Reproductive Success 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. We used a comparative approach to examine the effects of fragmentation on three forest-nesting migrants: Ovenbird (*Seiurus 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 midwestern regions. Distribution of individuals between fragmented and contiguous forests appeared to vary among species and regions, but total nest failure was significantly higher in fragments than contiguous forests in both regions for all species ($p = 0.053$). We attributed greater nest failure to increased nest predation ($p = 0.093$) and increased brood parasitism by the Brown-headed Cowbird (*Molothrus ater, $p = 0.009$*). In addition to greater total nest failure, partial nest failure due to cowbird parasitism led to a reduction in the number of host fledglings. Although the causes of nest mortality appeared to be species specific, total nest failure and partial nest failure acted in concert to reduce the number of offspring per adult for all three species on fragments. 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 continguous forests appeared to be population sources. Assuming constant mortality during winter, projected growth indicated that without immigration Ovenbird and Red-eyed Vireo populations should become extinct on fragments in both regions and Wood Thrush populations should be maintained or slightly decline on fragments. Populations of all three species should increase in contiguous habitats in both regions without emigration. We suggest that habitat fragmentation reduces local reproduction and may have ramifications for the entire population. 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.*

Éxito reproductivo de las aves migratorias en hábitats fuente y sumidero

Resumen: *La fragmentación del hábitat reproductivo en Norte América ha estado relacionada con la disminución de las aves migratorias Neotropicales que anidan en los bosques. En este estudio usamos un método comparativo para examinar el efecto de la fragmentación sobre tres aves que anidan en los bosques:* Seirus aurocapillus, Vireo olivaceus, *y* Hylocichla mustelina. *Monitoreamos el éxito reproductivo en 28 parcelas en bosques fragmentados y continuos, en dos regiones geográficas en el medio-oeste de los Estados Unidos. La distribución de los individuos entre bosques fragmentados y continuos pareció variar entre especies y regiones, pero el fracaso total de los nidos fue significativamente más alto en los fragmentos que en los bosques continuos, en ambas regiones para todas las especies ($p = 0.053$). Atribuímos los mayores fracasos de los nidos a la mayor depredación ($p = 0.093$) y al mayor parasitismo por parte de* Molothrus ater *($P = 0.053$). Además del mayor fracaso total de los nidos, los fracasos parciales, debidos al parasitismo por parte de* Molo-

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thrus ater, *condujeron a una reducción en el número de volantones de los huéspedes. Si bién las causas de la mortalidad en los nidos parecieron ser específicas para cada especie, los fracasos totales y parciales de los nidos actuaron en forma conjunta reduciendo el número de descendientes por adulto en los fragmentos para las tres especies. Usamos modelos simples de crecimiento poblacional para evaluar la viabilidad de las tres especies en hábitats fragmentados y contínuos en ambas regiones. En general, las poblaciones de los fragmentos parecieron ser poblaciones sumidero y las poblaciones en los bosques contínuos parecieron ser poblaciones fuente. Asumiendo una mortalidad constante durante el invierno, el crecimiento proyectado indicó que en ausencia de inmigración, las poblaciones de* S. aurocapillus *y* V. olivaceus *deberían extinguirse en los fragmentos en ambas regiones, y las poblaciones de* H. mustelina *deberían mantenerse o declinar levemente en los fragmentos. Las poblaciones de las tres especies deberían incrementar en los hábitats contínuos en ambas regiones en ausencia de migración. Sugerimos que la fragmentación del hábitat reduce la reproducción a una escala local y podría tener ramificaciones para las poblaciones a escalas espaciales mayores. La clara comprensión de la demografía poblacional, depende del análises de la dinámica demográfica dentro y entre las fuentes y los sumideros. Enfatizamos que, basta que se pueda determinar la escala espacial a la cual las poblaciones fuente y sumidero interactuan, la viabilidad a largo plazo de estas especies depende del mantenimiento de grandes áreas de bosques a lo largo y ancho del área reproductiva.*

Introduction

Many species of forest-nesting, Neotropical migrant songbirds have undergone significant population declines since 1966 (Robbins et al. 1989). Three nonexclusive hypotheses may explain these declines in migrant passerines (Askins et al. 1990; Wilcove & Robinson 1990; Finch 1991; Martin 1992; Faaborg et al. in press; Sherry & Holmes 1993): (1) increased mortality as they migrate between their wintering grounds in the Caribbean, Mexico, and Central America and their breeding grounds in North America; (2) increased mortality on wintering grounds because of anthropogenic changes in habitat (e.g., tropical deforestation) or other factors; and (3) reduced fecundity or fitness on breeding grounds because of anthropogenic habitat fragmentation or loss or other factors.

The habitat fragmentation hypothesis provides a framework for predicting changes 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 species distribution across habitats and that this shift in distribution results in population decline on local, regional, or range-wide scales, or (2) fragmentation decreases productivity or survival of birds nesting in fragmented habitats and this reproductive/survival dysfunction results in population decline on local, regional, or range-wide scales (Robbins 1979).

Fragmentation is expected to influence negatively those species that historically have inhabited large contiguous tracts of habitat with a relatively low edge density (Temple & Cary 1988). The reduction in reproductive success in the midwestern United States is related to the amount of forest cover and degree of fragmentation within a landscape (Robinson et al. 1995). In small fragmented habitats birds experience increased nest predation (Hoover et al. in press; Paton 1994), increased brood parasitism by the Brown-headed Cowbird (*Molothrus ater*, Robinson et al. 1993), and decreased pairing success (Gibbs & Faaborg 1990; Villard et al. 1993; Van Horn et al. in press). Together, these mechanisms may limit the reproductive success of forest-nesting migrants (Faaborg et al., in press) 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 & Holmes 1992) and may explain why most long-term declines of forest-nesting migrants appear in fragmented habitats (Askins et al. 1990).

To assess the fragmentation effects and the habitat size 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" (Robbins 1979). If reproduction does not compensate for adult mortality, then local populations are sinks: They will either become extinct or will be maintained via constant immigration from birds produced elsewhere (Brown & 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).

Many studies have used indirect methods to assess population viability including: utilizing artificial nests (reviewed by Paton 1994); documenting presence or absence of young produced on habitats of varying size (Porneluzi et al. 1993); and documenting the ratio of juveniles to adults on forests of varying size (Bollinger & Linder 1994; Donovan 1994). However, such indirect methods are insufficient to uncover the causes of reproductive dysfunction that ultimately limit populations on fragmented and contiguous forests. Because habitat features may affect reproduction and survival and therefore

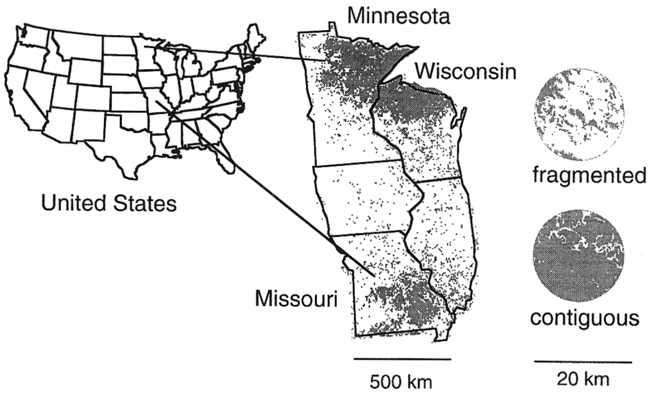


Figure 1. Location of four study areas and forest cover in the midwestern United States. Circles are examples of 10-km radius landscapes surrounding a fragmented and contiguous study plot, shading depicts forest cover.

alter the demography of a population, direct examination of fitness components in relation to habitat patterns at local sites and across regions is needed (Martin 1992). A few studies have examined directly species-specific characteristics of reproductive success of forest birds in either fragmented (Gibbs & Faaborg 1990; Robinson 1992; Roth & Johnson 1993) or contiguous habitats (Holmes & Sherry 1992); even fewer studies have examined these characteristics in both fragmented and contiguous landscapes (Villard et al. 1993; 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 midwestern regions. Our objectives were to (1) document 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 limit reproductive success of forest-breeding Neotropical migrant birds in fragmented and contiguous forests in these two geographic locations; and (3) assess 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 olivaceus*), and Wood Thrush (*Hylocichla mustelina*). All three species breed in U.S. midwestern and eastern deciduous forests. 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 & Sauer 1994). Breeding Bird Survey trends in the Midwest reflect range-wide trends (Thompson et al. 1993). As yet, whether the differential changes in population trends are related to differential responses to habitat fragmentation or to other causes is not clear.

Methods

Study Area

We studied the three species' distribution and reproductive success in Missouri (MO) and Wisconsin/Minnesota (WI/MN) in 1991 through 1993 (Fig. 1, Table 1). We selected these regions because they coincide with the center (WI/MN) and southwestern edge (MO) of the Ovenbird's breeding range. The former location is also the northwestern edge of the Wood Thrush breeding range whereas the Missouri location is the western center of its breeding range. Both regions are west-centrally located in the Red-eyed Vireo's broad breeding distribution.

Table 1. Mean location, habitat description, and landscape statistics of the 28 sites studied in Wisconsin/Minnesota (WI/MN) and Missouri (MO) in fragmented and contiguous landscapes.

Landscape	*Region*	*No. of sites*	*UTM coordinates (Easting, Northing)*	*Forest (%) cover (ha)**	*Mean patch size (ha)**	*No. of patches (ha)**	*Edge density (m/ha)**	*Mean core area index (%)**
Contiguous	WI/MN	6	5125960, 643090	92.84	29175	1	3.60	70.62
				(1.75)	(549.5)	(0)	(0.54)	(3.15)
Fragmented	WI/MN	6	5029620, 519786	31.31	550.49	26.50	7.31	10.85
				(12.91)	(613.01)	(11.40)	(1.80)	(15.14)
Contiguous	MO	8	666762, 4107719	95.06	26793.75	1	2.66	75.62
				(2.00)	(4890.09)	(0)	(0.82)	(4.41)
Fragmented	MO	9	577473, 4311684	32.03	674.57	20	8.49	7.59
				(10.27)	(511.92)	(7.88)	(1.49)	(4.04)

**All statistics are based on mean (standard deviation) of habitat characteristics within a 10-km radius surrounding each site.*

Within each region we examined bird demography in forest fragments in an agricultural landscape and in contiguous forests. For clarity, we refer to each landscape type (fragmented or contiguous) and region (MO or WI/MN) combination as a study area ($n = 4$; Fig. 1). We studied six to nine forest plots in each study area and treated these plots as replicates in distribution analyses. Nine fragmented study plots were in central Missouri and eight contiguous study plots were within the heavily forested Ozarks in southeast Missouri. In WI/MN six fragmented study plots were in the lower St. Croix River valley, and six contiguous study plots were within the heavily forested Chequamegan National Forest (WI). We studied all WI/MN plots in 1991 and 1992. In Missouri we studied nine fragmented plots and six contiguous forest plots in 1991; in 1992 we studied eight plots within fragmented and eight 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. 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). A forest tract was defined as 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 forest fragment tract ranged from 181 ha to 1872 ha, all fragments had similar edge density and percent core areas (Table 1). Average patch size within fragmented landscapes was 550.5 ha (WI/MN) and 674.57 ha (MO, Table 1). The contiguous forests in WI/MN and MO averaged 29,175 ha and 26,794 ha, 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 WI/MN 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 1994). In both regions the non-forested portion of fragmented landscapes was predominantly cool-season pasture and row crops.

Distribution and Abundance

We surveyed bird abundance at points located on a 150-m grid. Grid dimensions were 300 × 600 m where possible, given forest dimension constraints, and were established around randomly selected points. We surveyed 15 points at grid intersections located more than 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 10-min counts (Verner 1988). Three to four different observers conducted surveys at each point in each year to minimize observer bias (Verner and Milne 1989). Surveys began after territories were established and ended when most nests had fledged (May 5 through June 15 in MO; May 28 through July 2 in WI/MN).

In each 10-minute count we recorded bird detections within 50- and 70-m fixed radius circles as well as total (unlimited distance) detections. We computed the mean number of detections 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 ($n = 60$ 10-min counts). We used 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 from within 50 m and 70 m radii for between-study comparisons.

We compared mean 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. Plots within a landscape were used as the error term. We used a Type I error rate of 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 are).

Reproduction

We located and monitored nests on a subset of the study plots (four to five plots in each study area) in 1991 through 1993 to assess reproductive failure and cause-specific mortality in fragmented and contiguous forests in both regions. Nests that were located when active and were low enough (<10 m) 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. We monitored 142 Ovenbird nests, 62 Red-eyed Vireo nests, and 123 Wood Thrush nests. For each nest, we recorded the number of host and cowbird eggs, chicks, and fledglings every 3 to 5 days. We recorded each nest's fate as successful (nests that fledged at least one host species) or failed (nests that fledged no host species). We classified failed nests as: depredated (nests in which nest, eggs, or nestlings disappeared); abandoned (eggs or nestlings left unattended in nest); failed because of stochastic events (weather or other random events such as inadvertent trampling on a nest); or parasitized by cowbirds (no host young fledged 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 because of cowbird parasitism (parasitism failure) and the proportion of nests containing cowbird eggs or young (parasitism rate).

Daily Nest Mortality and Nesting Success

We calculated nesting success on a per nest basis using the Mayfield (1975) method. These estimates consider all nest failures regardless 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 study area as (1 − daily mortality). We assumed that daily survival was constant throughout the nest cycle (Mayfield 1975) and calculated nesting success as the daily survival rate raised to the exponent that reflects the length of the nesting cycle (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 (1 − nesting 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. Clutch size comparisons were difficult because of frequent host egg removal by Brown-headed Cowbirds on fragments and because many nests on fragments were located after they had been parasitized. In addition, we were not able to determine the exact length of the nesting cycle because we did not monitor nests daily. However, we do not believe 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 nest mortality differed among the four study areas using a Chi-Square analysis with multiple comparisons (Sauer & Williams 1989). We performed two additional comparisons for each to test directly the questions of interest: daily nest mortality on fragments versus contiguous forests and daily nest mortality in MO versus WI. We used a Type I error rate of 0.1 for all analyses to reduce the probability of committing a,Type II error.

To determine the mechanisms that limit reproductive success in fragmented and contiguous forests, we partitioned the total daily nest mortality into cause-specific components. For example, to determine how nest predation solely influenced daily nest mortality, we summed the total number of nest failures because of predation and divided that number by the total number of observation days. In the same manner, we summed nest failures caused by abandonment, stochastic events, and parasitism and calculated cause-specific daily nest mortality estimates for each of the four study areas. For each species we tested whether cause-specific daily nest mortality differed among the four populations, among fragmented and contiguous forests, and among regions using a Chi-Square analysis with multiple comparisons (Hines & Sauer, unpublished report). We considered P values less than or equal to 0.10 significant for these analyses.

Patterns of Daily Survival and Nesting Success

Our primary objective was to test whether fragmentation negatively affected the reproduction and viability of Neotropical migrant birds and whether these effects varied regionally. We analyzed each of the three forest-nesting, Neotropical migratory birds separately. Because these separate tests have relatively low statistical power, we used a combined probabilities test (Sokal & Rohlf 1981) to determine 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 & Rohlf 1981). As such, we tested whether daily mortality and cause-specific mortality of Neotropical migrants (Ovenbird, Wood Thrush, and Red-eyed Vireo combined) differed among landscapes and regions and considered P-values less than or equal to 0.10 significant.

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 successful 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 or 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

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: (1) the mean number of female offspring produced per adult female per year in a population (fecundity); (2) the probability that those offspring will survive to reproduce; and (3) 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 a closed 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 (Pulliam 1988). If

$$1 - \text{adult survivorship} = \text{mean number of female offspring/female/year} \times \text{juvenile survival},$$

then the population will replace itself (Ricklefs 1973). We 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. 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 in calculating the mean number of female fledglings produced per female per year. These assumptions represent a trade-off between intensively studying marked populations versus extensively studying populations across a large geographic scale. 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 our species-specific estimates of nesting success and nest failure (Mayfield method) were constant throughout the breeding season. Last, we assumed that the average number of female young that fledged per successful nest was constant throughout the breeding season. These last two assumptions were made because we monitored nests throughout the breeding season and considered these estimates as season-long statistics.

We calculated the mean number of female young per adult female per year from: the mean number of female young produced per successful nest, population specific estimates of nest success, the number of potential renesting attempts, and the number of potential broods per season. For example, we assumed that female Ovenbirds could fledge a maximum of one brood per year during our study and that females would renest once if their first nesting attempt failed. We determined the mean number of female young per successful nest and calculated how many young 100 adult females would produce throughout the breeding season. Nesting success was 0.27 for Ovenbird populations in MO fragments. An average of 1.58 female young were fledged per successful nest (assuming a 50:50 sex ratio of fledglings), so 27 females produced 42.66 female young and 73 females produced no young. All 73 females with a failed first attempt renested, 27% of which produced 31.14 female young. Thus, 74.1 female young were produced per 100 adult females or 0.74 female young per adult female per year.

The mean number of female young per adult female per year was calculated for Red-eyed Vireos and Wood Thrushes in a similar manner, but we assumed that an adult female could fledge a maximum of two broods per year (Martin, in press) and that females would renest if their first or second nesting attempts failed (Robinson, personal communication). In this manner, we utilized the population-specific nesting success estimates and fledging rates we derived from each of the four study areas.

We assumed that all juveniles of all species had a 0.31 probability of surviving to the following breeding season. Although direct estimates of this probability are lacking (because juvenile birds disperse widely, Greenwood & Harvey 1982), juvenile survival rates can be indirectly estimated based on data for adult mortality and female productivity (Rickleffs 1973). Greenberg (1980) and Temple and Cary (1988) hypothesized that juvenile survival was 0.31, or approximately 50% of adult survival, based on adult survival and fecundity calculations. This estimate agrees with computations for the Wood Thrush and Red-eyed Vireo (Noon & Sauer 1992) and has been used by other investigators that modeled population dynamics of forest-interior birds (Temple & Cary 1988; Thompson 1993, 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 is 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. Because these estimates were obtained from other sources and applied to the populations we studied, caution should be used when drawing inferences on rates of population change in our sites. 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. Although these survival estimates vary from study to study, they are 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 through time. We used the following two-stage population projection model to assess change in population size through time given current reproduction with no immigration or emigration:

$$N_{A(t+1)} = (N_{At} \times S_{At}) + (N_{At} \times F_t \times S_{Jt}),$$

where t = year of simulation, N_A = 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 $t + 1$, F_t 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 10-minute count × 1000 as a starting population size (for ease of interpretation) and projected population growth or decline over 20 years. Our point count estimates provide a reasonable, relative population size of adult females for each of the four study areas. Although singing males are predominantly counted with point counts, mist net capture data indicate that the sex ratios on fragments and contiguous forests in WI/MN and MO do not differ significantly (Donovan 1994; Porneluzi, unpublished, respectively). For the population growth models we used the average of the published adult survival estimates for each species. Annual adult survival averaged 0.62, 0.56, and 0.67 for Ovenbirds, Red-eyed Vireos, and Wood Thrushes, respec-

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, L) in Wisconsin/Minnesota and Missouri (region effect, R) in 1991 and 1992 (year effect, Y).

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

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

Species	*Region*	*Landscape*	*Year*	*N*	*Mean (<50 m)*	*SD (<50 m)*	*Mean (<70 m)*	*SD (<70 m)*	*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
		Cont	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
		Cont	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
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
		Cont	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
		Cont	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
		Cont	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
		Cont	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 (Frag) and contiguous (Cont) forests in Missouri (MO) and Wisconsin/Minnesota (WI/MN).

Species	*Region*	*Landscape*[a]	*Daily mortality failed by any cause*	*Cause of nest failure*[b]			
				Predation	*Parasitism*	*Abandonment*	*Stochastic*
Ovenbird	MO	Frag	0.0508	0.0424	0.0085	0	0
	MO	Cont	0.0384	0.0274	0	0.0110	0
	WI/MN	Frag	0.0626	0.0461	0.0033	0.0099	0.0033
	WI/MN	Cont	0.0336	0.0218	0	0.0101	0.0017
	χ^2, df (P)	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)
		Region	0.06, 1 (0.8028)	0.006, 1 (0.9387)	0.32, 1, (0.5674)	1.02, 1 (0.3120)	1.81, 1 (0.1784)
		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	Cont	0.0418	0.0386	0	0.0032	0
	WI/MN	Frag	0.0481	0.0385	0.0096	0	0
	WI/MN	Cont	0.0248	0.0124	0	0.0124	0
	χ^2, df (P)	Omnibus	3.12, 3 (0.3728)	6.31, 3 (0.0974)	1.06, 3 (0.7845)	0.04, 3 (0.9976)	—
		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)	—
Wood Thrush	MO	Frag	0.0456	0.0312	0.0144	0	0
	MO	Cont	0.0312	0.0220	0	0.0073	0.0018
	WI/MN	Frag	0.0398	0.0221	0.0089	0.0044	0.0044
	WI/MN	Cont	0.0182	0.0121	0	0.0061	0
	χ^2, df (P)	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)
		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 Probability	$-2\Sigma 1nP$,df, (P)	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)
		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)

[a] *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.*

[b] *Daily mortality is partitioned by cause of failure.*

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.

Species	*Region*[a]	*Landscape*[b]	*N*[c]	*Obs. days*[d]	*Daily mortality*	*Daily survival*	*Daily survival variance*	*Nest failure*	*Young per successful nesting attempt*[e]	*Fecundity per adult female per year*[f]
Ovenbird	MO	Frag	15	118.0	0.051	0.949	0.0004	0.730	1.58	0.74
		Cont	40	364.5	0.038	0.962	0.0001	0.620	2.15	1.32
	WI/MN	Frag	36	303.5	0.063	0.937	0.0002	0.803	1.65	0.59
		Cont	51	596.5	0.034	0.966	0.00005	0.579	2.00	1.35
Red-eyed Vireo	MO	Frag	2	12.5	0.160	0.940	0.011	0.991	0	0
		Cont	34	311.0	0.042	0.958	0.0001	0.686	1.57	1.46
	WI/MN	Frag	13	208.0	0.048	0.952	0.0002	0.735	0.83	0.63
		Cont	13	161.5	0.025	0.975	0.0002	0.495	1.43	2.00
Wood Thrush	MO	Frag	36	417.0	0.046	0.954	0.0001	0.732	1.07	0.85
		Cont	56	545.5	0.031	0.969	0.0001	0.586	1.51	1.75
	WI/MN	Frag	22	226.0	0.040	0.960	0.0002	0.681	1.21	1.12
		Cont	9	165.0	0.018	0.982	0.0001	0.399	1.50	2.40

[a] *Regions are Missouri (MO) and Wisconsin/Minnesota (WI/MN).*
[b] *Landscapes are fragmented (Frag) or contiguous (Cont).*
[c] *N = total nest sample size.*
[d] *Obs. Days = the total number of observation days pooled across all nests within the study area.*
[e] *Young per successful nesting attempt = the mean number of female fledglings per successful nesting attempt.*
[f] *Fecundity per adult female per year = the mean number of female offspring successfully fledged per adult female per year.*

tively. We used a value of 0.31 for juvenile survival of all three species in the population growth models and our calculated fecundity values in the population growth models.

Results

Distribution and Abundance

Ovenbirds were more abundant in WI/MN than MO (region effect), but abundance did not differ between fragmented and contiguous forests (landscape effect, Table 2). In MO detections averaged 0.80 and 0.72 in fragmented and contiguous forests respectively, whereas in WI/MN detections averaged 2.44 and 2.39 on fragmented and contiguous forests respectively (Table 3). Ovenbirds were more abundant in 1992 than 1991 especially in the WI/MN contiguous plots (region × landscape × year interaction, Tables 2 and 3), where mean detections increased from 1.78 to 3.00 detections per 10-min count.

Red-eyed Vireo abundance varied with the region and landscape (region × landscape interaction, Table 2). In WI/MN, vireo abundance averaged 1.82 and 2.19 detections per count on fragmented and contiguous forests respectively (Table 3). In MO, however, vireo abundance dropped from an average of 2.52 detections per count on contiguous forest plots to 0.70 detections per count on fragments (Table 3). Red-eyed Vireos increased from 1991 to 1992 in all four study areas (year effect, Tables 2 and 3).

Wood Thrushes were more abundant in MO than WI/MN (region effect, Table 2) and on fragments than contiguous forests (landscape effect, Table 2). In MO, Wood Thrush abundance averaged 0.47 and 0.26 in fragmented and contiguous forests, respectively (Table 3). Similarly, their abundance in WI/MN averaged 0.34 and 0.09 in fragmented and contiguous forests, respectively (Table 3). Abundance declined from 1991 to 1992 (year effect, Table 2), but this decline was most apparent in MO (region × year interaction, Table 2) where abundance decreased from 0.52 to 0.41 (Table 3).

Reproductive Success

The Chi-Square analyses used to determine if daily nest mortality and cause-specific daily nest mortality differed among the four populations, fragmented and contiguous forests, and regions were not statistically powerful tests. 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 mortality among populations is 0.12. Thus, if populations truly had different mortality 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 II error). Interpretation of non-significant differences in daily mortality should be made in light of the high Type II error rate. Even statistically non-significant differences can be biologically significant in terms of nesting success and population change.

OVENBIRD

Daily nest mortality of Ovenbird nests did not differ significantly among the four study areas (Table 4). In MO

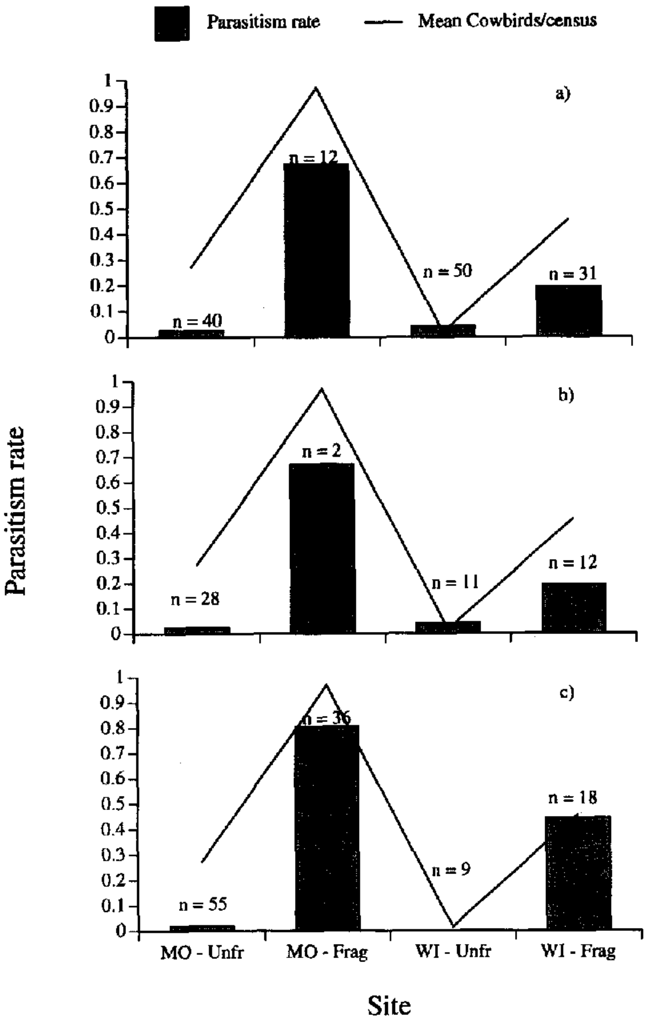


Figure 2. Parasitism rate, or the proportion of nests containing cowbird eggs or young in each study area, and the mean number of cowbirds detected per 10-min census in each study site for Ovenbird (a), Red-eyed Vireo (b), and Wood Thrush (c).

nest failure was 0.73 and 0.62 on fragments and contiguous sites, respectively (Table 5). Similarly, in WI/MN nest failure was 0.80 and 0.58 on fragments and contiguous sites, respectively (Table 5). These apparently large differences in nest failure reflect approximately a 0.025 difference in daily mortality between fragmented and contiguous forests (Table 5).

Daily nest mortality because of nest depredation accounted for the majority of nest failures (failure to fledge at least one host offspring) in all four study areas but did not differ between regions or landscapes (Table 4). Daily mortality because of nest abandonment was the second largest factor in nest failures and differed among the four study areas (Table 4). Abandonment caused failure in all study areas except the MO fragments and did not differ between regions or landscapes (Table 4).

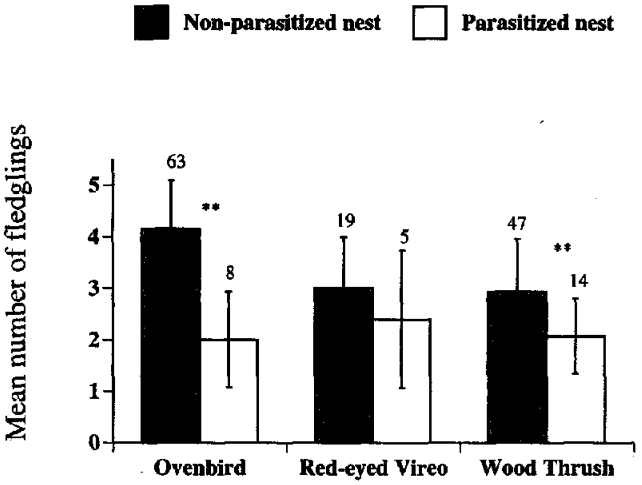


Figure 3. The mean number and standard deviation of Ovenbird, Red-eyed Vireo, and Wood Thrush fledglings in non-parasitized and parasitized nests that successfully fledged at least one host young. Nest samples are combined across all study areas.

Daily nest mortality caused by cowbird parasitism and stochastic events did not differ among the four study areas (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/MN respectively (Table 4). Failure because of stochastic events was recorded only in WI/MN, accounting for 5.27 and 5.06% of daily mortality on fragments and contiguous forests (Table 4). These estimates were not different from the MO populations.

Parasitism rates were low in contiguous forests; 1 out of 40 and 2 out of 50 nests were parasitized in MO and WI/MN forests, respectively (Fig. 2). On fragments 8 out of 12 and 6 out of 31 nests were parasitized in MO and WI/MN, respectively (Fig. 2). Across all study areas 71 nests successfully fledged at least one Ovenbird. 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, Fig. 3).

RED-EYED VIREO

Daily nest mortality of Red-eyed Vireo nests did not differ significantly among the four study regions (Table 4). In MO, nest failure was 0.99 and 0.68 on fragments and contiguous sites respectively (Table 5). In WI/MN nest failure was 0.74 and 0.49 on fragments and contiguous sites respectively (Table 5).

Daily mortality because of nest depredation accounted for the majority (≥50%) of nest failures in all four study areas but did not differ between regions or landscapes (Table 4). Nest predation accounted for 50% of daily mortality in WI/MN contiguous forests and >80% of daily mortality in the other three study areas (Table 4).

Daily mortality because of nest abandonment did not differ among the four study areas or between regions (Table 4). Nest abandonment was greater in contiguous landscapes than fragmented landscapes (Table 4) where failures because of abandonment accounted for 7.66 and 50% of daily mortality in MO and WI/MN contiguous habitats, respectively (Table 4).

Nest failure because of cowbird parasitism appeared only in WI/MN fragments, where 19.96% of daily mortality was attributed to parasitism (Table 4). Daily mortality because of parasitism did not differ among the four study areas, between regions, to or between landscapes (Table 4). Nest failure was not attributed to stochastic events in any of the four study areas (Table 4).

Three of 28 Red-Eyed Vireo nests were parasitized in MO contiguous forests; and 0 out of 11 nests were parasitized in WI/MN contiguous forests (Fig. 2). In MO fragments only 2 vireo nests were located, one of which was parasitized. In WI/MN fragments 8 out of 12 nests were parasitized (Fig. 2). 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 significantly from the mean number of vireo fledglings in non-parasitized nests (3.0; $T = 1.12$, $P = 0.277$, Fig. 3).

WOOD THRUSH

Daily nest mortality of Wood Thrush nests did not differ significantly among the four study areas or between regions (Table 4). However, daily nest mortality differed between landscapes (Table 4). In MO nest failure was 0.73 and 0.59 on fragmented and contiguous plots respectively, and in WI/MN nest failure was 0.68 and 0.40 on fragmented and contiguous plots, respectively (Table 5).

Failure because of nest predation accounted for at least 56% of daily mortality in all four study areas but did not differ among populations (Table 4). Failure because of abandonment accounted for 11 to 33.5% of daily mortality in both WI/MN study areas and MO contiguous forests but was not detected in MO fragments (Table 4). Nest failures because of stochastic events were detected in MO contiguous and WI/MN fragments and accounted for 5.8 and 11.1% of daily mortality (Table 4). Failures caused by abandonment and stochastic events did not differ among the four study areas, between regions, or between landscapes (Table 4).

Failure due to cowbird parasitism differed among the four study areas (Table 4). Fragments had higher daily mortality because of parasitism than contiguous forests (Table 4). On fragments parasitism accounted for 31.6 and 22.4% of daily mortality in MO and WI/MN respectively (Table 4). Alternatively, failures because of cowbird parasitism were not detected on contiguous forests in WI/MN or in MO (Table 4).

Parasitism of Wood Thrush nests was low to absent in contiguous forests: 1 of 55 nests in MO and 0 of 9 nests in WI/MN contained cowbird eggs or young. Conversely, 29 out of 36 and 8 out of 18 nests in fragments in MO and WI/MN contained cowbird eggs or young (Fig. 2). Across all study areas, 61 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, $T = 2.9$, $P = 0.0049$, Fig. 3).

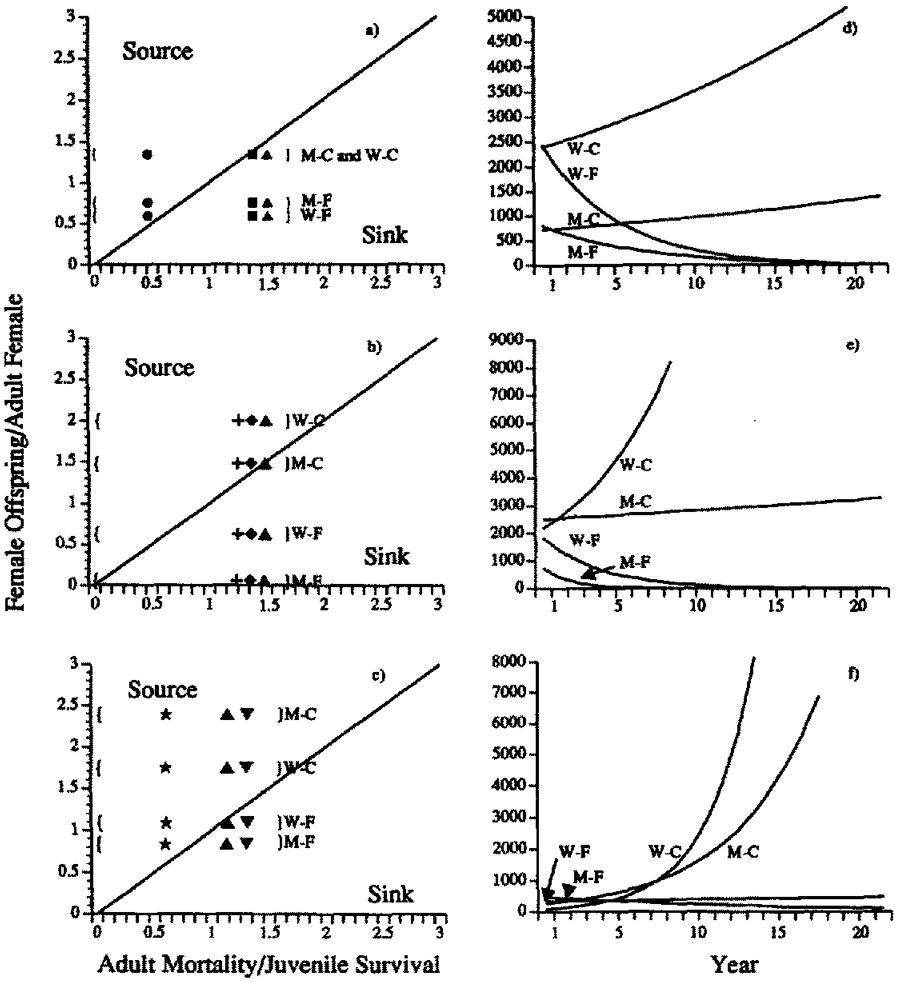
Daily Survival and Nesting Success

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, but did not differ among regions (Table 4). Nest failures because of predation and parasitism were greater on fragments than contiguous forests, whereas failures due to predation and parasitism did not differ between regions (Table 4). Failures because of abandonment and stochastic events did not differ between landscapes or regions (Table 4).

Neotropical Migrant Viability

Adult survival estimates for the Ovenbird vary greatly across studies (Fig. 4), ranging from 0.845 (Roberts 1971) to 0.540 (Savidge & 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 (Fig. 4a). Alternatively, when the adult survival value of 0.540 was used, none of the populations produced enough young to sustain the populations and all four populations was classified as sinks (Fig. 4a). 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. Mean female fledglings per adult female per year was 1.32 and 1.35 in MO and WI/MN contiguous forests respectively and 0.74 and 0.59 in MO and WI/MN fragments respectively (Fig. 4a, Table 5). 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 in fragments in both regions declined to near extinction within 20 years without immigration (Fig. 4d). Ovenbird populations in contiguous forests in both MO and WI/MN increased within 20 years and may function as population sources (Fig. 4d).

Annual adult survival estimates for the Red-eyed Vireo



	Reference	Location	ADULT SURVIVAL OVEN	 REVI	 WOTH
●	Roberts, 1971	Massachusettes	0.845	-	-
■	Faaborg and Arendt, in press	Puerto Rico	0.57	-	-
▲	Savidge and Davis, 1974	Pennsylvania	0.54	0.53	0.64
▲	Hann, 1937	Michigan	0.537	-	-
+	Nichols et al., 1981	Maryland	-	0.59	-
◆	Nichols et al., 1981	New Hampshire	-	0.57	-
▼	Roth and Johnson, 1993	Delaware	-	-	0.58
★	Robinson, unpubl.	Illinois	-	-	0.80

Figure 4. The source sink status of Ovenbirds (a), Red-eyed Vireos (b), and Wood Thrushes (c) based on juvenile survivorship rate = 0.31: Different published estimates of adult mortality are shown by different symbols. For example, using Roberts (1971) estimate of adult survivorship (0.845) of Ovenbirds, all four study populations (M-C = Missouri contiguous; W-C = Wisconsin/Minnesota contiguous; M-F = Missouri fragmented; W-F = Wisconsin/Minnesota fragmented) are classified as potential sources. Results of population simulations for the Ovenbird (d), Red-eyed Vireo (e), and Wood Thrush (f) in the four study areas. Initial population size (year 1) was derived from area-specific point count data × 1000.

ranged from 0.53 to 0.59 (mean survival estimate = 0.56, Fig. 4b). When juvenile survival was 0.31, the contiguous populations in both MO and WI/MN were classified as potential sources for all estimates, whereas fragmented populations in MO and WI/MN were classified as sinks (Fig. 4b). When the mean adult survival was used (0.56) and juvenile survival was 0.31, recruitment of 1.42 female fledglings per adult female per year was needed to balance adult mortality. Mean female fledglings per year was 1.46 and 2.0 in MO and WI/MN contiguous forests and 0 and 0.63 in MO and WI/MN fragments, respectively (Fig. 4b, Table 5). 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 (Fig. 4b). When the mean demographic values were used in population growth models, populations in fragments in both regions declined to near extinction within 20 years, whereas populations in contiguous forests in MO and WI/MN increased through time and potentially serve as sources (Fig. 4e).

Annual adult survival rates for Wood Thrush varied from 0.58 (Roth & Johnson 1993) to 0.80 (Robinson, unpublished). When the adult survival rate of 0.80 was used, all four populations produced enough young to compensate for adult mortality (Fig. 4c). When the adult survival of 0.58 was used, fragments in both MO and WI/MN were classified as sinks whereas contiguous forests in MO and WI were classified as sources (Fig. 4c). When the average adult survival value of 0.67 and juvenile survival value of 0.31 were used, recruitment of 1.06 female offspring per adult female per year was needed to compensate for adult mortality (Fig. 4). Mean female fledglings per year was 1.75 and 2.4 in MO and WI/MN contiguous forests and 0.85 and 1.12 in MO and WI/MN fragments respectively (Fig. 4c, Table 5). Populations in contiguous forests in both MO and WI/MN were classified as sources, whereas populations in WI/MN fragments apparently broke even and populations in 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 these demographic values and without immigration or emigration, Wood Thrush populations in contiguous forests in both regions dramatically increased through time, whereas growth in WI/MN fragments was low relative to population growth in contiguous habitat, and growth in MO fragments was slightly negative (Fig. 4f).

Discussion

Because our primary goal was to document reproductive success in 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 & Faaborg 1990; Van Horn et al. in press) found in smaller fragments in the Midwest. Thus given large fragment size, we did not expect that distribution would be significantly affected by fragmentation. Yet our focal species were distributed differently among fragmented and contiguous habitats: Ovenbird distribution did not differ in either MO or WI/MN; Red-eyed Vireos were less abundant in MO fragments but not on WI/MN fragments; and Wood Thrushes were more abundant in both MO and WI/MN fragments compared to contiguous habitats.

Without species-specific knowledge of patterns of dispersal or site faithfulness, it is difficult to explain these distributional differences between fragments and contiguous forests. They may reflect geographical variation in the distribution of required resources (Brown 1984). Alternatively, this variation may result from dispersal differences related to source-sink dynamics and distance to major source areas (Maurer & Villard 1994). If the few young produced on fragments emigrate to breed elsewhere, dispersal from contiguous to fragmented subpopulations is necessary to maintain fragment population size. By contrast, within-forest dispersal may predominate in contiguous forest populations, which may be less variable than movement between fragmented and contiguous subpopulations.

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

Although cause and effect was not established, our results support the hypothesis that fragmentation of breeding habitat reduces the reproductive success of forest-nesting migratory birds even when fragments are large (>500 ha). 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. Increased nest predation and parasitism in fragments caused an increase in daily mortality. We suggest that landscape features in fragmented habitats may be more suitable for predator and parasite populations than in contiguous landscapes (Andren 1992; Thompson et al. in press; Donovan et al. in press).

Independent analyses of all three species show that daily nest mortality tended to be higher ($0.10 < p < 0.22$) in fragments compared to contiguous habitats in both MO and WI/MN. The nonsignificant landscape trends can be interpreted in two ways 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; Type II error rate = 0.88). Alternatively, Mayfield daily nest survival may not truly differ between these populations. We measured daily nest survival as the probability that a nest would fledge at least one host young, ignoring partial nest loss. The number of nests that failed to fledge at least one host young in fact may not differ between fragmented and contiguous forests. However, our results demonstrate that partial nest loss from cowbird parasitism can influence the population's ability to maintain itself through time by reducing the number of female fledglings. 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 these effects would not be detected when nesting success is calculated on a per nest basis. Despite the problems with small sample sizes and nesting success calculations, we believe the patterns detected are real. When we combined our data with others in the region, the relationship between nesting success and parasitism levels were significantly correlated with several fragmentation indices for our focal species and several other forest-nesting migratory birds (Robinson et al. 1995).

Although fewer young were produced per adult in fragments compared to contiguous forests, the mechanisms that lower reproductive success in fragments appeared to be species-specific. Predation reduces Ovenbird and Red-eyed Vireo nesting success in fragments, and cowbird parasitism reduced the mean number of fledglings per successful nest. By contrast, cowbird parasitism significantly reduces Wood Thrush nesting success, decreasing the probability that a Wood Thrush nest would fledge at least one host offspring and decreasing the mean number of offspring in successful nests. Thus, fragmentation negatively affected reproduction in all three species, but the mechanism of this reduction varied among species.

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 in the breeding season may be structured as a network of sources and sinks, where more productive source areas effectively subsidize or rescue unproductive sink areas (Pulliam 1988; Brown & Kodric-Brown 1977; Stacey & Taper 1991; Rolstad 1991). If this is so, the relevant demographic unit for long-term management of these species is a system of subpopulations that are linked by dispersing individuals (Hanski & Gilpin 1991; Villard et al. 1992; Harrison 1994).

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 source-sink dynamics. 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 overall population size and longevity (Pulliam 1988; Howe et al. 1991). Genetically, sinks may contribute to a more diverse gene pool (Lande & Barrowclough 1987), but this benefit is lost if immigrants and emigrants are not successfully exchanged among subpopulations (Howe et al. 1991).

Sinks may be a detriment in that constant immigration from sources to sinks (fragments) may exert a negative influence on the larger population (Davis & Howe 1991). 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 heavily forested landscapes throughout the breeding range until the geographic scale at which source and sink populations interact can be determined.

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