# REPRODUCTIVE SUCCESS OF WOOD THRUSHES IN FOREST FRAGMENTS IN NORTHERN INDIANA

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ABSTRACT.—I monitored 278 Wood Thrush (*Hylocichla mustelina*) nests in 14 forest fragments (range 7 to 500 ha) in northern Indiana to explore patterns of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), nest predation, and reproductive success. Density of thrushes was negatively related to area of forest fragments. Cowbirds were common throughout the landscape, but I found no relationship between their abundance and forest area. Overall, 90% of the thrush nests were parasitized by cowbirds ($\bar{x}$ = 2.4 cowbird eggs per nest). The number of cowbird eggs per thrush nest was not related to forest area, abundance of host species, or distance to a forest edge but was positively related to thrush abundance. Nest predation rates averaged 58% and were lower than those reported in much of neighboring Illinois but also were unrelated to forest area and distance to a forest edge. The combination of cowbird parasitism and nest predation resulted in relatively low reproductive success ($\bar{x}$ = 0.6 thrush fledglings per nesting attempt). I estimated that Wood Thrushes in northern Indiana made an average of three nesting attempts per breeding season (based on 17 color-marked females) and had relatively low seasonal fecundity ($\bar{x}$ = 0.9 female fledglings per adult female per season). Nonetheless, considerable annual variation in seasonal fecundity suggested that some sites exceeded the source-sink threshold in some years. Regardless, the overall landscape appeared to be part of a regional sink for Wood Thrushes, although its negative influence on regional demography was not as severe as elsewhere in the midwestern United States. The poor demographic balance in much of the agriculturally dominated Midwest suggests that conservation efforts for Wood Thrushes and other Nearctic-Neotropical migrants should be directed at preserving and enhancing possible source habitats in regions where parasitism by cowbirds and nest predation are reduced. *Received 9 October 1998, accepted 8 July 1999.*

TWO GENERALIZATIONS have emerged from recent research on the breeding success of Nearctic-Neotropical migrant landbirds (hereafter, "Neotropical migrants"). First, population surveys of Neotropical migrants conducted on a local scale may be difficult to interpret without knowledge of breeding behavior and demography (Brawn and Robinson 1996). Second, effects of forest fragmentation on Neotropical migrants differ among geographic areas, particularly between the eastern and midwestern United States (Robinson et al. 1995).

Although bird surveys can be valuable tools for assessing regional population trends of Neotropical migrants (e.g. Robbins et al. 1989, Hagan et al. 1992, Peterjohn et al. 1995, James et al. 1996), such methods are based on observations of singing males that may not provide reliable indices of local breeding densities

(Gibbs and Faaborg 1990, Gibbs and Wenny 1993, Porneluzi et al. 1993). In the extreme, Brawn and Robinson (1996) found no negative population trends based on local bird surveys conducted in the Midwest, yet reproductive success was below levels necessary to maintain viable populations in the absence of immigration. For many Neotropical migrant species, surplus individuals from highly productive source habitats may immigrate into sink habitats where reproduction fails to balance adult mortality (Pulliam 1988, Pulliam and Danielson 1991). One result of such source-sink dynamics is a time lag between the collapse of local breeding success and the detection of population declines based on local bird surveys (Brawn and Robinson 1996). Thus, the combination of measuring breeding success on a local scale and surveying populations on a regional scale may be necessary to evaluate long-term population viability of Neotropical migrants.

Several studies in the eastern United States have shown positive relationships between

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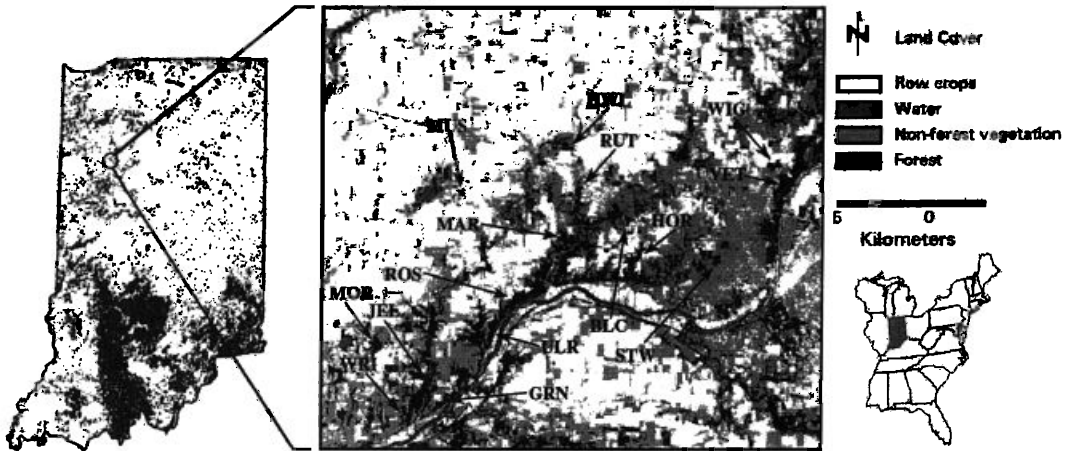
FIG. 1.   Forested habitat in Indiana, and the 58,000-ha Indian-Pine Watershed. Non-forest vegetation includes winter wheat, golf courses, fallow fields and lawns. Wood Thrushes were studied in the 15 study sites labeled on the map. ROS and ULR are two study sites within a single forest fragment.

nesting success and forest fragment size (e.g. Porneluzi et al. 1993, Hoover et al. 1995). Reduced breeding success in small forest patches may result from edge effects because Brown-headed Cowbirds (*Molothrus ater*) and mammalian and avian predators occur at higher densities within edge habitats (Brittingham and Temple 1983, Wilcove 1985, Paton 1994). Nonetheless, breeding success in moderate-sized fragments (>100 ha) and continuous forests in the eastern United States appears to be sufficient to maintain viable populations of Neotropical migrants (Holmes et al. 1992, Porneluzi et al. 1993, Hoover et al. 1995). In contrast, even relatively large forest fragments in the Midwest (200 to 2,200 ha) do not support viable populations of Neotropical migrants (Donovan et al. 1995, Trine 1998). As a result, Brawn and Robinson (1996) suggested that the agricultural portion of the Midwest acts as a sink in which all woodlot populations must be bolstered by constant immigration from areas with extensive forest, such as southern Indiana, northern Wisconsin, or southeastern Missouri.

I tested the regional-sink hypothesis (Brawn and Robinson 1996) by measuring the breeding success of Wood Thrushes (*Hylocichla mustelina*) in an agricultural landscape in northern Indiana that rivals the degree of forest fragmentation reported by Robinson (1992) and Brawn and Robinson (1996). I monitored Wood Thrush nests and conducted local bird surveys within 14 forest patches to (1) investigate rela-

tionships among densities of breeding birds, cowbirds, and reproductive success of Wood Thrushes; (2) measure the intensity of predation and cowbird parasitism on Wood Thrush nests; (3) describe variation in nesting success of Wood Thrushes among and within forest fragments; and (4) estimate the seasonal fecundity of Wood Thrushes within forest fragments. My study extends the geographic breadth of our knowledge about the reproductive success of Wood Thrushes, documents substantial annual variation in nesting success, and uses the renesting frequency of color-marked females to estimate seasonal fecundity.

STUDY AREA AND METHODS

*Study sites.*—I conducted the study in the 58,000-ha Indian-Pine Watershed, Tippecanoe and Warren counties, Indiana (Fig. 1). I established 15 study sites in 14 different forest fragments that ranged from 7 to 500 ha and varied in their degree of isolation, vegetation composition and structure, and surrounding land use (Fig. 1, Table 1). Less than 9% of the watershed was forested. I sampled vegetation within each fragment using methods modified from James and Shugart (1970). In addition, land-cover data for the landscape were derived from a Landsat Thematic Mapper image collected on 12 April 1986 (pixel width = 30 m) using PC-ERDAS image-processing software (see Gustafson et al. 1994), and fragment area and percent forest cover were estimated using FRAGSTATS (McGarigal and Marks 1995).

*Local bird surveys.*—From late May through mid-June in 1994 and 1995, I surveyed breeding birds us-

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TABLE 1. Characteristics of the northern Indiana study sites based on the methods of James and Shugart (1970).

| Site | Area (ha) | Isolation[a] | Sample points[b] | % Canopy cover | Basal area (m²/ha) | Tree density (no./ha) | Dominant tree species (m²/ha)[c] | Woody stems (no./ha)[d] | % Ground cover[e] |
|---|---|---|---|---|---|---|---|---|---|
| BLC | 11 | 18.2 | 8 | 68 | 30.0 | 278 | SM (8.0), SH (6.2) | 8,418 | 70 |
| GRN | 50 | 29.2 | 10 | 66 | 29.3 | 401 | WO (10.4), RO (5.2) | 3,367 | 35 |
| HOR | 379 | 15.7 | 13 | 97 | 44.0 | 635 | BL (17.0), WA (7.7) | 7,261 | 55 |
| HWL | 32 | 5.6 | 8 | 84 | 20.7 | 497 | SH (4.0), WO (3.5) | 5,676 | 70 |
| JEL | 490 | 27.1 | 13 | 92 | 28.7 | 487 | RO (5.7), WA (4.3) | 3,571 | 50 |
| MAR | 91 | 24.6 | 17 | 92 | 34.6 | 474 | WO (9.3), SM (5.5) | 4,622 | 65 |
| MOR | 42 | 13.8 | 10 | 90 | 33.9 | 381 | SM (6.9), WO (6.5) | 2,398 | 55 |
| MUS | 7 | 4.0 | 8 | 61 | 33.5 | 356 | SH (9.4), WO (7.4) | 6,696 | 60 |
| ROS | 436 | 16.8 | 14 | 80 | 31.6 | 438 | WO (9.6), TP (5.8) | 6,487 | 48 |
| RUT | 168 | 18.5 | 8 | 96 | 31.6 | 298 | WO (14.7), SM (6.5) | 8,355 | 71 |
| STW | 23 | 11.2 | 8 | 86 | 42.1 | 340 | BW (10.3), SM (9.9) | 5,485 | 47 |
| ULR | 436 | 23.4 | 15 | 97 | 39.4 | 497 | BW (9.8), RO (5.3) | 3,810 | 54 |
| VET | 321 | 14.6 | 10 | 90 | 41.5 | 471 | WO (21.4), RO (6.0) | 5,442 | 49 |
| WIG | 25 | 25.9 | 10 | 97 | 24.9 | 368 | WO (5.0), SM (3.8) | 8,593 | 44 |
| WRI | 25 | 22.0 | 8 | 93 | 33.2 | 472 | BW (5.8), WA (5.0) | 5,293 | 63 |

[a] Percent forest cover within a 3-km radius of study site.
[b] Sampling points were circular plots with 10-m radius (0.03 ha).
[c] SM = sugar maple (Acer saccharum), SH = shagbark hickory (Carya ovata), WO = white oak (Quercus alba), RO = red oak (Quercus rubra), BL = black locust (Robinia pseudoacacia), WA = ash (Fraxinus spp.), TP = tulip poplar (Liriodendron tulipifera), and BW = black walnut (Juglans nigra).
[d] Woody stems included shrubs and saplings at least 1.5 m in height and less than 10 cm in diameter at 1.5 m above the ground.
[e] % of the ground obscured by herbaceous vegetation at 1.5 m above ground.

ing fixed-radius point counts (Hutto et al. 1986). I established an area-dependent number of survey points (4 to 8 points) every 150 m along transects at least 150 m apart and 70 m from the forest edge. I mapped singing males within a 70-m radius of each survey point for 6 min on fair-weather days from 0530 to 0930 EST. I replicated each survey point three times during the breeding season. I sampled six sites (HOR, JEL, MAR, ROS, STW, and VET) in both years, and because avian abundance patterns in these sites were similar between years, I used two-year means in statistical analyses. I sampled the remaining sites in either 1994 or 1995.

I calculated the mean number of birds detected at each site to estimate the relative density of Wood Thrushes, cowbirds, cowbird hosts, and avian predators. I used the mean number of female cowbirds detected per point count as my measure of cowbird abundance. I distinguished between males and females using "rattle" calls (Rothstein et al. 1988), which are predominantly given by females (S. K. Robinson pers. comm.). Cowbird hosts included species known to be parasitized by cowbirds in neighboring Illinois (Robinson 1993), including most Neotropical migrants (73%) and one-third of all species breeding in the watershed. Avian predators included Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), and Common Grackles (*Quiscalus quiscula*).

*Monitoring thrush nests.*—I searched for Wood Thrush nests from May through August, 1994 to 1996. I did not study all sites in all years, and I used estimates of cowbird parasitism, nest predation, and reproductive success pooled across years for sites studied in multiple years. Two of the study sites (ROS and ULR) were within the large forest fragment that snakes along the Wabash River (Fig. 1). When investigating relationships involving fragment area, I used mean values from these sites. The sample sizes at some sites (e.g. WRI, VET, BLC, MOR, GRN) were low but represent all or nearly all of the breeding pairs of Wood Thrushes in these patches.

I checked the contents of thrush nests every other day using mirrors mounted to telescoping poles. I estimated the density of nests by dividing the number of simultaneously active nests into the area searched within each study site. I mapped the location of nests on aerial photographs (1:2,400 or 1:4,800) and estimated their distance to the nearest forest edge (i.e. an opening of more than 0.2 ha; Brittingham and Temple 1983).

In 1996, I marked females with unique combinations of colored leg bands to determine the frequency of renesting during the breeding season. I marked the females nesting in HOR, HWL, MUS, ROS, and STW but could follow only a subset of 17 females for the entire breeding season. Some of the marked females apparently left the fragments after their first breeding attempts failed, whereas others remained

in the study sites, but I was unable to locate all of their nesting attempts.

*Estimating parasitism, predation, and reproductive success.*—I counted the number of thrush and cowbird eggs and nestlings during each nest visit. Because cowbirds typically laid eggs in Wood Thrush nests in the early stages of incubation, I used those nests that persisted at least six days into incubation (half the incubation period) for my estimates of cowbird parasitism. I estimated intensity of cowbird parasitism as the maximum number of cowbird eggs observed in thrush nests; however, this was a minimum estimate because some cowbird eggs were laid and ejected by conspecifics between nest visits (pers. obs.). Unparasitized clutches produced late in the breeding season (hatching after June 15) were smaller than those produced earlier (early median = 4 eggs, $n = 8$; late median = 3 eggs, $n = 12$). Therefore, to calculate the reduction in Wood Thrush clutch size due to parasitism, I subtracted the minimum number of Wood Thrush eggs incubated from an expected clutch size of 4 or 3 eggs for early and late nests, respectively.

I estimated daily mortality rate during the 13-day incubation period using the Mayfield (1975) method. I estimated the number of fledglings as the number of nestlings that survived to within two days of their expected date of leaving the nest (8 days old for cowbird nestlings and 11 days for Wood Thrush nestlings). I calculated nesting success as the probability that a nest produced at least one Wood Thrush or cowbird fledgling (Mayfield 1975). I estimated the number of thrush fledglings produced per nesting attempt as the number of young produced per successful nest attempt multiplied by Mayfield nesting success. Finally, I calculated the reduction in reproductive success of thrushes due to nest predation as the percentage of "original" Wood Thrush eggs (estimated as above) that would have been lost to predators in the absence of parasitism.

*Source-sink assessment.*—To evaluate the potential source-sink status for Wood Thrushes in each study site, I adopted the following equation to estimate the finite rate of increase:

$$\lambda = P_A + P_j\beta, \qquad (1)$$

where $P_A$ is adult survival rate from one breeding season to the next, $P_j$ is juvenile survival rate from fledging until the following breeding season, and $\beta$ is the mean number of juveniles produced in a breeding season by adult females (Pulliam 1988). Assuming closed populations, sources are those that maintain $\lambda > 1$, whereas sinks are those for which $\lambda < 1$.

I did not measure survival rate for Wood Thrushes breeding in northern Indiana. Instead, I adopted "conservative" and "optimistic" survival rates based on estimates of return rates for adult Wood Thrushes (58%, Roth and Johnson 1993; 70%, Trine 1998). Because no direct estimates of juvenile surviv-

al rates exist for Wood Thrushes (but see Anders et al. 1997), I used empirical estimates reported in the literature for other Neotropical migrants (28%, Nolan 1978; 35%, Sæther 1989). I estimated seasonal fecundity per female ($\beta$) by multiplying the mean number of breeding attempts for marked females in 1996 by the mean number of fledglings produced per nesting attempt. I then determined the seasonal fecundity required for $\lambda = 1$ (i.e. source-sink threshold) based on the conservative and optimistic estimates of adult and juvenile survival. If the observed seasonal fecundity was above the source-sink threshold for a given fragment, the population was considered a potential source. If the observed seasonal productivity was below the threshold, the population was considered a sink.

*Statistical analyses.*—I used least-squares linear regression (SAS 1989) to test for relationships between measures of abundance, cowbird parasitism, nest predation, reproductive success, and fragment area. Residuals were examined for normality and homogeneity of variance using graphical procedures (SAS 1989). Fragment area was $\log_{10}$-transformed to meet the assumption of normality. I considered linear relationships among these variables because similar patterns were reported in previous studies (Robinson 1993, Hoover et al. 1995). To describe the relationship between the square root-transformed number of cowbird eggs in Wood Thrush nests and date, I fitted a quadratic regression model to the data and used a stepwise approach to find the curve that best described the variation in the data (Sokal and Rohlf 1981). I conducted Wilcoxon matched-rank tests to compare predation rates during the egg and nestling stages and to compare the number of Wood Thrushes and cowbirds produced within study sites. I used the $t$ distribution because it is more accurate than the traditional $\chi^2$ approximation, particularly for small sample sizes (Conover 1980). I used a paired $t$-test to compare the reduction in Wood Thrush clutch sizes due to parasitism and predation within study sites. Finally, I used a chi-square test of independence to explore possible edge effects on cowbird parasitism and nest predation. Unless noted otherwise, I pooled data across years and considered results significant if $P \le 0.05$.

## RESULTS

*Wood Thrush abundance.*—The mean number of Wood Thrushes detected per point count and the density of nests were negatively related to fragment area (point counts, $R^2 = 0.30$, df = 12, $P = 0.06$; nest density, $R^2 = 0.45$, df = 12, $P = 0.009$). However, the number of fledglings produced per nesting attempt was related to neither measure of Wood Thrush abundance ($R^2 < 0.11$, df = 13, $P > 0.20$).

*Cowbird parasitism.*—There was no relationship between fragment area and the number of female cowbirds or the number of cowbird hosts detected per point count ($R^2 < 0.17$, df = 12, $P > 0.15$). Likewise, no relationship occurred between the number of female cowbirds and the number of possible cowbird hosts ($R^2 = 0.10$, df = 13, $P = 0.24$).

Cowbird parasitism, measured as the proportion of nests parasitized, varied from 58 to 100% among study sites (Table 2). I detected a significant negative relationship between the number of cowbird eggs per nest (intensity of cowbird parasitism) and hatching date of Wood Thrush nests (cubic regression model, $R^2 = 0.21$, df = 213, $P < 0.001$). More cowbird eggs were deposited in thrush nests at the onset of breeding and at the peak period of second clutches than in the interim or late in the breeding season.

Cowbird parasitism was not related to fragment area ($R^2 < 0.07$, df = 0.12, $P > 0.38$). However, a positive relationship existed between the mean number of cowbird eggs per thrush nest and thrush abundance at the 15 study sites (point counts, $R^2 = 0.26$, df = 13, $P = 0.05$; nest density, $R^2 = 0.30$, df = 13, $P = 0.03$).

The number of thrush nests parasitized by cowbirds was independent of distance from forest edge ($\chi^2 = 1.72$, df = 2, $P = 0.42$; using 0 to 50 m, 51 to 100 m, and >100 m from a forest edge). Similarly, the number of nests with 0, 1 to 3, or >3 cowbird eggs was independent of distance from forest edge ($\chi^2 = 2.28$, df = 4, $P = 0.69$).

*Nest predation.*—I located 278 Wood Thrush nests from 1994 to 1996. Nest predation rates averaged 57.9 ± SE of 3.7%. The daily predation rate was significantly higher during incubation than during the nestling stage (Wilcoxon test, $t = 2.79$, df = 28, $P < 0.01$; Table 2). I found no relationship between fragment area and the abundance of avian predators or Mayfield-adjusted predation rates ($R^2 < 0.04$, df = 12, $P > 0.50$). In addition, the number of nests depredated was independent of distance from edge ($\chi^2 = 2.42$, df = 2, $P = 0.30$).

*Reproductive success.*—Nesting success was 39.3%, and only 0.6 Wood Thrushes were produced per nesting attempt (Table 2). Neither measure of reproductive success was related to fragment area ($R^2 < 0.06$, df = 12, $P > 0.38$). The percentage of nests that produced at least

TABLE 2. Nest parasitism, nest predation, and reproductive success of Wood Thrushes in the northern Indiana study sites.

| Site | $n$ | % Nest parasitism | WOTH eggs[a] | BHCO eggs[b] | % Clutch difference[c] | Incubation DMR[d] | Nestling DMR[d] | WOTH young[e] | Nesting success[f] | No. WOTH per attempt |
|------|-----|------|------|------|------|------|------|------|------|------|
| BLC  | 5   | 100  | 2.5  | 3.0  | 28.6 | 0.039 | 0.023 | 1.0 | 44.5 | 0.4 |
| GRN  | 5   | 100  | 2.8  | 2.4  | 21.4 | 0.022 | 0.026 | 1.7 | 53.6 | 0.9 |
| HOR  | 66  | 97   | 2.1  | 2.2  | 40.4 | 0.042 | 0.011 | 1.4 | 49.6 | 0.7 |
| HWL  | 19  | 68   | 2.5  | 1.8  | 30.4 | 0.042 | 0.008 | 1.5 | 44.6 | 0.7 |
| JEL  | 15  | 100  | 2.2  | 2.8  | 32.6 | 0.033 | 0.031 | 1.7 | 43.3 | 0.7 |
| MAR  | 19  | 58   | 2.8  | 1.0  | 15.8 | 0.022 | 0.023 | 2.4 | 50.9 | 1.2 |
| MOR  | 6   | 100  | 2.2  | 2.2  | 31.3 | 0.067 | 0.033 | 2.0 | 16.4 | 0.3 |
| MUS  | 27  | 93   | 2.0  | 2.4  | 43.3 | 0.054 | 0.021 | 1.5 | 31.6 | 0.5 |
| ROS  | 40  | 82   | 2.1  | 2.7  | 36.7 | 0.028 | 0.025 | 1.6 | 40.2 | 0.6 |
| RUT  | 7   | 71   | 2.3  | 2.9  | 30.0 | 0.016 | 0.065 | 1.3 | 37.1 | 0.5 |
| STW  | 45  | 91   | 2.2  | 1.9  | 37.1 | 0.034 | 0.023 | 1.5 | 38.6 | 0.6 |
| ULR  | 11  | 91   | 2.0  | 2.8  | 41.9 | 0.017 | 0.010 | 1.4 | 70.6 | 1.0 |
| VET  | 5   | 100  | 1.6  | 2.2  | 57.9 | 0.115 | 0.000 | 1.0 | 20.3 | 0.2 |
| WIG  | 5   | 100  | 1.7  | 2.3  | 50.0 | 0.083 | 0.030 | 0.6 | 21.6 | 0.2 |
| WRI  | 4   | 100  | 1.3  | 3.7  | 66.7 | 0.059 | 0.040 | 1.5 | 26.8 | 0.4 |
| Mean | 19  | 91   | 2.2  | 2.4  | 37.6 | 0.045 | 0.025 | 1.4 | 39.3 | 0.6 |

[a] Mean minimum number of Wood Thrush (WOTH) eggs observed during incubation.
[b] Mean maximum number of Brown-headed Cowbird (BHCO) eggs observed during incubation.
[c] Clutch size relative to clutch size of unparasitized nests.
[d] Daily mortality rate (DMR) during incubation or the nestling period based on the Mayfield method (1975).
[e] Mean number of WOTH nestlings fledged from nests that produced at least one WOTH and/or BHCO.
[f] [(daily nest survival rate during incubation)[13] × (daily nest survival rate during the nestling period)[13]] × 100.

one cowbird fledgling was significantly greater than the percentage that produced at least one Wood Thrush (Wilcoxon test, $t = 2.21$, df = 28, $P = 0.03$). The reduction in Wood Thrush clutch size as a result of parasitism ($\bar{x} = 37.6 \pm 3.4\%$) was similar to the potential reduction due to nest predators in the absence of parasitism ($\bar{x} = 36.9 \pm 3.4$; paired $t = 0.16$, df = 28, $P = 0.88$).

Based on the 17 color-marked females followed in 1996, the mean number of nesting attempts per season was 3.1 (range 2 to 4). All but one of the marked females initiated a nesting attempt in July, and 65% were still nesting in early August. I located more renesting attempts of successful pairs than of unsuccessful pairs. As a result, nesting success of the 17 color-marked females was nearly 1.6 times higher than that for all nests combined, and the color-marked females probably attempted fewer broods than those with lower nesting success. Therefore, my estimate of nesting attempts per season was conservative for this landscape.

*Source-sink assessment.*—Only 13% of the study sites had seasonal fecundity values above the conservative source-sink threshold, whereas 53% of the sites exceeded the source-sink threshold based on the optimistic survival estimates for adults and juveniles (Fig. 2).

Landscape-level population stability can be assessed by calculating how many Wood Thrush juveniles are recruited into the landscape relative to the number of adults that die. This calculation assumes that (1) forest patches in the watershed are adequately sampled, (2) nest density in areas sampled was representative of the entire fragment, (3) juvenile and adult survival rates were consistent among forest fragments, and (4) juveniles returned to their natal landscape. Using the conservative survival rates and the productivity levels and nest densities observed in each fragment, I estimated that the ratio of adult mortality to juvenile recruitment within the landscape was 1.53:1.

DISCUSSION

In contrast to other areas in the midwestern United States (e.g. Brawn and Robinson 1996), some forest fragments in northern Indiana support populations of Wood Thrushes that are potential sources, at least in some years. Nonetheless, the relatively few source populations in this landscape did not compensate for decreased reproductive success within the abundant sinks, supporting the regional-sink hypothesis of Brawn and Robinson (1996).
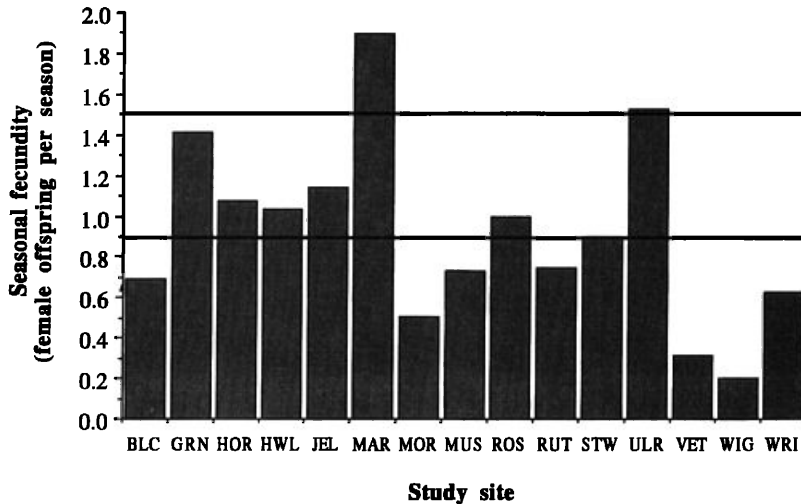
**FIG. 2.** Seasonal fecundity of female Wood Thrushes at the 15 study sites. Estimates are based on the number of female fledglings raised per nesting attempt multiplied by the mean number of broods attempted (3.1 broods) by 17 color-marked Wood Thrushes in 1996. Upper line is the level of productivity at the conservative source-sink threshold (based on 58% and 28% survival for adults and juveniles, respectively). Lower line is the source-sink threshold based on the more optimistic survival rates of 70% for adults and 35% for juveniles. Seasonal fecundity between these lines is near the source-sink threshold and would require more precise estimates of juvenile and adult Wood Thrush survival to classify accurately.

*Wood Thrush abundance.*—The breeding density of Wood Thrushes in small forest patches may have resulted from increased disturbance that created dense stands of saplings that are often used by nesting thrushes (Table 1). Alternatively, conspecific attraction (or social facilitation) may have encouraged settlement of Wood Thrushes that were searching for territories in forest patches that already contained breeding pairs (Smith and Peacock 1990). Nevertheless, the generally poor reproductive success of Wood Thrushes in small woodlots suggested that these sites did not provide high-quality habitats, in contrast to inferences that may be drawn from local surveys of breeding density (Van Horne 1983, Vickery et al. 1992).

*Cowbird parasitism.*—In my study, neither the number of female cowbirds detected per point count, the percentage of nests parasitized, nor the number of cowbird eggs per Wood Thrush nest was negatively related to fragment area as predicted by the fragmentation hypothesis (Wilcove et al. 1986). Apparently, female cowbirds have saturated this and other midwestern landscapes (Robinson 1992, 1993; Hoover and Brittingham 1993).

In the two most isolated woodlots studied (HWL and MUS), I detected few cowbirds

overall and no females. Although point-count sampling does not yield a direct measure of density, it produces a relative index of abundance, assuming equal detectability of cowbirds among study sites. Based on my point counts, either cowbirds spent little time in isolated woodlots searching for hosts' nests, or such woodlots were searched by a single (quiet) female. As a result, some Wood Thrushes occasionally may escape cowbird parasitism in isolated woodlots.

The lowest rate of cowbird parasitism occurred at MAR, a moderate-sized fragment. The density of breeding Wood Thrushes was also lowest at this site (0.10 nests per ha vs. 0.33 at the other sites). In fact, the density of Wood Thrushes was positively correlated with the number of cowbird eggs deposited in their nests. If cowbirds find nests of different host species with the same probability and show no host preference or numerical response, the relative density of Wood Thrush nests should not affect the number of cowbird eggs they receive. Instead, female cowbirds either specialized on common hosts such that rare hosts may have escaped intense cowbird parasitism (but see Robinson 1993), or they preferred Wood Thrushes over other hosts. Cowbird speciali-

zation also may have explained the seasonal pattern of parasitism on Wood Thrush nests. The number of cowbird eggs per thrush nest was relatively high when thrushes were highly synchronous in their nesting stage (i.e. early when thrushes began nesting, and again when successful breeders renested).

The rate of cowbird parasitism in my study was close to that predicted by Robinson et al. (1995) based on low forest cover (<10%) in the watershed. Nonetheless, the reduction in clutch size due to cowbird parasitism (37%) was not as extreme as the 71% reduction reported by Brawn and Robinson (1996) for Wood Thrushes that nested in a similar agricultural landscape. Despite the similar percentage of Wood Thrush nests parasitized, the two landscapes differed in the intensity of parasitism; Wood Thrush nests in central Illinois contained an average 4.6 cowbird eggs (Robinson 1992), which is nearly twice the average number of cowbird eggs that I found.

Cowbird parasitism of Neotropical migrants in eastern North America typically is much lower than in the Midwest (e.g. Holmes et al. 1992, Porneluzi et al. 1993, Roth and Johnson 1993, Gale et al. 1997). In addition, studies in eastern forests (e.g. Gates and Gysel 1978) and in more highly forested midwestern regions (e.g. Brittingham and Temple 1983, Temple and Cary 1988) reported that the percentage of nests parasitized and the number of cowbird eggs per host nest decreased as distance from a forest edge increased. I found no evidence of an edge effect for cowbird parasitism. In fact, such effects tend to appear only at intermediate levels of cowbird density (Gates and Gysel 1978, Brittingham and Temple 1983, O'Conner and Faaborg 1992).

*Nest predation.*—Nest predation was common in this landscape (58%) but was not as high as levels reported for Wood Thrushes in central Illinois (82%; Robinson 1992). As with cowbird parasitism, nest predation was independent of forest area and distance to edge in my study. Nest predators such as Blue Jays, raccoons (*Procyon lotor*), opossums (*Didelphis marsupialis*), and eastern chipmunks (*Tamias striatus*), typically show higher densities in small than in large forests tracts (Wilcove 1985, Small and Hunter 1988, Hoover et al. 1995). In addition, many studies have shown a gradation in predation rates as a function of distance from a habitat edge, and the most conclusive studies suggest that edge effects occur within 50 m of an edge (Paton 1994). In my study area, all but the largest fragments (>300 ha) were highly dissected and contained little interior habitat (Fig. 1). Nonetheless, neither my study nor that of Robinson (1993) detected a consistent effect of proximity to edge on rates of nest predation.

*Reproductive success.*—Nesting success of Wood Thrushes in my study was higher than that reported for a similar landscape in central Illinois (Robinson 1992, Robinson et al. 1995). In addition, estimates of the reduction of reproductive success attributed to cowbird parasitism and nest predation suggested that both were equally important sources of mortality. Wood Thrushes are larger than most Neotropical migrants that cowbirds parasitize and are better able to raise both their own and cowbird offspring (Robinson 1993). Predation rates vary among breeding Neotropical migrants, and Wood Thrushes had the lowest daily nest mortality rates among the ground- and shrub-nesting Neotropical migrants studied by Donovan et al. (1995) and Robinson et al. (1995). Therefore, some of my conclusions about reproductive success in Wood Thrushes may not be applicable to Neotropical migrants in general.

*Source-sink assessment.*—The number of female fledglings produced per adult female in one of my sites (MAR; Table 3) approached that reported for intact forests such as Great Smoky Mountains National Park (Simons and Farnsworth 1995), whereas productivity in others sites was so low that recruitment could not possibly balance mortality (Fig. 2). In contrast, no woodlots in northern and central Illinois were self-sustaining (Brawn and Robinson 1996), and even those as large as 2,000 ha in southern Illinois appeared to be sinks (Trine 1998).

Although 13% of my study sites were at or above the source-sink threshold (Fig. 2), none was a source habitat in all years. For example, MAR fledged an average of three female offspring per adult female in 1994, but fewer than half that number in 1996. Similarly, STW clearly was a sink in 1994 (0.2 female fledglings per adult female) but approached the productivity needed for a stable population in 1996 (1.1 female fledglings per adult female). Thus, a temporal pattern of source-sink dynamics occurred across the landscape, with periodic good and bad years within sites. Trine (1998)

TABLE 3. Annual variation in nest parasitism, nest predation, and reproductive success of Wood Thrushes breeding in the northern Indiana study sites that were observed in multiple years.

| Variable | Study site | | | | | | |
|---|---|---|---|---|---|---|---|
| | HOR | HWL | JEL | MAR | MUS | ROS | STW |
| **1994** | | | | | | | |
| No. of nests | 15 | — | 8 | 5 | — | 11 | 10 |
| % Nest parasitism | 100 | — | 100 | 80 | — | 82 | 90 |
| Nest predation[a] | 34.8 | — | 44.5 | 22.7 | — | 44.9 | 52.4 |
| No. exposure days[b] | 248 | — | 131 | 97 | — | 177 | 147 |
| Mean no. young per successful attempt | 1.9 | — | 1.8 | 2.5 | — | 1.3 | 0.5 |
| Mean no. young per attempt | 1.2 | — | 1.0 | 1.9 | — | 0.6 | 0.2 |
| **1995** | | | | | | | |
| No. of nests | 17 | 6 | 7 | 9 | 12 | 12 | 16 |
| % Nest parasitism | 100 | 83 | 100 | 44 | 100 | 89 | 93 |
| Nest predation[a] | 54.7 | 41.2 | 70.0 | 45.8 | 43.2 | 63.9 | 51.9 |
| No. exposure days[b] | 204 | 84 | 90 | 142 | 183 | 130 | 179 |
| Mean no. young per successful attempt | 1.4 | 2.0 | 1.5 | 2.8 | 1.6 | 1.8 | 1.4 |
| Mean no. young per attempt | 0.6 | 0.8 | 0.5 | 1.3 | 0.8 | 0.5 | 0.6 |
| **1996** | | | | | | | |
| No. of nests | 34 | 13 | — | 5 | 15 | 17 | 19 |
| % Nest parasitism | 88 | 67 | — | 60 | 87 | 76 | 84 |
| Nest predation[a] | 54.7 | 51.6 | — | 65.4 | 77.3 | 45.6 | 52.7 |
| No. exposure days[b] | 450 | 178 | — | 73 | 163 | 215 | 258 |
| Mean no. young per successful attempt | 1.2 | 1.4 | — | 1.5 | 1.4 | 1.7 | 2.0 |
| Mean no. young per attempt | 0.5 | 0.7 | — | 0.5 | 0.3 | 0.7 | 0.8 |

[a] $1 - [(\text{daily nest survival rate during incubation})^{13} \times (\text{daily nest survival rate during nestling period})^{13}] \times 100$.
[b] Total number of days that nests were observed.

also documented considerable annual variation in reproductive success in midwestern forest tracts, emphasizing the importance of collecting data in multiple years before assessing source-sink status of fragments.

The scale at which source-sink dynamics operate for Wood Thrushes is unknown. Juveniles are rarely detected returning to natal areas (Roth and Johnson 1993), and many probably disperse long distances. Nonetheless, variation in productivity among my study sites suggests the potential for source-sink dynamics within the landscape, although the number of recruits produced in source habitats is not sufficient to overcome the population deficit produced by forest patches that act as sinks. Not all forest fragments in northern Indiana are sinks in all years, but my results concur with other studies that suggest that agricultural portions of the midwestern United States act as regional sinks for Wood Thrushes and other Neotropical migrants (Donovan et al. 1995, Robinson et al. 1995, Brawn and Robinson 1996, Bollinger et al. 1997, Trine 1998). This conclusion should be

considered tentative, however, because relatively few studies (including mine) have collected all the necessary estimates of demography (i.e. survival rates and measures of seasonal breeding productivity). Collecting such data will require long-term studies of populations with marked individuals (e.g. Nolan 1978, Holmes et al. 1986, Roth and Johnson 1993) but will provide the basis for improving the current understanding of source-sink dynamics of Neotropical migrants that breed in the midwestern United States.

Temporal variation in reproductive success and the scale of source-sink dynamics complicate conservation strategies for Neotropical migrants in the midwestern United States. Unlike the eastern United States, forest area is not a good predictor of reproductive success in the Midwest, at least when the total amount of forest cover is low. Enhancing large tracts where cowbird parasitism and nest predation are reduced, such as in southern Indiana, northern Wisconsin, and southeastern Missouri, cur-

rently is the best strategy for conserving Neo-tropical migrants in the Midwest.

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