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REPRODUCTIVE SUCCESS OF NEOTROPICAL MIGRANTS IN A FRAGMENTED ILLINOIS FOREST

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ABSTRACT.—In June–July 1991–1992, we replicated the mist-netting methods of Robinson (1988, 1992), who captured birds in forest fragments adjacent to Lake Shelbyville in east-central Illinois in 1985–1986. Of all forest-interior Neotropical migrants that were captured, a much high proportion were hatching year (HY) birds in 1991–1992 (29%) than in 1985–1986 (8%), indicating higher reproductive success. The numbers of Brown-headed Cowbirds (*Molothrus ater*) and the frequency of their parasitism were significantly lower in 1991–1992 than in 1985–1986. However, despite these improvements, reproductive success for Neotropical migrants was still low, presumably because of high levels of nest predation. A significantly lower percentage of adult birds captured in 1991–1992 were forest-interior Neotropical migrants than in 1985–1986 (35% vs 48%). *Received 22 March 1993, accepted 16 July 1993.*

In the past 20 years, there has been a marked increase in concern over the apparent population declines of many species of birds that breed in temperate North America and winter in the tropics (Neotropical migrants) (e.g., Briggs and Criswell 1978, Keast and Morton 1980, Robbins et al. 1989b, Askins et al. 1990, Hagan and Johnston 1992). These declines have tended to be most severe for species nesting in the interior of larger tracts of forest (i.e., forest-interior species; Terborgh 1989, Askins et al. 1990).

Forest fragmentation on the breeding grounds and deforestation in the tropics have frequently been mentioned as likely causes of the population declines of these birds (Askins et al. 1990, Terborgh 1992). On the breeding grounds, forest fragmentation reduces not only the quantity of habitat but also the suitability of that which remains for forest-interior Neotropical migrants (Whitcomb et al. 1981, Robbins et al. 1989a). Birds nesting in small forest fragments often suffer from high levels of brood parasitism by Brown-headed Cowbirds (scientific names given in Appendix I; Chasko and Gates 1982, Brittingham and Temple 1983, Robinson 1992), nest predation (Gates and Gysel 1978, Wilcove 1985, Wilcove et al. 1986, Temple and Cary 1988, Yahner and Scott 1988, Robinson 1992), and, perhaps, competition from non-forest or forest-edge species that invade the interior of small forest fragments (Ambuel and Temple 1983, Wilcove and Robinson 1990).

Perhaps nowhere have these detrimental effects been documented more dramatically than in the small forest fragments adjacent to Lake Shel-

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byville in east-central Illinois. Here, Robinson (1988, 1992) and Wilcove and Robinson (1990) documented extremely high levels of nest parasitism and nest predation in 1985–1986. For example, 76% of all nests of Neotropical migrants were parasitized by Brown-headed Cowbirds, with an average of 3.3 cowbird eggs per parasitized nest. Approximately 80% of all open-cup nests were destroyed by predators. As a result, this study has frequently been cited as a "worst case scenario" (Robinson 1990) of the detrimental effects of forest fragmentation on the breeding grounds for Neotropical migrants (e.g., Terborgh 1989, 1992; Roth and Johnson 1993).

In 1991–1992, we investigated reproductive success of Neotropical migrants to determine whether population sizes of Neotropical migrants had declined in these woodlots as a result of poor reproductive success and to determine if reproductive success was still as low as Robinson had found in 1985–1986. To answer these questions, we used Robinson's (1992) methodology for his midsummer mist-net samples.

STUDY AREA AND METHODS

Our study sites were three small woodlots (14-, 25-, and 65-ha) bordering Lake Shelbyville in Shelby and Moultrie counties, east-central Illinois (39°N, 88°W) and were the same sites studied by Robinson (1992). Efforts were concentrated in the largest woodlot, a 65-ha fragment (known as "the Boot") bordered by the lake to the north and by corn and soybean fields to the south. This woodlot is dissected by numerous intermittent streams with large white oaks (*Quercus alba*) scattered among dense young oaks and hickories (*Carya* spp.) on the ridge tops (see Linder 1992, Robinson 1988 for more details).

We mistnetted birds using the methodology of Robinson (1992 and pers. commun.) as closely as possible. We relocated Robinson's netlines and opened our nets at approximately the same places and times as he did in 1985–1986. We also netted the same areas for two consecutive years (1991 and 1992) as did Robinson. Between 15 and 25 mist-nets (black, 12 m, 36 mm mesh, 4 tier) were strung end-to-end along the netline and opened for three consecutive days from 06:00–12:00 h EDT. After the third day, the nets were moved to the next adjacent area. A total of five areas was sampled. Netting began on 20–21 June after the primary breeding season for most forest-nesting passerines and ended on 20–24 July before fall migration. Each area was sampled twice, once between 20 June–5 July and once (two weeks later) between 6–24 July.

All birds that were captured were banded with U.S. Fish and Wildlife Service aluminum bands, aged by plumage characteristics and skull pneumatization (Pyle et al. 1987, USFWS 1991), measured, and released. Birds were aged as either adult, "after-hatching-year" (AHY), or recently fledged, "hatching-year" (HY) birds. Compared to Robinson's studies, we spent relatively little time searching for nests or recently-fledged family groups.

We compared our mist-netting data with those of Robinson primarily through chi-square (χ^2) tests of the numbers of birds caught. Tests have one degree of freedom unless noted otherwise. We pooled data from 1991 and 1992 as Robinson did for 1985 and 1986. We used data published in Robinson (1988 and 1992) where possible and Robinson's unpublished data otherwise. We have followed the categorizations of Whitcomb et al. (1981) and Freemark and Collins (1992) to distinguish Neotropical migrant species from permanent

TABLE 1

HATCHING YEAR (HY): ADULT (AHY) RATIOS FOR FOREST-INTERIOR NEOTROPICAL MIGRANTS IN MIST-NET SAMPLES FROM LATE JUNE THROUGH MID-JULY, IN BOTH 1985–1986 (ROBINSON 1992) AND IN 1991–1992 IN FOREST FRAGMENTS ADJACENT TO LAKE SHELBYVILLE, ILLINOIS

	HY: AHY ratio	
Species	1985–1986	1991–1992
Great Crested Flycatcher	0.1 (19)[a]	0.6 (13)
Eastern Wood-Pewee	0.2 (12)	0.9 (13)
Acadian Flycatcher	0.0 (5)	0.2 (15)
Wood Thrush	0.1 (46)	0.6 (21)
Red-eyed Vireo	0.0 (2)	0.6 (19)
Kentucky Warbler	0.3 (14)	0.0 (8)
Worm-eating Warbler	0.0 (4)	1.0 (2)
Ovenbird	0.0 (11)	0.3 (13)
Louisiana Waterthrush	0.5 (3)	1.0 (2)
Scarlet Tanager	0.0 (7)	0.2 (13)
Total HY: Total AHY	0.1 (123)	0.4 (119)

[a] Numbers in parentheses are total numbers caught (HY + AHY) for each species.

residents and short distance migrants. These references were also used to categorize species as either "forest interior" or "edge" species (see Appendix I). Permanent residents and short-distance migrants are referred to collectively as "local" species.

We used HY percentages (or HY: AHY ratios) as our index of reproductive success. We assume that high reproductive success will result in a high proportion of HY birds in our mist net samples. We believe that HY percentages (or HY : AHY ratios) provide a reasonable index of reproductive success and population sizes for comparative purposes between Robinson's data and our own. Others (e.g., Karr 1981, Robinson 1992) have discussed the benefits and limitations of using mist-netting data to infer breeding success and population dynamics. Therefore, we will attempt to "generalize cautiously" (Robinson 1992:416) from our data.

RESULTS

For all forest interior species combined, we captured a significantly higher proportion of HY Neotropical migrants (29% of 119 Neotropical migrants) in 1991–1992 than did Robinson in 1985–1986 (8% of 123) ($\chi^2 = 18.1$, $P < 0.001$). Furthermore, our HY: AHY ratios were higher for nine of the 10 species of Neotropical migrants reported by Robinson (1992, Wilcoxon signed rank test, $P < 0.01$, Table 1). However, the proportion of all the adult (AHY) birds that we captured that were forest-interior Neotropical migrant species (35% of 243 adult birds) was significantly lower than Robinson's figure (48% of 236, $\chi^2 = 8.7$, $P < 0.005$). Considered individually, seven of the 10 species had fewer adults captured in 1991–1992 compared to 1985–1986 (Table 1), but this result was not statistically significant (Wilcoxon signed rank test, $P > 0.10$).

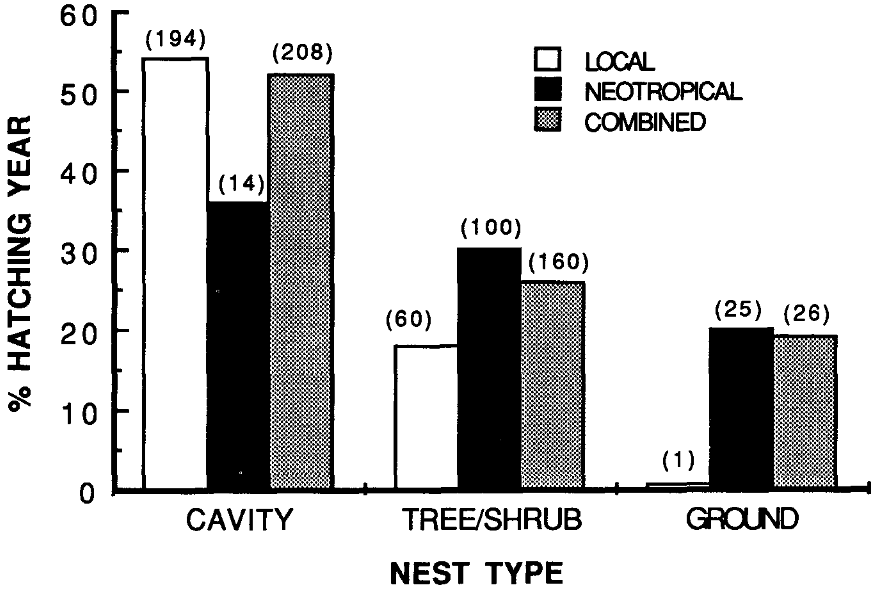

FIG. 1. Percentages of birds caught in mist-net samples in late June through mid-July, 1991–1992 that were hatching year (HY) for three groups of species with different nest types. "Tree/shrub" nesters are species that do not nest on the ground or in cavities. Sample sizes (total caught; HY + AHY) are in parentheses. For local and Neotropical species combined, the HY percentage varied significantly among nest types ($\chi^2 = 31.9$, df = 2, $P < 0.001$).

HY birds made up similar proportions in both 1991–1992 and 1985–1986 when all local species where pooled (45% vs 42% of 264 and 201 individuals, respectively; $\chi^2 = 0.6$, $P > 0.50$). In both studies, the HY proportion was significantly higher for local species than for Neotropical migrants ($P < 0.005$).

Our index of reproductive success varied significantly by nest type ($P < 0.001$, Fig. 1). For all species combined, cavity nesters had the highest proportion of HY birds (52% of 208 in 1991–1992, 44% of 131 in 1985–1986) and ground nesters had the lowest (19% of 26 in 1991–1992, 12% of 33 in 1985–1986). However, within a nest type, the proportion of birds that were HY did not differ between local species and Neotropical migrants (1991–1992 data, $\chi^2 < 2.7$, $P > 0.10$, Fig. 1).

Fewer Brown-headed Cowbirds were caught in 1991–1992 than in 1985–1986. Cowbirds made up 10% of all birds captured in 1985–1986 (N = 324) compared to 2% (N = 383) in 1991–1992 ($\chi^2 = 17.1$, $P < 0.001$). They were the third most abundant species captured in mist-nets in 1985–1986 but only the 16th most abundant species in 1991–1992. Species that build open cup nests but are known to reject cowbird eggs (i.e., "rejector" species, Rothstein 1975, Appendix I) had a significantly higher percentage of HY individuals among the birds Robinson captured in 1985–1986 (49% of 39) than did all other species combined (22% of 285; $\chi^2 = 12.9$, $P < 0.001$). HY birds made up only 25% of the individuals of rejector species captured in 1991–1992 (8 of 32), a proportion that was marginally lower than that for all other species combined (41% of 371; $\chi^2 = 3.1$, $P < 0.10$).

Return rates of AHY Neotropical migrants between the first and second years of both Robinson's study and ours were similarly low (15% and 19% respectively, $\chi^2 = 0.2$, $P > 0.50$). Return rates for local species were lower (14% in 1991–1992, 7% in 1985–1986).

Results from the few nests and recently-fledged family groups that we observed generally supported our mist-netting data. Only 25% of the open-cup nests (3 of 12) that we found contained eggs or nestlings of cowbirds compared to 67% (49 of 73) for Robinson (1992; $\chi^2 = 7.7$, $P < 0.01$). Of seven recently-fledged family groups of Neotropical migrants observed in 1991–1992 (1 Scarlet Tanager, 1 Red-eyed Vireo, 2 Kentucky Warbler, 2 Ovenbird, 1 Wood Thrush), five had host young only (71%) compared to 33% (7 of 21) for the same species in 1985–1986 (Robinson 1992; Fisher's exact test, $P = 0.10$). Only one of the seven groups (14%) contained only cowbird fledglings (vs 12 of 21 in 1985–1986 [Robinson 1992], Fisher's exact test, $P = 0.06$).

DISCUSSION

Based on the fact that our HY : AHY ratio for forest-interior Neotropical migrants in 1991–1992 was about four times greater than was Robinson's (1992) in 1985–1986, it appears that reproductive success of these species in the Lake Shelbyville area has improved significantly in the past five years. Reproductive success for Neotropical migrants in these forest fragments may not always be as low as it was in 1985–1986. In fact, the HY : AHY ratio for forest-interior Neotropical migrants in 1991 alone was nearly 1.0 (and virtually identical to the HY : AHY ratio for local species that year). Thus, this index of reproductive success has varied nearly an order of magnitude (HY : AHY ratios of 0.1 to 1.0) in the past 5–6 years. An important question is how frequently do these "good years" occur? They may be relatively rare, however, as our HY : AHY ratio for Neotropical migrants dropped back to 0.25 in 1992 (still 2.5 times higher than in 1985–1986).

One explanation for the higher reproductive success of Neotropical migrants in 1991–1992 was the apparent reduction in cowbird parasitism, suggested by four pieces of data. First, we caught a much lower proportion of cowbirds in our mist-net samples (2% vs 10%) than did Robinson. Second, although we found only 12 nests, the proportion of nests that were parasitized was half that found in nests in 1985–1986. Third, most of the recently-fledged families of Neotropical migrants that we observed contained only host young, in contrast to Robinson's (1992) findings. Finally, rejector species appeared to have higher reproductive success in 1985–1986 but somewhat lower reproductive success in 1991–1992 compared to species that accept cowbird eggs. This suggests that cowbird parasitism may have been an important factor limiting reproductive success for many species of open-cup nesters in 1985–1986 but not in 1991–1992. Why the frequency of cowbird parasitism should have dropped is unclear to us. However, the fact that the relative abundance of all forest-interior Neotropical migrant adults combined (i.e., common cowbird hosts) declined significantly between the studies may be a partial explanation. The precipitous drop (i.e., >50%—Table 1, see also Robinson 1992) in the population size of the Wood Thrush, an especially vulnerable cowbird host, may be particularly significant. However, two other common cowbird hosts (Red-eyed Vireo and Scarlet Tanager) appeared to have increased since 1985–1986.

Despite the fact that reproductive success appeared to be over three times higher for forest-interior Neotropical migrants during our study, overall productivity for these species was still low. Only 29% of the Neotropical migrants we captured were fledglings (HY) compared to 45% for all local species, 54% for cavity-nesting local species in general, and 67% for the Tufted Titmouse (51 of 76) in particular. High levels of nest predation appeared to be the primary cause of this low reproductive success during our study. Cavity-nesting species, less vulnerable to predation than open-nesting species (Ricklefs 1969), had significantly higher proportions of HY birds than did non-cavity nesting species (52% vs 25%), for all species combined (Neotropical + local). Ground-nesting species, probably the most vulnerable to mammalian predators, had the lowest proportion of HY birds (19%) despite the fact that these species should be the most likely to be captured in our mist nets. Thus, the higher reproductive success for local species largely reflects the preponderance of cavity-nesting species in this group (and the near lack of ground-nesting species) compared to the Neotropical migrants. Artificial nest studies (Linder 1992, Bollinger, unpubl. data) in our study area also indicate very high levels of nest predation, primarily due to mammals such as raccoons (*Procyon lotor*). Over 90% of the artificial nests that we placed in these woodlots were disturbed by predators within six days.

Whereas cowbird parasitism may have abated somewhat in the 5–6 years since Robinson's study, high levels of nest predation, especially on open-nesting species, continue. Robinson's (1988, 1992) conclusion that these woodlots represent population sinks for Neotropical migrants still appears to be correct. However, these sinks may not be quite as "deep" as originally proposed. Long-term studies are necessary to determine how frequently good reproductive years for Neotropical migrants occur in this fragmented forest.

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APPENDIX I

CLASSIFICATION OF BIRDS CAPTURED IN MIST NETS IN FOREST FRAGMENTS ADJACENT TO LAKE SHELBYVILLE, ILLINOIS ACCORDING TO MIGRATORY STATUS

Species	Migration[a]	Habitat[b]	Nest type
Northern Bobwhite (*Colinus virginianus*)	L	—	G
Yellow-billed Cuckoo (*Coccyzus americanus*)	N	I	T/S
Ruby-throated Hummingbird (*Archilochus colubris*)	N	E	T/S
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	L	—	C
Red-bellied Woodpecker (*Melanerpes carolinus*)	L	—	C
Downy Woodpecker (*Picoides pubescens*)	L	—	C
Hairy Woodpecker (*Picoides villosus*)	L	—	C
Northern Flicker (*Colaptes auratus*)	L	—	C
Eastern Wood-Pewee (*Contopus virens*)	N	I	T/S
Acadian Flycatcher (*Empidonax virescens*)	N	I	T/S
Great Crested Flycatcher (*Myiarchus crinitus*)	N	I	C
Blue Jay* (*Cyanocitta cristata*)	L	—	T/S
Black-capped Chickadee (*Parus atricapillus*)	L	—	C
Tufted Titmouse (*P. bicolor*)	L	—	C
White-breasted Nuthatch (*Sitta carolinensis*)	L	—	C
Carolina Wren (*Thryothorus ludovicianus*)	L	—	C
Blue-gray Gnatcatcher (*Polioptila caerulea*)	N	E	T/S
Eastern Bluebird (*Sialia sialis*)	L	—	C
Wood Thrush (*Hylocichla mustelina*)	N	I	T/S
Gray Catbird* (*Dumetella carolinensis*)	L	—	T/S
Brown Thrasher* (*Toxostoma rufum*)	L	—	T/S
Red-eyed Vireo (*Vireo olivaceus*)	N	—	T/S
Prothonotary Warbler (*Protonotaria citrea*)	N	E	C
Worm-eating Warbler (*Helmintheros vermivorus*)	N	I	G
Ovenbird (*Seiurus aurocapillus*)	N	I	G
Louisiana Waterthrush (*S. motacilla*)	N	I	G
Kentucky Warbler (*Oporornis formosus*)	N	I	G
Summer Tanager (*Piranga rubra*)	N	E	T/S
Scarlet Tanager (*P. olivacea*)	N	I	T/S
Northern Cardinal (*Cardinalis cardinalis*)	L	—	T/S
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	N	E	T/S
Indigo Bunting (*Passerina cyanea*)	N	E	T/S
Common Grackle (*Quiscalus quiscula*)	L	—	T/S
Brown-headed Cowbird (*Molothrus ater*)	L	—	—
Northern Oriole* (*Icterus galbula*)	N	E	T/S
American Goldfinch (*Carduelis tristis*)	L	—	T/S

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[a] Migration status, habitat type, and nest types: L (local)—included both residents and short-distance migrants; N (Neotropical migrant); I, (forest interior); E (forest edge); C (cavity); G (ground); T/S (tree/shrub). Species with an asterisk are known to reject cowbird eggs.

[b] Local species were not classified according to habitat. Neotropical migrants classified as "interior and edge" species by Whitcomb et al. (1981) and Freemark and Collins (1992) are here listed as either "interior" or "edge" for comparison with Robinson (1992).