

LONG-TERM DYNAMICS OF A WOOD THRUSH POPULATION BREEDING IN A FOREST FRAGMENT

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ABSTRACT.—The dynamics of a population of Wood Thrushes (*Hylocichla mustelina*) in a Delaware woodlot from 1974 through 1990 did not meet all predictions of the forest-fragmentation hypothesis, which posits that declining abundance of Neotropical, migratory, forest songbirds results from poor reproduction in, and immigration to, forest fragments. Abundance declined at an average rate of 4% per year over the period 1978 through 1987, equalling the national decline found by the Breeding Bird Survey for those years, but recovered by 1990 to pre-decline levels. Abundance of previous residents followed a similar pattern, the only population component to do so. Abundance of new immigrants and of returning, locally produced young was generally stable. Throughout the study, reproductive rates were high enough to maintain the population at the return rates observed early and late in the study. However, a sustained episode of reduced production per female and of an increased percentage of adults failing to produce any young generally coincided with the decline in abundance. When the failure rate later dropped, return rate and abundance subsequently increased. We conclude that a period of elevated, predation-caused failure prompted greater emigration by an ever-younger, less-site-faithful population. High emigration coupled with stable immigration, stable recruitment of local young, and even normal mortality of residents would yield a declining population. A regional predation episode could cause a broader decline in abundance through several mechanisms that could reduce the number of available immigrants. Received 25 March 1991, accepted 9 November 1992.

CONCERN THAT populations of forest songbird species breeding in North America and wintering in the Neotropics are declining is widespread (Aldrich and Robbins 1970, Whitcomb 1977, Briggs and Criswell 1979, Robbins 1979, Terborgh 1980, 1989, Hall 1984, Askins et al. 1990, Hagan and Johnston 1992). Evidence of a general decline in one of these species, the Wood Thrush (*Hylocichla mustelina*), comes from several sources. Using results from Breeding Bird Survey routes in the eastern United States and Canada, an area covering essentially all of its breeding range, Robbins et al. (1989b) determined that Wood Thrush abundance decreased at a rate of 4.0% per year from 1978 to 1987. Holmes and Sherry (1988) reported a decline of 3.6% per year from 1969 to 1986 in similar data from New Hampshire. Although one study recorded small increases in Wood Thrush densities on a few plots (Wilcove 1988), and one reported little change on one plot (Serrao 1985), most recent studies of local abundance have observed large declines over time periods of various lengths (Askins and Philbrick 1987, Johnston and Winings 1987, Roth 1987, Holmes and Sherry 1988, Leck et al. 1988, Wilcove 1988, Terborgh 1989:42-43). These include studies of

isolated woodlands in Maryland, District of Columbia, Delaware, and Connecticut, as well as plots in extensive forest in Tennessee and New Hampshire.

One hypothesis to account for such declines suggests that fragmentation of the breeding habitat is important (Robbins 1979, Whitcomb et al. 1981). Wood Thrushes breed in a variety of deciduous forest types (James et al. 1984), including woodlots of only a few hectares (Galli et al. 1976, Temple 1986, Robbins et al. 1989a) and residential areas with some closed canopy (Roth 1987). Timber harvest, conversion to agriculture, and urbanization have left many eastern forests highly fragmented. For example, in Maryland, 59% of forest tracts are less than 8 ha and 85% are less than 20 ha; in Delaware, the corresponding numbers are 44% and 84% (Brooks and DiGiovanni 1989).

Local abundance can decline through decreased production and recruitment of local young, decreased immigration, increased deaths of residents, or increased emigration of adults. One prediction of the fragmentation hypothesis is that productivity of migrant birds nesting in forest fragments will be held below replacement levels by high rates of predation and brood

parasitism (Brittingham and Temple 1983, Wilcove 1985, Terborgh 1989:47–59). Small fragments have little forest-interior habitat and a large proportion of forest-edge habitat. Some nest predators and the Brown-headed Cowbird (*Molothrus ater*), a brood parasite, may concentrate their activities near forest edges and, thereby, in much of the area of smaller fragments (Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985, Temple and Cary 1988). Abundance of such species may have increased in the last 10 to 15 years as a result of new agricultural practices, urbanization, and reduced numbers of hawks and mammals that prey on the nest predators, thereby exaggerating their impact. Fragmentation also isolates woodlots. Isolation may lower immigration rates, and immigration may be critical to maintaining populations in small fragments (Butcher et al. 1981, Whitcomb et al. 1981, Askins and Philbrick 1987). The fragmentation hypothesis does not predict increased mortality or emigration of adults, although the latter may be a consequence of reduced reproductive success.

Intensive, long-term studies of fragmented populations can help resolve the importance of forest fragmentation to population dynamics. Unfortunately, no such studies involving simultaneous estimates of abundance and rates of reproduction, immigration, and return for a Neotropical forest migrant have been published. Studies on American Redstart (*Setophaga ruticilla*) and Black-throated Blue Warbler (*Dendroica caerulescens*) in extensive New Hampshire forests come closest to that ideal and are the most exhaustive to date (Sherry and Holmes 1992, Holmes et al. 1992). Here we report such data from a study of Wood Thrush breeding in a forest fragment in northern Delaware. We focus on the period 1978 through 1987, which Robbins et al. (1989b) identified as one of general decline for Wood Thrush populations and during which the study population declined. We also discuss trends before and after that period. The patterns observed are consistent with some, but not all, predictions of the fragmentation hypothesis. We propose verbal models of local and regional dynamics that accommodate both the consistencies and inconsistencies, including the recent return to pre-1978 levels.

METHODS

Study site.—The study site is a 15-ha woodlot on the University of Delaware Experimental Farm in

Newark, Delaware. The woodlot (hereafter, UDW) has been protected by a chain-link fence since 1979. Agricultural and athletic fields surround about 95% of UDW; a suburban highway borders the remainder, separating it from a housing development built in the 1960s. The nearest habitats occupied by Wood Thrush are residential areas about 0.8 km distant. In recent years, deciduous forest cover in the surrounding county has declined (by 7% between 1974 and 1984; MacKenzie 1989), while urbanization has increased.

UDW was not used for agricultural purposes after about 1900 (Steinhauer 1974). The area is mesic, with an intermittent stream and vernal ponds. The tree canopy is dominated by *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Acer rubrum*, *Quercus alba* and *Q. rubrum*. *Cornus florida*, *Carpinus caroliniana*, and *Nyssa sylvatica* are important in the subcanopy, and a well-developed shrub layer is composed primarily of *Viburnum* spp., *Clethra alnifolia*, *Lindera benzoin*, and *Smilax* spp. Minor changes in the vegetation have occurred during the study. Some patches of *Viburnum dentatum*, the shrub most often used for nesting, have declined, but new ones have developed. Some die-off of oaks (*Quercus*) has occurred since about 1985, and a 1-ha section of pole-sized *A. rubrum* has self-thinned and matured. See Longcore et al. (1966) and Gorman and Roth (1989) for more details.

Potential predators of eggs and nestlings common at the site include Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), Common Grackles (*Quiscalus quiscula*), gray squirrels (*Sciurus carolinensis*), and raccoons (*Procyon lotor*). Black rat snakes (*Elaphe obsoleta*) are uncommon. Predators that might prey on adult Wood Thrushes have included a resident pair of Great Horned Owls (*Bubo virginianus*) and occasional red foxes (*Vulpes vulpes*), feral cats (*Felis silvestris*), and migrating hawks (*Accipiter* spp.). American Robins (*Turdus migratorius*) are the only other thrushes nesting at the site. There is little human use of UDW in the nesting season except for our research team.

Data collection.—Each year from 1974 through 1990, Roth and coworkers tried to capture and mark with unique combinations of colored bands all Wood Thrushes breeding in UDW. One to four workers were on the site almost daily between late April and mid-August. Locations of singing, calling, and foraging birds were recorded. Singing males were attracted with song playbacks and captured with mist nets for banding. Females were netted near nests or in foraging areas. Mist nets also were set frequently at other sites in the woods to ensure the banding of all birds and to help determine home ranges. Whenever possible, young birds were banded in nests we could reach (below 5–6 m) a few days before fledging. With rare exception, others were captured and banded shortly after they fledged.

Efforts also were made to find all Wood Thrush nests and to determine their ownership and productivity. We are confident that few successful nests escaped discovery. Plotting seasonal chronologies of

nesting pairs shows few had sufficient time away from known nests to produce young from an unfound nest, and unbanded fledglings that could not be assigned to a known nest were rarely captured or seen, except in 1979. No effort to find nests was made in 1979; we report no reproductive data for that year. However, 13 young birds were banded when encountered.

From 1980 through 1983, a 3-ha peninsular portion of the site was not studied. In other years, this area held, on average, about 20% of the residents, fledglings, and new immigrants found in the rest of the plot. Assuming that the unstudied part held these same proportions in 1980 through 1983, we added 20% (rounded to the nearest whole number) to the numbers observed in those years.

Data analysis.—The abundance values are counts, not estimates, of the total number of residents present during the season. We used resightings, recaptures and nesting information to determine how many and which birds were resident on the site. Residents are defined as Wood Thrushes with territories, nests, or a sustained presence during the breeding period, and those observed only a few times, but that bred on the site in a previous or subsequent year. We included the occasional individuals that died or established residency in midseason. Thus, total residents may not equal two times the number of pairs.

Success in banding all known residents has been greater than 88% in all years except 1974 (76%). In general, the number of new immigrants was the number of residents not banded previously. However, 10 resident females in 1974 and 3 in 1975 were not banded; several of these likely returned and were banded as "new" residents in the next year. In calculating the number of immigrants and previous residents for 1975 and 1976, we assumed these birds returned at the same rate as marked ones. In no other year did more than two residents of each sex go unbanded; no corrections were made for those years because the effect would be minimal.

Return rate for each sex was the percent of marked residents present in UDW in year t that was also resident in year $t + 1$. This is a conservative estimate of survival rate because birds could be alive elsewhere. However, it does not decline systematically toward the end of the study, unlike estimates based on the minimum number known alive (Nichols and Pollock 1983). We made no correction for missing birds that returned in a later year. Such cases were infrequent and never involved more than one banded adult of each sex in a year; correcting for such missing birds would not alter the analysis in any notable way (unpubl. data).

Annual fledgling production was the number of young known to have fledged, plus an estimate of the number fledged from nests with unknown success. Nests were occasionally found after all activity had ceased at them. The nesting chronologies of nearby residents indicated that some of these almost certainly were nests of known birds and were not active

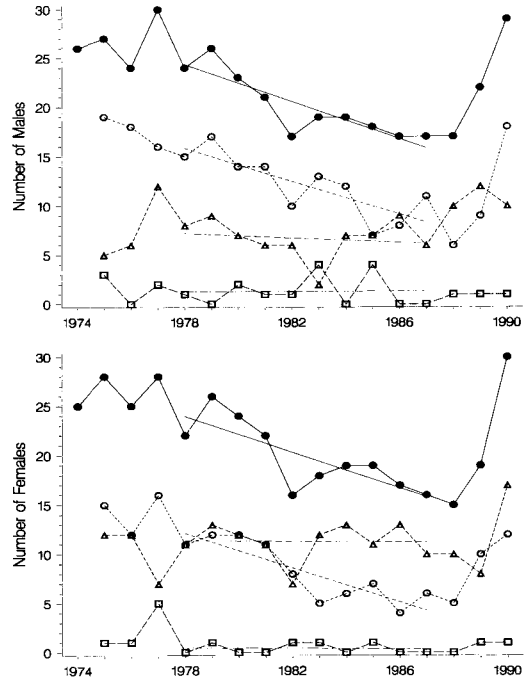


Fig. 1. Abundance of resident male and female Wood Thrushes at study site, 1974–1990 (solid circles) and of components of population: resident in previous year (open circle); new immigrant (triangle); and local young (square). Straight lines are least-squares regressions for 1978–1987 (see text). Sex ratios differ from 1:1 in years when a bird arrived in midseason and mated with a bird previously mated to another or a male remained unmated throughout season.

long enough to have produced fledglings. In 37 of 709 total nests, that determination was not possible; we estimated that these nests fledged the same number as the mean for all nests with known outcomes that year. Return rate of fledglings is the percent of birds that were born and banded on the site in year t that returned to breed in any later year.

We tested differences in return rates between the sexes with paired t -tests, male and female rates for each year forming the pairs. For the 1978–1987 period of decline, we examined trends over time for return, reproductive, and immigration rates by regressing the annual rates against year.

RESULTS

The number of residents on the site averaged around 26 birds of each sex during the early years of the study, then dropped in 1978–1982 (Fig. 1). Numbers remained low and remarkably stable at about 17 pairs through 1988, then rose dramatically, reaching their highest level of the

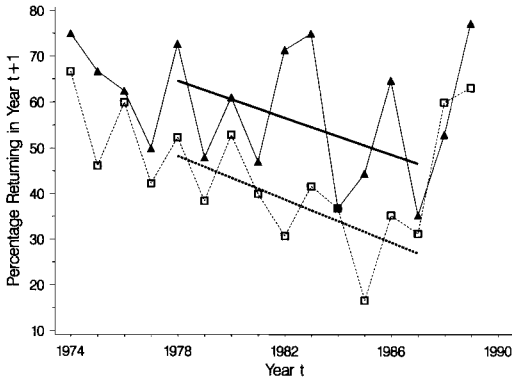


Fig. 2. Return rates of resident Wood Thrushes at study site, 1974–1990: males, triangles and solid line; females, squares and dashed line. Regression lines as in Figure 1. Return rate for year t is percentage of those banded in year t that returned in next year $t + 1$ and does not include unidentified birds known to be present, nor those estimated to be present (see Methods).

entire study in 1990 (Fig. 1). During 1978–1987, the number of males and females declined at an average rate of 3.8% and 3.5% per year, respectively, very near the rate calculated by Robbins et al. (1989b) for Wood Thrushes over their entire breeding range in the same period. This trend was significant for both sexes (both $P < 0.01$; $r^2 = 0.63$ for females, 0.77 for males).

The return rate of resident females had a pattern similar to that of population abundance: higher in the early years of the study, declining in the middle years, and increasing again in the last two years (Fig. 2). The decline during the 1978–1987 period was significant ($P = 0.03$, $r^2 = 0.46$). The data are suggestive that the return rate of resident males, though more variable, declined (Fig. 2) in the 1978–1987 period, although the trend was not statistically significant ($P = 0.25$, $r^2 = 0.16$). As with females, return rates increased in 1988 and 1989. Males returned at a higher rate than females in all but two years; mean return rate over all years (females 45%, males 59%) differed significantly between the sexes ($P < 0.001$).

Experiments conducted in 1984–1986 could have influenced return rates. In 1984, collars were put on 43 nestlings in 17 nests of 15 pairs for 1 to 2 h on one to six days in a diet study; four nestlings, each in a different nest, died as a result. All four pairs produced other young during the year. In 1985, none of 32 young collared in 12 nests of 10 pairs died. In 1986, 36

young in 15 nests of 12 pairs received an oral dose of carbaryl or a control solution in a toxicity study; 14 nestlings from 8 nests died, including all young in 4 nests. Three of those four pairs produced no young from their other nests; the fourth produced one. We tested two hypotheses: that return rates of birds with manipulated nests were less than ones with unmanipulated nests; and that return rates of birds with a manipulation-caused nest failure were less than those with unmanipulated nests. The first was rejected for all years and the second for 1986, the only year when manipulations caused failures, for each sex separately and for both sexes combined (Fisher exact test, all $P > 0.23$). Although some of the tests had small samples ($n = 2$ to 4 birds) and, thus, little power, we found no evidence of manipulations affecting return rates. A third conceivable test—unmanipulated birds with failed nests versus ones with manipulation-caused failure—would duplicate the second test because all unmanipulated birds in 1986 had a failed nest.

The changing return rates caused changes in the number and proportion of experienced residents (those that had been residents at UDW in a previous year) in the population. Those changes in number of experienced residents closely paralleled changes in total abundance for both sexes, notably shown by the regression lines for 1978–1987 (Fig. 1). Those declines were significant (both $P < 0.01$, $r^2 = 0.75$ for females, 0.64 for males). For females, the effect on composition was especially conspicuous in 1983–1988. Experienced residents were only 24 to 37% of the residents compared with 48 to 57% before the decline (1975–1977) and 40 to 53% as abundance increased (1989–1990). Low proportions also occurred for males (35–47%), though later (1985–1989) and with an exception (65%, 1987). Experienced residents were greater than or equal to 53 to 75% of the males before and after the low point.

The number of fledglings produced on the site generally declined with the population decline and rose with the subsequent increase. After 78 fledglings in 1974, the number remained below 70 until 1989; extremes were 29 in 1986 and 108 in 1990. The decline during the 1978–1987 period was not significant ($P = 0.11$, $r^2 = 0.32$). As noted above, 4 nestlings in 1984 and 14 in 1986 died as a result of experiments. In 1985, another three nestlings died after their mother became entangled in a closed mist net

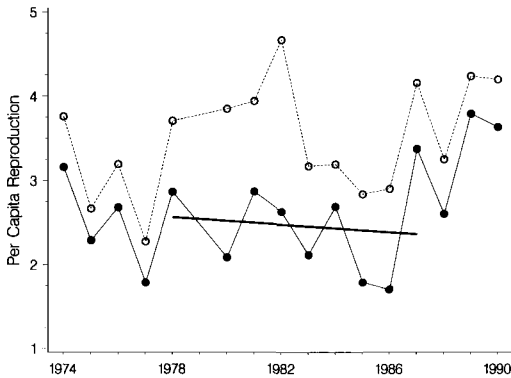


Fig. 3. Production of Wood Thrush fledglings per female (solid circles and lines) and per successful female (open circles, dashed line) at study site, 1974-1990. Straight line is least-squares regression for 1978-1987.

and died. Had these nestlings fledged, the slight tendency for fewer fledglings to be produced in years of low population would be weakened.

The number of fledglings produced per resident female varied annually but with no persistent decline overall (Fig. 3; for 1978-1987, $P = 0.78$, $r^2 = 0.01$). Successful fledging of the nestling fatalities noted above would have raised the annual values for 1984-1986 to 2.89, 1.95, and 2.53, respectively. The means (\pm SE) for 1974-1977 (2.49 ± 0.29) and 1978-1987 (2.45 ± 0.19) were equal. However, these means cloud a notable pattern: values dropped below 3.0 in 1975, not to exceed it again until 1987, two years before abundance increased. The overall mean number of fledglings per female was 2.62.

Fledglings per successful female (those fledging ≥ 1 young per year) should slightly exceed but closely track production per female normally. It did so in 1974-1977 and 1987-1990 (Fig. 3). In 1978-1986, the tracking generally held, but the gap between the two lines widened markedly. Two co-occurrences are notable. The increased production per successful female coincided with a period of increased failure rate (percent of residents fledging no young in a season; Fig. 4). Thus, fledglings per female held at about 2.5 because of increased production by the successful females. Second, a brief episode of moderate (19%) parasitism by Brown-headed Cowbirds occurred in 1976 and 1977 (Roth unpubl. data). A longer (1983-1987), more intense episode (35-65% parasitism) coincided with the drop in production by successful females. Notably, production rebounded in 1987

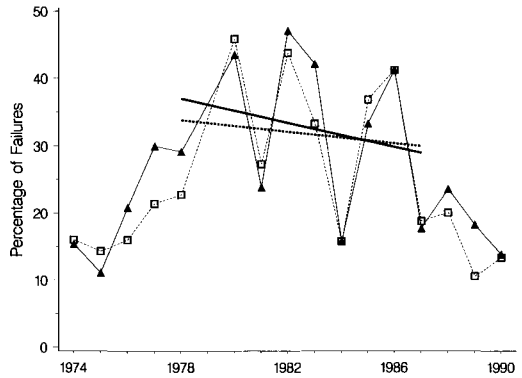


Fig. 4. Percent of resident males (triangles, solid line) and female Wood Thrushes failing to fledge young in a year at study site. Straight lines are least-squares regressions for 1978-1987 (see text).

despite 65% parasitism because failure rate dropped by one-half (Fig. 4).

Failure rate was low in 1974-1977 ($\bar{x} = 18.1 \pm 2.1$) and 1988-1990 ($\bar{x} = 16.6 \pm 2.0$), but was much higher in 1978-1987 ($\bar{x} = 32.2 \pm 2.6$). Failure rate actually began increasing in 1977 and returned to initial levels in 1987 (Fig. 4). Failure rate did not increase significantly during the 1978-1987 decline in abundance ($P > 0.55$, both sexes). Over the entire study, failure rate was significantly correlated with fledglings per female ($P = 0.007$, $r^2 = 0.412$, $n = 15$).

Few fledglings ("local young") returned to breed at UDW: 13 females and 21 males or 5% of all fledglings (Fig. 1). These include four females and one male that did not return to UDW until their second year after fledging. In eight years one or no young returned, and only in four years did more than two return. The most returning in one year was seven in 1977, four of them born in 1976 and three in 1975. Return rate of fledglings varied little during 1978-1987 ($P = 0.47$, $r^2 = 0.08$), nor before or after.

The number of new immigrants also showed no significant trends in 1978-1987 (females $P = 0.90$, $r^2 < 0.01$, males $P = 0.37$, $r^2 = 0.10$). Immigrant numbers varied annually within a range of 6 to 9 males and 10 to 13 females, with few exceptions (Fig. 1). The relative stability of immigrant numbers, especially females, kept total abundance from further decline in 1983-1988 when abundance of previous residents was lowest. Exceptional female immigration swelled the population's resurgence in 1990, and two of the exceptionally high years for male immigrants were in the 1989-1990 recovery.

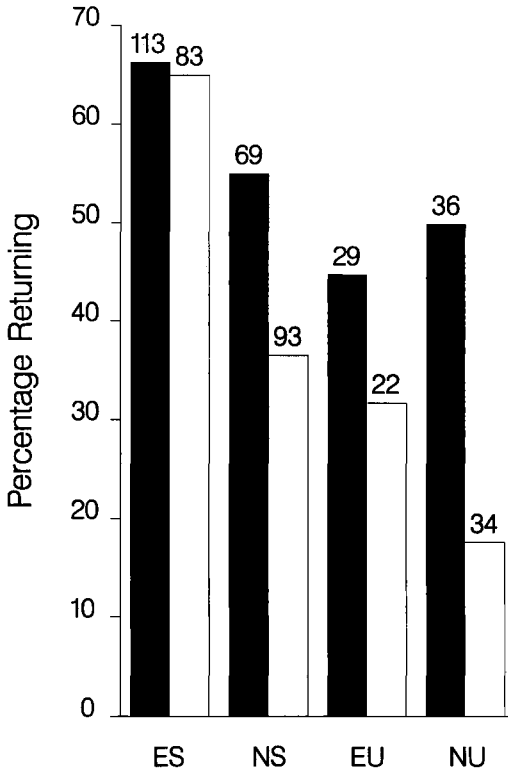


Fig. 5. Percent of times male (solid bars) and female (open bars) resident Wood Thrushes returned to study site in a subsequent year in relation to experience and breeding success. Experienced birds (E) = previous residents of UDW; novices (N) = first-time residents; successful breeders (S) = those that produced ≥ 1 young in the year; unsuccessful breeders (U) = those that produced no young. Sample sizes at tops of bars may include the same bird in different years.

We also looked for interactions between the dynamics already presented that could be relevant to the declining abundance and return rates. Because reproductive failure might induce emigration, we tested for a relationship between failure rate and return rate for residents. Female return rate declined significantly with increasing failure rate over all years ($P = 0.038$) though the r^2 was low (0.29). No trend was apparent for males ($P = 0.33$, $r^2 = 0.07$), and no trend occurred for either sex in 1978–1987.

The declining portion of experienced residents in the population (Fig. 1) increased the portion of residents that were novices to UDW. That change could have influenced return rates of residents (Fig. 2) because site fidelity can be related to age, gender, and success (Greenwood

TABLE 1. Results of chi-square tests for all comparisons of return rates of Wood Thrushes to study site in relation to gender, experience in UDW (E = previous resident, N = novice), and breeding success (S = successful, U = unsuccessful) as displayed in Figure 5.

Group	Comparison ^a	χ^2
Females	ES \geq EU	7.89
	ES \geq NS	14.25
	ES \geq NU	25.56
	EU = NS	0.23
	EU = NU	1.50
	NS > NU	4.13
Males	ES > EU	4.55
	ES = NS	2.32
	ES = NU	3.62
	EU = NS	0.64
	EU = NU	0.17
	NS = NU	0.24
ES	M = F	0.04
NS	M > F	5.50
EU	M = F	0.89
NU	M \geq F	8.12

^a All comparisons with $df = 1$. Symbols: > indicates $P < 0.05$; \geq indicates $P < 0.01$; = indicates $P > 0.05$.

and Harvey 1982). Over all years, experienced males ($n = 160$) returned at a 63% rate compared to 59% of 114 novices ($X^2 = 2.55$, $df = 1$, $P = 0.11$). Experienced females ($n = 115$) returned more often (59%) than novices (31% of 143; ($X^2 = 19.8$, $df = 1$, $P < 0.001$). Lack of experience and success, singularly and together, reduced return rate of both sexes but had a far greater effect on females (Fig. 5, Table 1). Novice status and failure had equally retarding, and additive, effects on female return rate (e.g. the rate for novice successful birds was intermediate between those of experienced successful and novice unsuccessful).

Another determinant of abundance can be production of young in the previous year. Total young produced by all pairs during the year should indicate the potential pool of local recruits for the next year. Because very few UDW natives recruited as residents (Fig. 1), the issue has little bearing on abundance at UDW. However, if UDW results reflected regional production levels, they might reflect also the pool of potential immigrants, a significant part of the resident population (Fig. 1).

Abundance of residents in year t was positively correlated with total young in year $t - 1$ (Table 2). However, that relationship is dominated by a strong correlation with number of returning residents—a component previously

TABLE 2. Values for correlation analysis between total fledglings from all Wood Thrush nests in study site in a previous year $t - 1$ and abundance of total residents, returning residents and new residents (local young plus immigrants) in the following year t .

Value	All residents			Returning residents			New residents		
	Total	Male	Female	Total	Male	Female	Total	Male	Female
r^2	0.554	0.511	0.571	0.544	0.413	0.579	0.156	0.044	0.133
P	0.002	0.003	0.001	0.002	0.010	0.001	0.145	0.452	0.182

discussed. Abundance also was strongly correlated between years. Because abundance affects production, the correlation between total young in year $t - 1$ and abundance in t is also, in part, an artifact of abundance itself. The more relevant relationship—between total young in $t - 1$ and number of new residents in t —was not significant (Table 2).

DISCUSSION

The dynamics of the Wood Thrush population at UDW did not neatly fit the predictions of the forest-fragmentation hypothesis. The hypothesis implies that fragmentation effects persist if fragments persist. Thus, the abrupt increase in abundance beginning in 1989, the increase in fledglings per female starting perhaps in 1987, and the abrupt decrease in failure rate in 1987–1990 would not be expected. High brood-parasitism rates, also predicted to occur in small woodlots, occurred only briefly, their timing and intensity unlikely to have affected productivity very much.

Contrary to prediction, immigration rates also did not decline despite a loss of forested habitat in the region. In fact, immigration of females increased sharply in 1990. Whitcomb et al. (1981) speculated that reduced immigration was the cause of declines in migrant populations at Cabin John Island, Maryland, with Wood Thrushes being one of the species involved. Our data show, however, that a population of Wood Thrushes can decline even when annual immigration rate remains unchanged.

The very low number of "local" young that became residents indicates that the UDW population depended on returning adults and immigration. That result fits the view of fragments as ecological sinks where productivity is insufficient to maintain a stable population (Pulliam 1988, Robinson 1992). However, we believe productivity was at least adequate for maintaining the population at UDW. Our reasoning is as follows. For a population to remain stable,

the product of production rate of female fledglings (P) and their survival rate (S) must equal adult female mortality (M ; Ricklefs 1973). We can use this relationship to calculate the juvenile survivorship rate needed to maintain the population, if we assume a 1:1 sex ratio at fledging and equal survival. During 1974–1976, when the population was fairly stable and failure rate had not begun increasing, return rate (a minimum estimate of survival) of adult females averaged 58%, so M was less than 42%. At this mortality rate, and the P in those years of 1.35 daughters (or 2.69 fledglings) per female, S would have had to be 31% to balance M and P . Estimates of first-year survivorship for several smaller tropical migrants are close to this: *Riparia riparia*, 35% (Saether 1989); *Hirundo rustica*, 28% (Saether 1989); *Delichon urbica*, 30% (Saether 1989); *Saxicola rubetra*, 34% (Saether 1989); *Ficedula hypoleuca*, 30% (Lack 1966:114); and *Dendroica discolor* 35% (Nolan 1978:470). Thus, 31% is a reasonable value. Juvenile survival rates of Wood Thrushes might be somewhat higher than in these species because adult mortality rates of these species are higher than adult mortality rates of Wood Thrushes, and among species, juvenile survival rates are positively correlated with body size (Saether 1989, Dobson 1990). Because normally high off-site dispersal makes return rate a poor estimate of juvenile survivorship, our best indication of adequate productivity is that our calculated S , using P and M values from when the population was stable, is of appropriate magnitude. This, of course, assumes that the published values were from stable populations. Further support comes from applying this equation to 1977–1986, when abundance and return rates declined and failure rate was high. In that period, M was 61% and P was 1.13, requiring an unrealistic S of 54%. That value is distorted by the inflated "mortality" rate of adults (i.e. return rate probably was low due to increased emigration, not necessarily mortality). Had M remained at the pre-decline level of 42%, productivity for 1977–

1986 would have been sufficient to require an S of only 37%. This is comparable to the pre-decline S and to the published values mentioned earlier.

Changes in abundance were determined primarily by changes in the return rates of adult females, another factor not directly predicted by the fragmentation hypothesis. Residents not returning to UDW either died during the breeding or nonbreeding season, or they emigrated. We found little evidence of breeding season mortality. We have direct evidence of only three residents dying at UDW from predators or unknown causes and one resident male dying off-site in midseason. The deaths were scattered throughout the study period.

We do not know to what extent factors operating outside the breeding season might have contributed to the decline of return rates. Habitat destruction in transient areas or increased hazards, such as towers, could have led to greater migratory mortality. Even so, we do not know why their effects would have lessened recently.

Survival on the wintering grounds also could have varied during our study. Wood Thrushes winter mainly in moist, primary forests and secondary woodlands of eastern Mexico and the Caribbean slope of Middle America (AOU 1983, Lynch 1989, Rappole et al. 1989, Blake and Loiselle 1992, Petit et al. 1992, Powell et al. 1992). Much of the primary forest in these areas has been cleared over the period (Sader and Joyce 1988, Estrada and Coates-Estrada 1988, Hartshorn 1992). Some authors have suggested this loss as a factor in the decline of some migrant species (e.g. Vogt 1970, Terborgh 1980, 1989, Rappole and Morton 1985, Robbins et al. 1989b, Petit et al. 1992, Powell et al. 1992). Some Wood Thrushes wintering in tropical Mexican forests are territorial and sedentary (Rappole and Warner 1980, Rappole et al. 1989, Winker et al. 1990), while many using secondary scrub habitats are not and may have lower survivorship (Rappole et al. 1989, Winker et al. 1990, Blake and Loiselle 1992). Clearing primary and older secondary forests could reduce overall survivorship. However, an explanation that invokes increasing mortality as the cause of lower return rates and abundance also must accommodate the reversal of those trends after 1987. Gradually increasing winter mortality may have been occurring, but our evidence points more strongly to emigration as the primary dynamic of the decline at UDW.

Declining habitat conditions may prompt increased emigration. Such changes in conditions have been negligible at UDW; wet, shaded areas, moderate understory vegetation, and tall trees, which are important features of Wood Thrush habitat (Bertin 1977, James et al. 1984, Roth 1987), have persisted. The high density, proportion of returning residents, and productivity in 1990 show that UDW has not undergone a permanent decline in attractiveness.

Poor success also may induce emigration (Greenwood and Harvey 1982, Bollinger and Gavin 1989, Slagsvold and Lifjeld 1990). The positive correlation between total fledglings in one year and abundance of returning residents in the next attests to that, as does the negative correlation between failure rate and return rate of females. The period of declining abundance and return rate coincided with the period of depressed production per female and of elevated failure rate. We suspect that such a sustained level of failure reflects unusually high predation pressure. We believe predation was involved because no other factor likely would cause so many failures in a multibrooded species. We saw no evidence of starvation or toxic death of broods and no unusual number of unhatched eggs, abandoned nests, or non-nesting residents. By its completeness, failure should have a greater impact on site fidelity than would partial loss of a season's effort. Failure affected both experienced and novice females. The low return rate of even successful novices shows that novice status alone carries a high probability of not returning to a site. Reduced productivity, probably caused by predation, is the one dynamic we found to be consistent with predictions of the fragmentation hypothesis. Its episodic nature, however, differs from the implied notion that those effects are unidirectional.

We offer the following explanation of the patterns we observed. A period of increased failure, presumably predator-induced, occurred from the late 1970s through the mid-1980s. This failure, perhaps aggravated by episodes of cowbird parasitism, probably increased emigration, especially among novice females. Thus, new immigrants, dominated presumably by young birds, failed to return and become "old faithfuls." That effect, coupled with normal mortality of older birds, and perhaps higher mortality over winter, reduced the number of returnees. Consequently, the population became younger

and more fickle in the face of reproductive failure, yielding a self-perpetuating decline in abundance. A steady flow of immigrants and local young kept the population from declining further. In 1987, the failure episode ended, production increased, and two years later, return rates and abundance increased.

Because abundance declined at UDW, in the Breeding Bird Survey data, and in other studies at similar rates, we suggest a model based on the dynamics we found to explain the broader decline of the Wood Thrush. If the failure episode was regional, emigration also would have increased for most fragments. If so, we should have seen increased immigration at UDW, but we did not, perhaps because the immigrant pool was reduced. This may be why new birds did not fill vacancies of nonreturnees. Reduction of the pool could have occurred in several ways. Fewer young were being produced to enter the pool, more so if mortality of breeders was increasing. Any mortality over winter or in migration also would reduce the pool of immigrants and of returning residents. The increased movement of emigrants, prompted by reproductive failure or birds displaced by habitat loss, might carry with it increased risk of mortality. Finally, emigrants might be moving long distances out of the region. The result would be a broad, regional decline in abundance until predation or parasitism subsided, success improved, and emigration slowed. This model accommodates the possibility of a regional episode of excessive predation or parasitism, increased emigration associated with such failure and the reversal of the pattern. It leaves room for the possibility of increased mortality in all parts of the annual cycle and likely would be most apparent in a highly fragmented landscape.

We lack solutions to two important puzzles. First, we have not determined the predator(s) that caused the high failure rate and whether the episode of failures corresponded with a period of greater predator abundance, which also ended. The same predators are cited repeatedly in the literature, but with virtually no data documenting their individual patterns of spatial or temporal abundance, nor their impact on real nests in forest fragments. Gray squirrels, Common Grackles, Blue Jays, black rat snakes and raccoons have been observed or implicated as predators of eggs and nestlings at UDW (Roth unpubl. data), but we too lack data on their abundance. Cowbirds clearly were not a critical

factor, although they apparently are in the Midwest (Brittingham and Temple 1983, Temple and Cary 1988, Robinson 1992).

The second puzzle is: if we invoke emigration without mortality to explain the lower return rates, where did the emigrants go? Our evidence suggests that it was not nearby. No birds from UDW were among the 91 adults netted during an intensive study (1980–1983) of a population in a residential area 1.6 km away, nor did any of the many nonreturners from there appear in UDW (Roth 1987, unpubl. data). Only two residents (both male) have been recovered off site, about 43 and 4 km from UDW (Roth unpubl. data). Checks of about 140 Wood Thrushes (mostly males) in other forest fragments within 10 km have never found a resident from UDW (Roth unpubl. data). These results also could be evidence of high off-site mortality.

The immigration and reproductive rates maintained at UDW throughout the study period demonstrate that a moderate-sized, suburban woodlot can be an attractive, successful breeding habitat for Wood Thrushes. A network of such woodlots, each providing immigrants for others, might be sufficient to maintain a metapopulation if return and reproductive rates equalled those at UDW in the early and late years of our study. Our data, however, suggest that Wood Thrushes are vulnerable to the predator pressures predicted by the fragmentation hypothesis, pressures that may wax and wane. We also caution that numerous factors, including size, quality, and frequency of fragments can affect the dynamics of a plot and that abundance on a single plot may not indicate the general pattern (Sherry and Holmes 1991, Villard et al. 1992). For example, abundance in refugia such as UDW may increase, remain stable longer, or decline less rapidly than general abundance in the face of continued deforestation as residents from altered sites move to protected areas. See Bierregaard and Lovejoy (1989) and Bierregaard (1990) for an Amazonian example.

We have reported the dynamics of a Neotropical migrant's decline in a suburban woodlot, a decline similar in timing and magnitude to a geographically broader one. Our results and general model may have wider application to the decline of Neotropical migrants, but one should be cautious when looking for generalizations. Three examples will illustrate.

Wood Thrushes are less area-sensitive, at least in occurrence, than most Neotropical migrants (Temple 1986, Robbins et al. 1989a). Thus, one should not conclude from our results that a 15-ha forest is sufficient breeding habitat for other species. Second, Wood Thrushes are vulnerable to cowbird parasitism, but the cowbird's impact varies spatially and temporally. We already have noted the very different rates between UDW and Robinson's (1992) Illinois forests. Locally, parasitism in a wooded residential area 1.2 km from UDW was 26 to 56% of nests receiving eggs in 1980–1982 versus 0 to 6% at UDW (Roth 1987, unpubl. data). Finally, studies of Black-throated Blue Warbler and American Redstart populations point, as does our investigation, to increased predation and lower nesting success for migrants in fragmented forests (Holmes et al. 1992, Sherry and Holmes 1992). In our study and theirs, productivity (though indexed differently) influenced abundance in the next year, but by different routes. In the New Hampshire studies, which only considered males, changes in abundance depended heavily on recruitment of second-year birds; in UDW, changes in abundance were more strongly influenced by the return rate of previous residents. Both can be affected by predation on nests though the latter, as a response to reproductive success or failure, has not been considered in other studies of Neotropical migrants. Until additional intensive, local, long-term studies of the kind reported here are conducted in other locations and on other species (on both the breeding and wintering grounds), it will be difficult to confirm the generality and magnitude of forest-fragmentation effects on bird populations.

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