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FOREST AREA AND HABITAT QUALITY FOR NESTING WOOD THRUSHES

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ABSTRACT.—For Neotropical migrants, rates of nest survival and brood parasitism are thought to decline with the area of the forest fragment in which the birds nest. Using the Wood Thrush (*Hylocichla mustelina*), we conducted the first test of the "area" hypothesis based on direct measures of annual production and related demographics of marked individuals. We predicted that productivity per female and per ha, proportion of females nesting successfully each year, and return rates of adults would decrease and that rates of nest predation and brood parasitism and the ratio of yearlings:older adults would increase with a decrease in area of forest. Intensive season-long banding, nest finding, and nest monitoring to determine the annual production of all residents yielded data for two annual (1991 and 1992) tests in which we compared mean results from 14 small fragments (≤2.1 ha) with those from a 15-ha site, the University of Delaware Woods (UDW). Fledglings per female and per ha, and percent of females fledging ≥2 young per year, were lower, and percent of nests lost to predation and percent of nests parasitized were higher, in small fragments than in the larger tract at UDW in both years. The ratio of yearlings:older adults was significantly higher in small fragments for males and tended to be so for females in 1991, but neither result occurred in 1992. Return rate for each sex was lower in small fragments in the only year tested. The 17.5 ha of small fragments collectively produced many fewer young per female and per ha than the 15-ha UDW. Three analyses indicated that the small fragments were population sinks, whereas UDW probably was a source of recruits. Although a few small fragments equaled the UDW in some measures of quality, our data support the area hypothesis in relation to quality of breeding habitat. *Received 30 September 1997, accepted 18 February 1998.*

MANY SPECIES OF NEOTROPICAL MIGRATORY BIRDS that have declined in abundance since the late 1970s breed in eastern deciduous forests (see Askins 1993). One hypothesis to explain these declines centers on reduced reproductive success of birds nesting in forest fragments. The hypothesized scenario is that the reduced area and increased amount of edge of fragments result in a greater abundance of small predators and of the parasitic Brown-headed Cowbird (*Molothrus ater*). Increased nest predation and brood parasitism, in turn, reduce the reproductive success of vulnerable species in the fragments to below-replacement levels. Consequently, widespread fragmentation could contribute to declines in these species (Askins 1993, 1995). Some research, however, has shown that conditions in the landscape around a fragment (e.g. forest cover, cowbird feeding areas) also may influence predation, parasitism, or pairing success (Villard et al. 1993, Van Horn et al. 1995, Robinson et al. 1995, Brawn and Robinson 1996, Gale et al. 1997). Thus, reproductive success of birds in equal-sized areas can differ among landscapes, and success can be higher in one area than in a larger one (see Van Horn et al. 1995). Nevertheless, within a landscape, fragment size is an important factor in avian nesting success and a consideration in land-use decisions related to bird conservation (Brawn and Robinson 1996).

In essence, the "area" hypothesis states that habitat quality for nesting Neotropical migrants declines with fragment area (here, "quality" implies reproductive success). Support for the area hypothesis has come from studies that estimated reproductive success in various ways: (1) rate of brood parasitism (e.g. Donovan et al. 1995); (2) disturbance rate on artificial nests (see Askins 1995); (3) rate of nest survival as estimated by the Mayfield (1975) method (e.g. Robinson 1992, Donovan et al. 1995, Hoover et al. 1995, Robinson et al. 1995,

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Brawn and Robinson 1996); (4) fledglings per nest and predation rate for first-brood nests (Møller 1991); and (5) indexes to nesting success that rely on interpreting behavior of adult birds (e.g. Porneluzi et al. 1993). These indirect methods, necessary in large-scale studies that have time and effort constraints, have been useful in shaping our understanding of fragmentation effects. Unfortunately, the methods generally yield data that are not easily translated to actual annual productivity at the individual, population, or habitat levels (see Donovan et al. 1995, Brawn and Robinson 1996). Such values are useful in understanding and modeling the dynamics of populations and in assessing whether forest fragments are population sources or sinks (Van Horne 1983, Pulliam 1988). Although time- and effort-intensive, season-long tracking of individuals and their nests can yield productivity data directly; such tracking also provides insight into the effects of partial losses of clutches and broods (from parasitism and predation) on productivity. We are not aware of any studies of area effects that have used values of actual productivity per unit area or per female, or that have measured the proportion of females that are successful in a single nesting season. Productivity per unit area, as a function of the number of nesters and their annual production, expresses the quality of a unit of habitat. The proportion of females that is successful reflects the breadth of success among individuals. How well indirect methods estimate actual productivity remains to be determined. Nevertheless, if the area hypothesis is correct, direct measures of productivity also should decline with area. Furthermore, rates of predation and parasitism on nests should vary inversely with area if they are the agents of the reduced reproductive success.

Poor habitat quality also should manifest itself in the age structure of the population and site fidelity of adults using the habitat. If larger areas are of better quality and are preferred over smaller sites, and if birds can recognize the difference during habitat selection, we should expect despotic or preemptive settling behavior (Fretwell 1972, Pulliam and Danielson 1991) by older, dominant birds over younger, subordinate birds in the larger sites. The result should be higher ratios of yearlings:older birds in smaller areas. Variation in age ratios among habitats has been reported (e.g. Pärt and Gustafsson 1989; Sherry and Holmes 1989, 1991; Holmes et al. 1996; Hunt 1996), and in one study the age ratio varied among sites of different sizes (Møller 1991). Because yearlings commonly have lower reproductive success (e.g. Sæther 1990, Johnson 1994, Black 1996), this predicted ratio could be a factor in the lower productivity of smaller fragments. Consequently, age ratios could be a potential index of habitat quality.

Site fidelity can vary directly with reproductive success and age, especially for females, which in general are less site-faithful than males (Greenwood and Harvey 1982, Payne and Payne 1993, Roth and Johnson 1993). Another consequence of reduced area, then, may be a lower return rate of adults because of poor reproductive success. If less site-faithful yearlings predominate in smaller areas, the effect of poor success on return rates should be even more pronounced. Roth and Johnson (1993) concluded that declining return rate, driven by increased rates of predation and annual failure, and uncompensated by increasing immigration, was the major dynamic in an 11-year decline of a local population of Wood Thrushes (*Hylocichla mustelina*). A lower return rate to a site also might result in a lower mean age of adults, further reducing the mean productivity of a site.

Using the above arguments, we developed nine predictions from the hypothesis that habitat quality for a forest-nesting Neotropical migrant declines with size of forest fragments. We tested these predictions with banded Wood Thrushes nesting in forest fragments in a human-modified landscape. The predictions were that populations in smaller areas, relative to larger ones, should: (1) produce fewer fledglings per female and (2) per hectare; (3) have a smaller portion of females fledging ≥2 young per year; (4) have a higher rate of nest predation and (5) of cowbird parasitism; (6) have a higher proportion of yearling males and (7) females; and (8) have a lower return rate of resident males and (9) resident females.

The design of our study also allowed us to test the prediction that the collective productivity from numerous small fragments will be less than that from a single fragment of area equal to the sum of the smaller ones. This prediction is a variation on the debate over the probability that a single, large refuge will sustain more species than will several small refuges of the same total area, the so-called "SLOSS" debate (Simberloff and Abele 1982, Wiens 1989).

METHODS

Species and general design.—The Wood Thrush is a Neotropical migrant that has declined notably during recent decades as measured by the Breeding Bird Survey and in local studies (Askins 1993, Roth et al. 1996). Nests of the species can be subject to high rates of predation and brood parasitism (Roth and Johnson 1993, Robinson et al. 1995, Brawn and Robinson 1996, Roth et al. 1996). Moreover, Wood Thrushes are area-sensitive in their occurrence, but they are less so than many forest-dwelling Neotropical migrants and may nest in wooded residential areas and in forest fragments as small as 0.3 ha (Temple 1986, Roth 1987, Robbins et al. 1989; but see Friesen et al. 1995). Their use of very small fragments facilitated our study design.

If habitat quality declines with fragment area, then poor conditions should be especially apparent in the smallest patches that a species occupies, all else being equal. Wood Thrushes nest in fragments small enough that demographic characteristics of the residents can be determined in several fragments simultaneously to yield replicated samples for a given size category. Means with variances from such samples can then be compared statistically with results from fragments of other sizes, an approach not heretofore used for direct measures of demographic characters.

Study areas.—Our study sites were 14 "small" fragments of 0.2 to 2.1 ha (total of 17.5 ha) and one "larger" fragment of 15 ha, the University of Delaware Woods (UDW). All fragments were surrounded largely by a matrix of cropland, mowed grass, meadow, open water, or paved roads and parking lots. Some forest cover (another fragment) lay near a few sites but never along more than one side and always separated from the site by canopy or understory breaks of ≥15 m. The area is a developing, semirural to residential/commercial landscape at the lower edge of the Piedmont-Coastal Plain transition. All sites lay within 11 km of one another at nine locations in and near Newark, Delaware, the 15-ha site being roughly in the center. Three small fragments and the UDW site occurred singly, and five locations had two or three small fragments. At two of these locations, two sites were separated by canopy and understory breaks of about 22 m. In all other cases, gaps between sites at the same location were 65 to 100 m wide.

None of the 15 sites was strictly independent, especially at the multisite locations, because predators, cowbirds, and thrushes could have moved among sites. Such movement by thrushes was probably uncommon. We saw thrushes cross between only two of the sites and only a few times. We detected only one shift to an adjacent site by a banded pair between nestings, even though turnover of residents was common (see Results). On a longer time frame, no banded birds from small fragments appeared in UDW in later years (Roth et al. 1996). We have no information about movements of predators or cowbirds.

UDW has been the site of a Wood Thrush demographic study since 1974 (Roth and Johnson 1993). *Quercus* spp., *Liquidambar styraciflua, Acer rubrum, Liriodendron tulipifera, Fagus americana,* and *Nyssa sylvatica* dominated the canopy. *Cornus florida, Viburnum dentatum, Carpinus caroliniana, Clethra alnifolia,* and *Lindera benzoin* were predominant in the healthy understory and shrub layer. Several small, ephemeral ponds and overflow from a small, intermittent stream and a nearby field occurred in wet periods, providing wet to moist soils over half of the site. See Gorman and Roth (1989) for more details.

The small fragments resembled parts of UDW in terms of vegetation composition and structure, moisture regime, and age. We chose the small fragments from January to March 1991 based on perceptual similarities to UDW and known Wood Thrush habitat therein, and sometimes on the presence of old nests. Details of each site are in Weinberg (1993).

Demographic data.—Our data came from an intensive banding and nesting study conducted on each site from May through August in 1991 and 1992 using methods previously used at UDW (Roth and Johnson 1993). We attempted to color band all adults and young and to find all nests in each fragment. Through nest monitoring, mist netting, and mapping, we determined the owners and productivity of the nests and the number of adults on a site. Typically, we checked nests from a distance once a day, and we determined the contents of nests that we could reach (≤9 m) with the aid of a ladder and mirror on an extendible pole every one to two days (sometimes every two to three days on the small fragments owing to time constraints). We determined status and the number of young in the higher nests from behavior of the adults and by counting heads. Frequent visits allowed us to count young at fledging time regardless of nest height. We did not try to census predators nor to assign losses to particular types of predators.

We measured productivity on a breeding-season basis, i.e. as fledglings per female per year, rather than per nest. Our fledglings-per-female values were the total number fledglings from all nests on a site divided by the number of females that nested at least once on the site during the year. Productivity per hectare for a plot was the total number of fledglings divided by the area of the site. Our criterion for a successful female in determining percent of females successful was that she fledged at least two young per year, which is twice the value used by Roth and Johnson (1993). We believe that this more rigorous criterion is more appropriate. Wood Thrushes typically attempt to rear two broods per year in Delaware, and fledging only one young per year is a mediocre performance based on 20 years of data from UDW, where the among-year mean was 2.6 young per female (range 1.7 to 3.6; Roth et al. 1996). Our criterion also is closer to the production level that might be required for demographic replacement or population stability. Roth and Johnson (1993) reported annual productivity of 2.7 young per female for a period of stable density. Our criterion also is twice the conservative, widely used value (i.e. at least one young fledged) for success of a single nest.

None of our productivity measures would be altered by extrapair paternity because none of them is male-based. No evidence of egg-dumping in Wood Thrushes, which could bias female-based measures, is known (Roth et al. 1996). When calculating percent of nests lost to predation, we considered only nests that we knew had contained eggs or young. For percent of nests parasitized by cowbirds, we used only nests for which we knew the number and type of eggs (i.e. thrush or cowbird) to reduce bias in our determination. For example, nests too high for checks of contents could have held cowbird eggs that did not hatch and so would be counted as unparasitized nests. Similarly, counting such nests as parasitized only because a cowbird nestling was visible would bias the rate upward (see Appendix for how many nests met our criterion vs. the total number of nests and nests with eggs on each site). We classified unbanded adults as yearlings (i.e. in first breeding season) or as older birds based on the shape of their rectrices (Weinberg and Roth 1994) or, in the case of banded birds, on their histories. Return rates were the percent of banded residents on a site in 1991 that returned to the site in 1992. We did not check for returns of 1992 residents in 1993.

Analysis.—We compared the mean of each value for the 14 small fragments with the value from UDW by a one-sample *t*-test within each year. In this design, a value for UDW is not viewed as a mean of 15-ha fragments; it has no variance. Instead, UDW is a standard with which "experimental" (reduced area) fragments are compared. Thus, we tested if values for the smaller areas differed in the predicted direction from that for the larger one. The number of small fragments that we compared with UDW in a particular test represents *n* comparisons to the standard (Zar 1996). UDW was the standard because no other similarly gathered data existed, and logistical limits precluded replication of sites that large. The sample size for small fragments (i.e. the number of sites with data) varied among the different tests and years depending on availability of data from a site. Each year was a separate test. All tests were one-tailed because we predicted the direction of difference. We followed Askins et al. (1990) in treating patterns with $P \leq 0.1$ as significant. Our approach differs from Møller (1991), who used nests as the sample unit to get a mean for a series of sites of similar size and pooled data from eight years. Gale et al. (1997) compared results for Worm-eating Warblers (*Helmitheros vermivorus*) from multiple small sites (21 to 56 ha) with one larger site, but they used pairs as the sample unit and pooled data from two years and from their small sites.

To test the prediction that a single larger site would be more productive than a collection of small sites of similar total area, we compared the number of fledglings produced on the 15-ha UDW with the total number fledged from the 17.5 ha scattered among the 14 small fragments. We compared only the total number of fledglings because the issue was the productivity of the two habitat configurations.

RESULTS

We saw or heard Wood Thrushes in every small fragment at least briefly in both years. In the 11 small fragments that held resident Wood Thrushes in 1991, we detected 30 males, 32 females, and 60 nests; at UDW we found 26 males, 26 females, and 58 nests. In 1992, we found 39 males, 38 females, and 62 nests on 13 occupied small fragments versus 27 males, 27 females, and 59 nests at UDW. Based on our frequent searches and the nest-monitoring, banding, and mapping data, we probably found all or nearly all nests.

The higher number of residents in small fragments versus UDW reflected a generally higher within-season transience of nesters on small fragments. More than half of the pairs on small fragments had only one known nest and left the site after that attempt, which usually was a failure. New birds arrived throughout the season. At only a few small fragments was the season's complement of birds present at one time. For example, only four and five pairs occurred simultaneously at one site used by seven and eight pairs in the two years. Turnover was much lower at UDW, where each year one pair nested once and disappeared. Only one male and one female in 1991, and one male in 1992, arrived in midseason; none of them nested to our knowledge. Although slightly more females used small fragments versus the UDW in a season (1.8 females per ha vs. 1.7 in 1991; 2.2 vs. 1.8 in 1992), the density of simultaneous residents was lower in the small fragments (1.0 vs.1.7 per ha in UDW 1991; 1.5 vs. 1.8 per ha in 1992). With one exception (sites SF8 and SF9; Appendix), results from sites at the same lo-

TABLE 1. Demographic and productivity features (values are means; see footnote) of Wood Thrushes at the University of Delaware Woods (UDW) and in small fragments (SF).

	1991			1992		
Variable	UDW (n)[a]	SF (SE, n)[a]	P[b]	UDW (n)	SF (SE, n)	P
Fledglings per female	3.62 (26)	1.91 (0.50,11)	***	3.70 (27)	1.09 (0.34, 13)	***
Fledglings per ha	6.30 (15)	3.29 (1.19, 14)	**	6.70 (15)	3.14 (1.05, 14)	***
% Females with ≥2 young per year	88.5 (26)	51.4 (0.12,11)	**	85.2 (27)	30.8 (0.9, 13)	***
% Predation	23.2 (56)	41.4 (9.9, 11)	*	28.6 (56)	65.3 (9.4, 11)	***
% Parasitism	0.0 (53)	34.5 (12.0, 11)	**	3.7 (53)	20.7 (7.8, 10)	*
% Yearling males	20.0 (25)	44.0 (11.4, 10)	*	55.6 (27)	51.7 (10.4, 12)	ns
% Yearling females	32.0 (25)	42.7 (11.8, 10)	ns	57.7 (26)	50.9 (12.6, 10)	ns
Male return rate (%)	46.1 (26)	24.1 (9.8, 9)	**	—	—	—
Female return rate (%)	38.5 (26)	17.1 (7.0, 8)	**	—	—	—

[a] For UDW, n equals the number of females, males, ha, or nests; for SF, n equals the number of sites with data. SE calculated only for small fragments.

[b] Probability that result in predicted direction is random. ns, $P > 0.10$; *, $P \leq 0.10$; **, $P \leq 0.05$; ***, $P \leq 0.01$.

cation differed considerably. See Appendix for these and other data for the individual study sites.

We banded two to five males and one to five females in 1991 on each of the various small fragments (27 males and 22 females in all) from which we could calculate return rates in 1992. At UDW, 25 male and 25 female residents carried bands during 1991. In our overall banding effort, which we used in identifying nest owners, we estimate that we banded at least 93% of the resident males and 74% of the females during the two years on the small fragments. At UDW, the values were 96% and 100%, respectively.

Of the 16 tests of the predictions over two years (Table 1), 14 outcomes were in the predicted directions: 10 at $P \leq 0.05$, 3 at $P \leq 0.10$, and 1 (percent female yearlings in 1991) not significant ($P = 0.39$). In the two cases where differences were opposite to prediction, age ratios in 1992, the reversals were by small margins. Notably strong and consistent across years were the results for measures directly related to reproductive success: fledglings per female and per ha, percent females with ≥2 young, and percent of nests experiencing parasitism or predation. Productivity in small fragments was 29 to 58% of that in UDW by the three ways we calculated it, but the percent of nests lost entirely to predation was 188 to 228% of that in UDW. Cowbird parasitism in the small fragments exceeded the negligible rates in UDW.

The percent of yearling males in small fragments greatly exceeded that in UDW in 1991, as predicted, but it was slightly lower than the UDW value in 1992, one of the three failed predictions. Female age ratio in both years accounted for the other two failures; it had the same pattern as for males, but the 1991 difference lacked statistical significance. The ratios for both UDW and the small fragments were higher in 1992 than in 1991, especially at UDW. Finally, and also as predicted, return rates of both males and females to small fragments were lower, by half, than those for UDW.

When we treated all small fragments as one sample to compare productivity in the collective small fragments with that in UDW, the small fragments were considerably less productive. In 1991, 32 females produced 58 young on the small fragments versus 26 females fledging 94 young at UDW. In 1992, 38 females produced 41 young on the small fragments versus 100 young from 27 females at UDW. Because UDW and the collective small fragments were single sample units in this analysis, no statistical comparisons were possible.

DISCUSSION

Our results support the hypothesis that habitat quality of forest fragments for nesting Neotropical migrants declines with area. On average, smaller fragments were of lower quality for Wood Thrushes than the larger UDW. Discussion of the general forest fragmentation scenario has emphasized higher levels of predation and parasitism as the principal causes of lower productivity in fragments. We found substantial support for this argument in both years.

Small fragment size had a multi-dimensional effect on productivity. The lower annual production of young per female in small fragments reflected the average effect on individual females. The low proportion (≤0.51) of females fledging ≥2 young per year on small fragments, our criterion for success, showed that the low average production per female was a result of many females fledging very few, if any, young rather than from uniformly low production by all females. Production per hectare expressed the quality of small fragments as units of breeding habitat. Small fragments produced half as many young per ha as did UDW, despite slightly more females having used the small fragments during a season and despite slightly more nests being built on small fragments. Thus, small fragments had poor production because of poor success of the birds, not because fewer birds nested there. All three aspects of productivity were negatively affected by the repeated total losses of nests to predation, failures followed by emigration, and failures following midseason arrival that usually were too late to permit renesting.

Higher predation pressure (partial and total losses of clutches and broods) in small fragments versus UDW was probably the major cause of the lower productivity in the small fragments in both years. We do not know if the higher predation on nests came from a higher abundance of predators or from vegetation conditions that increased the efficiency of predators. We noticed no exceptional differences between UDW and the small fragments in evidence of likely nest predators such as Blue Jays (*Cyanocitta cristata*) and raccoons (*Procyon lotor*). None of the small fragments nor the UDW had chipmunks (*Tamias striatus*) or red squirrels (*Tamiasciurus hudsonicus*). Common Grackles (*Quiscalus quiscula*) nested in one small fragment, but fledging rate of the thrushes there equaled those in UDW. Black rat snakes (*Elaphe obsoleta*) occasionally were seen on some of the small fragments but occurred very rarely at UDW.

The rate of cowbird parasitism was higher in small fragments than in UDW but still was typical for Wood Thrushes in the Mid-Atlantic and Northeast regions (Hoover and Brittingham 1993). The very low rates of parasitism at UDW were similar to typical historic rates for that site (Roth and Johnson 1993, Roth unpubl. data) and to the 2 to 10% reported from 100- to 1,300-ha forests in New York and Pennsylvania (Hahn and Hatfield 1995, Hoover et al. 1995). Cowbirds can have a notable influence on productivity if parasitism and predation are additive effects (Roth et al. 1996), but the high predation rates in the small fragments rendered parasitism largely irrelevant there. Wood Thrush productivity did not differ between parasitized and unparasitized nests in the small fragments during both years (*t*-test, $P = 0.32$; Weinberg and Roth unpubl. data).

Our study is the first to examine the area-productivity relationship using direct determination of annual production per female and per hectare. In Denmark, Møller (1991) found that the number of fledglings per first-brood nests of several species decreased with decreasing area of small (≤2.6 ha) woodlands. Gale et al. (1997) found no effect of fragment size on the ratio of successful (≥1 young fledged per year) to unsuccessful pairs of Worm-eating Warblers, perhaps because of favorable landscape effects. Most support for the area hypothesis has come from studies that indirectly estimated success of nests (i.e. ≥1 young fledged) or productivity. Our results suggest that the lower nest success in fragments reported by others (e.g. Robinson 1992, Donovan et al. 1995, Hoover et al. 1995) does translate to lower annual production.

Our other predictions addressed other responses that birds should make to lower-quality breeding habitats. The first of these predicted that more yearlings should occur in the small fragments because yearlings (males, at least) are likely to be relegated to suboptimal sites by older birds. This prediction held, especially for males, in 1991. Møller (1991) also found higher proportions of yearlings in smaller woodlands for four species. The fact that our results were reversed in 1992, however, prompts caution in the use of age ratios as indicators of habitat quality, at least in short-term studies. An anomaly at UDW contributed to the reversed result. The number of yearling females there doubled to 15 from 1991 to 1992, and yearling males tripled to 15, both very exceptional levels based on 1974 to 1995 data (Roth and Johnson 1993, Roth unpubl. data). Among the yearlings was a record of 12 (six of each sex) UDW-hatched birds, a value that rarely has exceeded two in the past (Roth and Johnson 1993, Roth unpubl. data). That the number and proportion of yearlings increased in both

UDW and the small fragments suggests a regional increase in yearlings or a decrease in older birds in 1992. Indeed, the number of previous residents at UDW dropped from 18 males and 13 females to 12 and 10, respectively, from 1991 to 1992, apparently creating openings for yearlings that normally would have been displaced elsewhere or have become floaters. Sherry and Holmes (1991) reported age ratios that varied temporally and spatially in American Redstarts (*Setophaga ruticilla*) and showed how such variation can affect research conclusions.

The basis of our final two predictions, that return rates for males and females would be lower in smaller areas, was that return rate should reflect habitat quality because site fidelity increases with reproductive success (e.g. Greenwood and Harvey 1982, Payne and Payne 1993, Roth and Johnson 1993). The prediction was supported. Return rates in small fragments were similar to the poor 19% estimate for a 65-ha Illinois site with very high predation and parasitism rates (Robinson 1992). Furthermore, the mean rate for the small fragments was less than (males) or equal to (females) the long-term average at UDW for the worst-case cohort there—females that fledged no young in their first year at UDW (Roth and Johnson 1993). The connection between success and return rate held within small fragments. Females that returned in 1992 averaged 4.5 ± SE of 0.65 (n = 4) fledglings per year in 1991 versus 1.7 ± 0.36 (n = 21) for non-returnees; in UDW, the difference was negligible: 3.8 ± 0.55 (n = 10) for returnees versus 3.7 ± 0.56 (n = 15) for non-returnees (Weinberg and Roth unpubl. data). The greater discrepancy in small fragments further suggests that they provided poorer habitat than UDW. Because age can influence reproductive success and return rate, one might expect the higher proportion of yearlings on small fragments to have caused the difference in return rates between UDW and small fragments. However, for a sample of banded females for which we had reproductive data, return rates (15 and 17%, respectively) and productivity (2.2 fledglings per female per year for both age classes) of 12 yearling and 13 older females on small fragments were equal in 1991; comparable values for yearlings and older birds at UDW were 38% versus 41% for return rates and 3.63 versus 3.82 fledglings per female per year (Weinberg and Roth unpubl. data). Thus, the poor quality of the small fragments affected birds of both age groups equally.

Our study offered an opportunity to compare overall production by thrushes in one larger patch of forest versus several smaller areas, an aspect that bears on whether a species persists at a site. Debate of this issue has focused on the variety of species supported within patches (Wiens 1989). Our test was apt because all of the small fragments were in sufficient proximity and similar enough in topography and vegetation to simulate a fragmented UDW. Treating the small fragments as one unit showed the "several smaller areas" approach to habitat protection to be a poor one. In two years, the collective 17.5 ha of small fragments produced 99 young from 70 female "residencies" (some females resident in both years) versus 194 young from 53 female residencies in the 15-ha UDW. Even on this small scale, one "large" site, itself a fragment, proved better in terms of productivity by Wood Thrushes.

The low productivity of the small fragments suggests that they were ecological sinks producing too few young to maintain a stable population (Van Horne 1983, Pulliam 1988, Pulliam and Danielson 1991), an expansion of Lidicker's (1975) original use of the sink concept. Put as a question in a broader context: were the small fragments together a net contributor of new breeders to the larger metapopulation? First, we used Roth and Johnson's (1993) method to answer this question.

For a population to be stable and self-sustaining, production of female fledglings per female (P) times their survival rate to the next breeding season (S) must equal M, the mortality rate of adult females (Ricklefs 1973). Roth and Johnson (1993) assumed a 1:1 juvenile sex ratio, i.e. that P was half the total production of fledglings, and that the mortality rate of females was 1 − return rate, a rough measure of mortality that also includes dispersal. (For a single site, but perhaps not for a metapopulation, the distinction between mortality and dispersal is a moot point; in either case, the birds are absent from the site.) For the UDW thrushes, S ranged from 31 to 37% (Roth and Johnson 1993), which is close to published estimates for several migrant passerines. Because their value of S seemed reasonable, and because they used values of M and P estimated during a period of numerical stability, Roth and Johnson (1993) concluded that productivity at UDW was adequate to maintain the population. For the same analysis here, we treated 1991 and 1992 as one period for a larger temporal scale. Using these values, we calculated S for UDW for the period, where $M = 1 - 0.39$ or 0.61, and $P = 1.85$ female young per adult female. Our estimate of S was 0.33, which is very close to the previous values for UDW. We conclude that productivity probably was adequate at UDW to match mortality in 1991 and 1992. In contrast, for all small fragments combined, $M = 0.80$ and $P = 0.70$; i.e. not enough young were fledged to compensate for non-returning females, even if all young survived over winter. For the population to be stable, S would have to be >1.0, an impossibility. Thus, small fragments appear to be sinks.

Pulliam (1988) used these same components to indicate source-sink status. Using the above notation, his Equation 5a would be $\lambda = (1 - M) + SP$, where λ = the finite rate of increase. A value of $\lambda < 1$ indicates a sink, and $\lambda > 1$ indicates a source. Using the values above, UDW in 1991 and 1992 was borderline, i.e. $\lambda = 1.00$. For the small fragments, even an unlikely juvenile survival of 1.00 would yield $\lambda = 0.90$. Using the lower, more realistic $S = 0.33$ from UDW, λ would be 0.59 for the small fragments. By both analyses, the small fragments were sinks by virtue of both low productivity and high female "mortality" (i.e. low return rate). The latter probably had a sizable emigration component, a response to low reproductive success. Whether from mortality or emigration, the low return rates nevertheless mean that most previous breeders were absent from the small fragments and had to be replaced by immigrants.

Another way to evaluate source-sink status is to determine if the number of fledglings that a site contributes is higher or lower than the number of immigrants it absorbs from the larger metapopulation. UDW produced 94 and 100 fledglings in 1991 and 1992, respectively, and took in only 16 and 21 immigrants (Roth unpubl. data). In contrast, the small fragments collectively produced 58 and 41 young in the two years, whereas in the only year with data (1992), immigrants numbered 55 (Weinberg unpubl. data). The small fragments produced barely enough young to match the large number of immigrants, leaving no margin for the inevitable mortality between fledging and adulthood. This analysis also shows that collectively, the small fragments were sinks and UDW was a source.

Our results show that very small fragments should not be viewed as suitable breeding habitat for Wood Thrushes or as substitutes for larger areas of intact forest. UDW may have held a source population, and in four year-site cases, small fragments outproduced UDW on a per-unit basis (see Appendix). However, these results do not imply a minimum fragment size for sustaining a viable population of Wood Thrushes. At best, they suggest that in some cases the negative effects of fragmentation may be offset by exceptional habitat or landscape conditions (Robbins et al.1989, Donovan et al. 1995, Robinson et al. 1995, Brawn and Robinson 1996, Gale et al. 1997). Furthermore, most of the small fragments (24 of 28 "small fragment-years") attracted nesting birds, but in 20 of them the number of fledglings per female was lower than at UDW (Appendix). These results confirm what others have noted (Dow 1969, Roth 1979, Van Horne 1983); viz. presence and/or abundance are poor indicators of habitat quality. Despite their generally poor quality, such small fragments merit retention. They provide alternative breeding habitat for individuals in regions where better habitat is occupied. Any production in them aids the persistence of the larger metapopulation (Howe et al. 1981, Pulliam 1988). The high proportion of yearlings, the high within-season transience, and the low return rates in the small fragments suggest that such sites are unlikely to be permanent "ecological traps" (sensu Gates and Gysel 1978) for the individuals using them. That is, most birds using them likely will seek better habitat. Thus, larger, higher-quality sites must also be available.

We note that our study included only one larger fragment and covered only two years. Other 15-ha forests may be more or less productive, and we do not know how UDW productivity compares with that of larger forests in the region. Productivity, annual success rate of females, return rate, and age composition have varied temporally in UDW, which calls for caution in interpreting short-term data (Roth and Johnson 1993). We do not know if the same was true in some or all of the small fragments.

A variety of factors (e.g. short-term changes in weather, abundance and type of predators, abundance of cowbirds, stochastic events during migration or on the wintering grounds) may alter local or regional demographics of a species (e.g. Wiens 1989; Sherry and Holmes 1991, 1992; Robinson 1992; Roth and Johnson 1993; Wiedenfeld and Wiedenfeld 1995; Brawn and Robinson 1996). Long-term, replicated studies of banded birds at multiple localities can offer clues as to how much population characteristics vary spatially and temporally. Such information is important in assessing the long-term significance to population viability of apparent changes in abundance and habitat quality.

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APPENDIX. Characteristics of Wood Thrushes resident in small fragments (SF) and at the University of Delaware Woods (UDW). Values for each small fragment were averaged for the tests of predictions against UDW values.

Site (ha)[a]	Male[b]	Females[b]	Nests with eggs (total nests[c])	No. fledged	Females with ≥2 fledglings[d]	No. nests depredated[e]	Parasitized nests / nests used in analysis[f]	Male returns[g]	Female returns[g]
1991									
SF1 (2.0)	2/3/0	1/2/2	9 (12)	5	1	6	2/7	2/5	0/3
SF2 (1.1)	2/1/0	0/1/2	4 (7)	3	1	2	0/4	0/3	0/1
SF3 (0.24)	0/0/0	0/0/0	—[h]	—	—	—	—	—	—
SF4 (0.77)	0/0/1	0/0/1	1 (1)	0	0	1	1/1	*[i]	*
SF5 (0.76)	1/2/0	0/3/0	3 (3)	2	1	2	0/3	0/3	0/3
SF6 (1.4)	0/2/0	0/2/0	3 (3)	8	2	0	2/3	0/2	1/2
SF7 (2.0)	0/0/0	0/0/0	—	—	—	—	—	—	—
SF8 (0.48)	0/1/0	1/0/0	1 (1)	0	0	0	1/1	*	*
SF9 (2.1)	1/0/1	1/1/0	3 (3)	4	1	1	1/3	0/1	*
SF10 (2.1)	1/4/0	3/2/2	9 (11)	5	2	6	0/6	3/5	1/5
SF11 (1.5)	3/0/0	3/0/0	7 (7)	13	3	2	0/7	2/3	1/3
SF12 (0.24)	0/0/0	0/0/0	—	—	—	—	—	—	—
SF13 (2.1)	1/1/0	1/1/0	4 (5)	7	2	1	2/4	1/2	0/2
SF14 (0.69)	1/2/0	1/2/0	6 (7)	11	3	1	0/6	0/3	1/3
UDW (15.0)	5/20/1	8/17/1	56 (58)	94	23	13	0/53	12/25	10/25
1992									
SF1	1/3/0	3/1/0	6 (8)	3	1	5	2/5	—	—
SF2	2/1/0	2/0/1	4 (6)	3	1	3	1/4	—	—
SF3	2/0/0	1/0/1	2 (2)	3	1	1	1/2	—	—
SF4	1/0/1	0/0/2	3 (3)	0	0	3	0/1	—	—
SF5	2/1/1	2/1/1	3 (5)	3	1	2	0/3	—	—
SF6	2/2/0	1/2/1	4 (5)	6	2	2	1/4	—	—
SF7	0/1/0	0/1/0	0 (1)	0	0	*	*	—	—
SF8	0/0/1	0/0/1	0 (1)	0	0	*	*	—	—
SF9	1/1/0	0/0/2	2 (6)	0	0	2	*	—	—
SF10	2/5/1	2/1/4	7 (9)	0	0	7	0/3	—	—
SF11	1/2/0	0/3/0	4 (5)	11	3	0	0/4	—	—
SF12	0/0/0	0/0/0	—	—	—	—	—	—	—
SF13	0/3/0	2/1/0	5 (7)	6	2	3	2/5	—	—
SF14	1/0/1	0/1/1	3 (4)	6	1	1	2/3	—	—
UDW	15/12/0	15/11/1	56 (59)	100	23	16	2/53	—	—

[a] SF and number identify 14 smaller fragments. The following groupings of small fragments occurred at the same location (see Methods): 1 and 3; 2 and 4; 5, 6 and 7; 8 and 9; 12 and 13 (see Weinberg 1993).

[b] Number of yearlings / older / undetermined age.

[c] Total nests includes all nests that reached complete lining stage but were abandoned or lost all eggs without content or predation being verified.

[d] Refers to number of young fledged on the site during a year; some females may have fledged young elsewhere. This value divided by number of females equals % females with ≥2 fledglings per year in Table 1.

[e] This value divided by nests with eggs equals % predation in Table 1.

[f] Ratio of these values equals % parasitism by Brown-headed Cowbirds in Table 1. Some nests with eggs could not be used in this analysis because of uncertainty regarding parasitism (see Methods).

[g] Number of birds resident and banded in 1991 that returned in 1992 over total residents banded in 1991. Ratio equals return rate in Table 1. Includes only birds counted as yearling or older in columns 2 and 3. No effort in 1993 to determine return rate of 1992 birds.

[h] No data because no Wood Thrushes were resident at site.

[i] Asterisk indicates where value could not be determined because of missing observations.