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FACTORS AFFECTING NESTING SUCCESS OF WOOD THRUSHES IN GREAT SMOKY MOUNTAINS NATIONAL PARK

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ABSTRACT.—Recent evidence suggests that the nesting success of forest-interior Neotropical migrants is lower in fragmented habitat. We examined the nesting success of Wood Thrushes (*Hylocichla mustelina*) in a large contiguous forest from 1993 to 1997. From a sample of 416 nests we tested for predictors of daily nest survival rates, including activity at the nest and vegetation parameters at the nest site. We tested whether disturbance during nest checks (as measured by the behavior of the adults) was related to subsequent nest predation. Females were more likely to vocalize when brooding chicks than when incubating eggs. However, we found no evidence that observer disturbance or Wood Thrush activity influenced daily nest survival rates. Wood Thrushes nested predominately in small hemlocks, generally surrounded by many other small hemlocks. However, survival rates of nests in hemlocks were not significantly different from those in other substrates. Overall, neither activity at the nest nor habitat in the vicinity of the nest was a good predictor of nesting success, and only one vegetation characteristic, a measure of concealment, was significantly correlated with successful nesting. Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) was extremely low (<2% of nests parasitized). However, nesting success was moderate (daily survival rate = 0.958) when compared with other published studies from more-fragmented landscapes. Our results suggest that daily nest survival rates do not increase monotonically from small to very large forest patches. *Received 31 August 1998, accepted 22 March 1999.*

GLOBAL DECLINES in Wood Thrush (*Hylocichla mustelina*) populations are evident from analyses of Breeding Bird Survey data (Robbins et al. 1989, Peterjohn et al. 1995). One possible cause of this decline is low nesting success in isolated forest remnants (Hoover et al. 1995, Robinson et al. 1995b). In a landmark study, Wilcove (1985) identified an inverse relationship between forest patch size and rates of predation on artificial nests. In that study, predation rates reported for Great Smoky Mountains National Park were the lowest recorded across a spectrum of sites that ranged from small fragments of suburban forest to large contiguous tracts of forest. Hoover et al. (1995) also found a positive relationship between forest patch size and Wood Thrush nesting success. Robinson et al. (1995b) concluded that the nesting success of Neotropical migrants (including the Wood Thrush) in forest fragments in the Midwest probably is insufficient to maintain the breeding populations in many fragments. Their findings suggest that populations of Neotropical migrants exhibit source-sink population structure (sensu Pulliam 1988) and that large contiguous tracts of forests, such as that within Great Smoky Mountains National Park, are important in sustaining regional populations.

Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) is another threat that could influence the sustainability of Wood Thrush populations. Populations of Brown-headed Cowbirds have increased markedly in this century (Terborgh 1989, Robinson et al. 1995a). Studies in forest patches in the Midwest have found that rates of parasitism are negatively correlated with the degree to which the surrounding landscape is forested (Donovan et al. 1995, Robinson et al. 1995b). Even within the largest remaining forest tracts in Illinois (1,500 to 3,000 ha), Trine (1998) found high rates of nest parasitism and a high incidence of multiple parasitism on Wood Thrush nests. In some cases, however, Wood Thrush nests in small, isolated forest patches experience consistently low rates of cowbird parasitism (Roth and Johnson 1993).

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In fact, in a Maryland woodlot, Link and Hahn (1996) considered the Wood Thrush to be the host species least likely to be parasitized by cowbirds.

Because of the large size of Great Smoky Mountains National Park (202,000 ha) and its location in the predominately forested landscape of the southern Appalachians, we expected to find high rates of survival and very low rates of brood parasitism for Wood Thrush nests. We also investigated additional factors that may influence nest survival. Specifically, we examined (1) whether Wood Thrush activity at the nest, both observer-induced and natural, increased the chance that a nest was discovered by a predator; and (2) whether the characteristics of the vegetation surrounding the nest were associated with nesting success.

Disturbance caused by investigators visiting nests may increase the chance that nests are discovered by predators (Martin and Roper 1988). We used the behavior of the adults during nest checks as an index of disturbance and examined the relationship between the amount of disturbance and predation. We also examined whether natural levels of activity at the nest affected nest survival. Skutch (1949) hypothesized that the activity of adults at a nest may make nests more obvious to predators. He proposed a positive relationship between nest predation rates and clutch size, a hypothesis that has been tested with several species. Larger clutches suffered higher rates of nest predation in studies of Great Tits (*Parus major*; Perrins 1965) and Black-billed Magpies (*Pica pica*; Redondo and Castro 1992). Studies of the Least Flycatcher (*Empidonax minimus*; Briskie and Sealy 1989) and Western Slaty Antshrike (*Thamnophilus atrinucha*; Roper and Goldstein 1997), however, failed to show this pattern. By comparing predation rates at natural and artificial nests, we tested the following hypotheses related to natural activity at the nest: (1) thrush nests fail more often than nearby artificial nests, (2) nests with chicks have lower survival rates than nests with eggs, and (3) nests with larger clutches are more likely to fail than nests with smaller clutches.

Vegetation characteristics at nests have been associated with nest predation in some studies (Martin 1988, 1996; Johnson 1997). Nest concealment may influence survival because highly concealed nests would be less likely to be discovered by predators. In a review of 36 studies from a number of bird taxa, Martin (1992) found 29 studies reporting an inverse relationship between nest concealment and rates of nest predation. Johnson (1997) found a significant linear relationship between an index of concealment and the number of Wood Thrush fledglings produced in Delaware, but this was only true in one year of a two-year study. We measured vegetation at nests and at adjacent sites to characterize Wood Thrush nest sites and to determine the extent to which features of the vegetation explained variations in nesting success in the park.

STUDY AREA AND METHODS

Study area.—Great Smoky Mountains National Park straddles the border of North Carolina and Tennessee at an elevational range of 300 to 2,020 m. Since its establishment as a national park in 1934, all logging has been prohibited and forest fires have been controlled, creating one of the largest contiguous tracts of forest in the eastern United States. We monitored 416 Wood Thrush nests on the Tennessee side of the park from 1993 to 1997. Sites ranged from an old-growth hardwood forest near the upper elevational limit of Wood Thrushes in the southern Appalachians (1,350 m), to a second-growth site on the park boundary (300 m) near the city of Gatlinburg.

Nest monitoring and nesting success.—We monitored nests every three days until they failed or the chicks fledged. Nest visits were brief (<1 min) to minimize disturbance, and when possible, we observed nests from a distance. Wood Thrush chicks normally fledge at about 12 days (Roth et al. 1996), but they will leave the nest as early as 10 days if disturbed. To prevent premature fledging, we did not visit nests if chicks were older than 10 days, and we considered chicks to have fledged if they survived at least 10 days after hatching.

We calculated daily nest survival based on Mayfield's (1975) method and calculated standard errors and performed z-tests following Johnson (1979). We tested for nest-tree preferences using a *G*-test to compare the ratio of nests in each of the two most frequently used tree species with the ratio of each species measured at non-nest sites. We also used logistic regression (SAS 1995, 1996) with a backward selection procedure and a 0.25 significance level criterion to test for the effects of multiple factors on nesting success (Table 1).

Activity at the nest.—In 1997, we recorded the behavior of adult thrushes during each nest check. The behaviors observed were assigned an activity score ranging from 0 to 3. An activity score of 0 was assigned when a female was observed on the nest and

TABLE 1. Variables used in logistic regression to evaluate nesting success in Wood Thrushes.

Variable	Description
DENS	Average of the four densiometer readings at nest
NUMTREES	Number of trees recorded in the wedge prism
NUMSHRB	Number of shrubs (<10 cm dbh) on four 12.5-m transects radiating from nest
NUMHEM	Number of hemlocks in the shrub layer
PERHEM	Percentage of shrubs that were hemlocks
YEAR	Year nest was monitored (entered as a categorical variable, 1994 to 1997)
HEM	Nest tree was (1) or was not (0) a hemlock
HEIGHT	Height of nest (m)
TREEHT	Height of the nest tree (m)
DISTTRNK	Distance of nest from trunk (m)
TREEDBH	Diameter at breast height of nest tree (cm)
CLUTCH	Size of clutch
DAY	Day from beginning of season on which nest was initiated

was not otherwise disturbed, or if the nest was unattended during a check and no thrushes were seen or heard in the vicinity. An activity score of 1 was recorded if the female (or occasionally the male perched by the nest) was flushed from the nest without making any audible vocalization. We recorded an activity score of 2 if the flushed bird emitted a call described as "bup bup" (Roth et al. 1996), which is considered to be the first-level agitation vocalization. If the thrush gave the second-level agitation call, described as "pit pit," the visit received a score of 3. We used a *G*-test of independence to test whether the activity score was related to the probability of nest predation following the visit.

To test whether natural activity at the nest increased the likelihood of predation, we placed a pair of artificial nests containing two Northern Bobwhite (*Colinus virginianus*) eggs near 65 active Wood Thrush nests in 1996 and 1997. One artificial nest was placed 25 m from the active nest in a randomly chosen direction. The other was placed 100 m from the active nest at an angle of 90° from the first artificial nest. Artificial nests were placed at the same height and in the same tree species as nearby active nests and were checked in the same manner as active nests.

We tested the hypothesis that activity near the nest increases the probability of nest predation and predicted that nest failure would be highest at active nests, next-highest at artificial nests 25 m away, and lowest at artificial nests 100 m away. Each set of three nests was monitored every three days to determine predation rates. We ended the experiment as soon as the first nest failed because if the Wood Thrush nest failed, the "activity" ceased.

We scored the results of each experiment by recording which nest(s) failed first. At the time one or more nests failed, the failed nest(s) received a score of 1 and the other nest(s) received a score of 0. Because we checked nests every three days, oftentimes more than one nest failed during the same interval between nest checks. We used a *G*-test of independence to test whether any of the three types of nests was more likely to fail first.

Vegetation characteristics.—We characterized the vegetation at 400 nests by recording the species of tree or shrub in which the nest was located, the heights of the nest and the nest tree, the diameter at breast height (dbh) of the nest tree, and the distance from the trunk to the nest. We recorded additional vegetation data at 355 of these nests. We counted the number and recorded the species of all trees in a wedge-prism point (basal-area factor 20; Husch et al. 1982) centered at the nest. We made four estimates of canopy cover using a spherical densiometer and counted the number of vertical woody stems less than 10 cm dbh and at least 1.5 m high (i.e. shrubs) within two transects (25 × 2 m) centered at the nest and oriented north-south and east-west. All vegetation sampling was conducted after nesting attempts had terminated.

We also measured vegetation at two "non-nest" plots 50 m from each of the above-mentioned 355 nests using the same methods as at the nests. Non-nest plots were located due east or west (chosen at random) and north or south (also chosen at random) from each nest.

RESULTS

Nesting success and daily survival.—Seven of the 416 Wood Thrush nests monitored contained one Brown-headed Cowbird egg. Five of these seven nests fledged a total of 14 Wood Thrushes and 4 cowbird chicks, suggesting that nest parasitism had only a negligible effect on Wood Thrush nesting success on our study area. Similarly, only nine nests were aban-

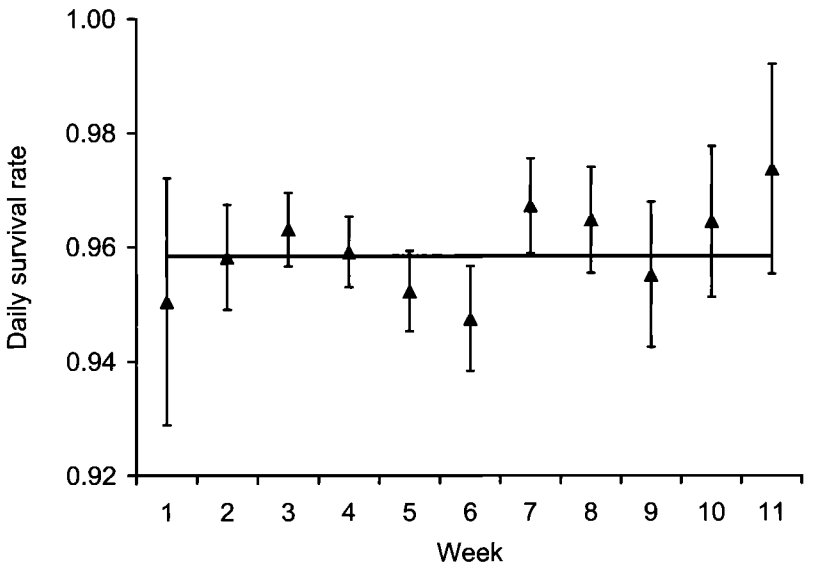

FIG. 1. Mayfield daily survival rates (± SE) for Wood Thrush nests throughout the nesting season (n = 416) pooled for 1993 to 1997. Horizontal line depicts the overall average.

doned with no evidence of predation (mostly during the egg-laying stage). In contrast, the majority of nests (225 nests) failed due to nest predation.

Of the 400 thrush nests where we recorded nesting substrate, 336 (84%) were in hemlocks (*Tsuga canadensis*) and 45 (11.3%) were in rhododendrons (*Rhododendron maximum*). No more than three nests were found in any other plant species (complete list in Farnsworth 1998). Slightly more than 84% of nests were in trees less than 10 cm dbh, so we used the proportion of shrub species recorded at non-nest sites as our measure of the availability of nesting substrates.

The overall Mayfield daily survival rate from 1993 to 1997 was 0.958 ± SE of 0.003. The total of 5,407 exposure days comprised 3,351 days for nests with eggs and 2,056 days for nests with chicks. Of the 225 nesting failures, 146 occurred during incubation and 79 during brood rearing. The resulting survival rates for nests with eggs (0.956 ± 0.004) and nests with chicks (0.962 ± 0.004) were not significantly different (z = 0.933, P = 0.35). When all nests from 1993 to 1997 were pooled, daily nest survival was fairly constant throughout the breeding season (Fig. 1). No two weeks were significantly different from each other (all $P > 0.05$). When all nests were combined for each year (Table 2), daily survival did not differ between years (all $P > 0.20$). Moreover, daily survival did not differ among sites (Table 2) at the three study sites where we had more than 50 nests (all $P > 0.15$).

Activity at the nest.—We checked nests, recorded activity scores, and returned three days later on 390 occasions during 1997. Activity was scored 0 on 185 occasions, 13% of which were followed by predation. Scores of 1 were followed by predation on 10% of 122 occasions, scores of 2 were followed by predation on 15% of 41 occasions, and scores of 3 were followed by predation on 10% of 42 occasions. Therefore, the probability of nest failure appeared to be independent of the activity of adult birds during our nest checks (G_{adj} = 1.23, df = 3, P = 0.75).

Of the 185 occasions when we scored nest disturbance 0, 74% occurred during incubation. Similarly, of the 122 occasions when we scored nest disturbance 1, 72% occurred during incubation. However, of the 41 occasions when we scored nest disturbance 2, only 54% occurred during incubation, and of the 42 occasions when we scored nest disturbance 3, only 52% occurred during incubation. Activity scores were significantly higher for nests with chicks than for nests with eggs (G_{adj} = 12.7, df = 3, $P < 0.01$).

Among the 65 sets of active and artificial

TABLE 2. Spatial and temporal variation in daily survival rates (±SE) of Wood Thrush nests.

Site/year	No. of active nests	No. of failed nests	Daily survival
		All years combined	
Albright	81	43	0.9608 ± 0.0059
Grassy	70	41	0.9564 ± 0.0067
Cosby	114	70	0.9499 ± 0.0058
Other sites	151	71	0.9641 ± 0.0042
		All sites combined	
1993	49	25	0.9614 ± 0.0076
1994	78	39	0.9605 ± 0.0062
1995	101	49	0.9622 ± 0.0053
1996	107	66	0.9529 ± 0.0057
1997	81	46	0.9571 ± 0.0062
Total	416	225	0.9584 ± 0.0027

nests, active nests were the first to fail 31 times, artificial nests 25 m from active nests were the first to fail 25 times, and artificial nests 100 m from active nests were the first to fail 22 times. These results are in line with our predictions, but the differences among treatments were no larger than what would be expected by chance alone (G_{adj} = 2.66, df = 2, P = 0.26). Therefore, we cannot reject the null hypothesis that the probability of nest failure is independent of activity at the nest.

Nest-site characteristics.—We observed significantly more shrubs at nest sites than at non-nest sites (two-tailed t-test, $P < 0.01$; Table 3). The composition of the shrub species also differed significantly between nests and non-nest sites. Hemlocks comprised more than 51% of the shrubs recorded near nests but only 33% of those at non-nest sites (t-test, $P < 0.01$).

Using the proportion of hemlocks in the shrub sample from non-nest sites as an estimate of hemlock availability, Wood Thrushes nested in small hemlocks more frequently than would be expected by chance (G_{adj} = 377, df = 1, $P < 0.001$). The next most common nesting substrate, rhododendron, was not used more frequently than expected (G_{adj} = 1.34, df = 1, P = 0.51). Nevertheless, we found no difference between daily survival rate of nests in hemlocks (185 failed nests in 4460.5 exposure days) and nests in all other species of shrubs (40 failures in 946.5 days; z = 0.11, P = 0.90).

We had sufficient data to include 284 nests in a logistic regression analysis. All variables listed in Table 1 were required for a nest to be included in the analysis. Of these nests, 116 fledged young and 168 failed. Six variables were included in the regression model, and only one, the densiometer reading, was significantly associated with nesting success (Table 4). Overall concordance (which measures how well the model predicted fledging success) was 65%, indicating that the variables used in the

TABLE 3. Comparison of vegetation measurements at Wood Thrush nests and non-nest locations. Values are $\bar{x}$ ± SD.

Vegetation measure	Nests (n = 355)	Non-nests (n = 722)	P
	Trees		
Number of trees	8.19 ± 2.82	8.16 ± 3.44	0.90
% Tulip poplar	38.6 ± 26.2	36.7 ± 28.9	0.30
% Hemlock	14.8 ± 16.4	13.7 ± 19.5	0.34
% Red maple	14.7 ± 16.8	14.6 ± 17.1	0.90
	Shrubs		
Number of shrubs	37.7 ± 20.8	28.0 ± 18.2	<0.01
% Hemlock	51.2 ± 29.2	33.4 ± 29.8	<0.01
% Rhododendron	9.0 ± 20.0	11.3 ± 23.1	0.11

TABLE 4. Results of logistic regression to evaluate nesting success in Wood Thrushes.

Variable	df	Parameter estimate	SE	χ^2	P
INTERCEPT	1	−1.94	1.12	2.97	0.08
DENS	1	−0.13	0.06	4.10	0.04
NUMSHRB	1	0.01	0.01	2.22	0.14
PERHEM	1	−0.73	0.44	2.77	0.10
YEAR	3	—	—	6.49	0.09
HEIGHT	1	0.18	0.12	2.19	0.14
CLUTCH	1	0.33	0.25	1.69	0.19

model provided only partial explanation for variation in nesting success.

DISCUSSION

Daily survival rates of Wood Thrush nests in our study area did not vary significantly among sites or years (Table 2), and they were similar over the course of the breeding season when data were pooled for all years (Fig. 1). The level of disturbance to adults caused by our nest checks was not associated with a higher probability of nesting failure. In similar studies, Martin and Roper (1988) and Mayer et al. (1997) also found no differences between survival rates of nests visited by observers and nests observed from a distance. We also found no evidence for an association between the activity of breeding adults at the nest and nest predation rate.

Our prediction that predation rates would be higher for active thrush nests than for nearby (25 to 100 m) artificial nests was not supported. This result differs considerably from that reported by Wilson et al. (1998). Using an experimental design that was similar to ours, Wilson et al. (1998) placed one artificial nest within 3 to 4 m of 58 active Wood Thrush nests in Pennsylvania and found that the artificial nests failed with greater frequency. This could happen if artificial nests were more visible (i.e. poorly concealed) than natural nests, or if adults actively protected or concealed their nests.

Interestingly, our disturbance scores during the nestling period were significantly higher than those during incubation, suggesting that parental investment accrued during later stages of the nesting cycle makes adult birds more prone to risky behavior in defense of their nests (Trivers 1972). However, we found no evidence that activity at the nest increased the probability of predation. Contrary to Skutch's hypothesis, daily survival rate did not differ between nests with eggs and nests with chicks, and we found no correlation between clutch size and probability of fledging. This suggests that Wood Thrush activity is not related to nest survival.

Hemlock was the most abundant potential nesting substrate, making up 33% of the shrubs within Wood Thrush territories. We found that Wood Thrushes used hemlocks as a nesting substrate more frequently (84%) than would be expected by chance. It is possible that we found more nests in small hemlocks because we developed a search image for nests in these locations. Although we attempted to locate all Wood Thrush nests in the areas we searched, we cannot be certain that such a bias was absent. However, 9 of the 10 nests that we found using radio telemetry (which presumably is free of such bias) also were placed in hemlocks (Farnsworth 1998). The apparent preference for hemlocks as a nest substrate suggests that Wood Thrushes employ a "needle in a haystack" nesting strategy. This hypothesis proposes that if predators preferentially search the plant species used for nesting, nests should be placed in the most abundant plant species in order to minimize the chance of discovery (Martin and Roper 1988, Filliater et al 1994). Hemlocks were more abundant surrounding Wood Thrush nests sites than at non-nest sites. Thus, birds appear to be placing their nests in local "haystacks" within the larger "haystack." However, the daily survival rate of Wood Thrush nests in hemlocks did not differ from that of nests in other substrates. Moreover, the relative abundance of hemlocks around nests was not correlated with nesting success (Table 4).

With the exception of the densiometer measure of canopy cover, no variables tested by logistic regression were strongly correlated with

nesting success. Densiometer values represent a measure of nest concealment because readings are made directly below the nest. This is a crude index of nest concealment because it is impossible to separate precisely which vegetation layers are most responsible for the overall densiometer reading. In most cases, however, lower values were associated with vegetation immediately above the nest. Despite many studies cited as evidence that nest concealment affects nest survival rates (see Martin 1992), few studies have taken an experimental approach. Howlett and Stutchbury (1996) manipulated the concealment of Hooded Warbler (*Wilsonia citrina*) nests and failed to show an effect of removing cover from around the nests.

The relatively low concordance (65%) of the logistic regression model indicates that habitat variables cannot explain all of the variability in nesting success of Wood Thrushes. Monitoring nests with remote cameras revealed that the relatively pristine habitats in Great Smoky Mountains National Park support an abundant and diverse predator assemblage that includes small rodents, squirrels, weasels, black bears (*Ursus americanus*), snakes, owls, and corvids (Farnsworth and Simons 2000). Our results support the conclusions of Filliater et al. (1994) that passerines have evolved under conditions of high nest predation, which provides strong selective pressure for the ability to renest quickly.

Nest survival rates reported for the Wood Thrushes from a variety of forested areas led us to expect that survival would be relatively high in Great Smoky Mountains National Park. Robinson et al. (1995b) found that nest survival rates for Neotropical migrants in general, and Wood Thrushes in particular, increased with the percentage of forest cover in the landscape. Similarly, Hoover et al. (1995) found that nesting success of Wood Thrushes in Pennsylvania increased as the size of forest fragments increased. Based on these trends, daily nest mortality rates in Great Smoky Mountains National Park, which is a large, contiguous forest patch within a mostly forested landscape, should have been 0.03 or lower (Robinson et al. 1995b: figure 4), and nesting success should have exceeded 70% (Hoover et al. 1995: table 1). However, our nest mortality rates were consistently near 0.04 (33% nesting success). This moderate level of nesting success, combined with current low levels of brood parasitism, probably allow the park to act as a population source for Wood Thrushes (Farnsworth 1998). However, the contribution of the park to sustaining Wood Thrush populations on larger spatial scales warrants further investigation.

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Literature Cited

Briskie, J. V., and S. G. Sealy. 1989. Determination of clutch size in the Least Flycatcher. Auk 106: 269–278.

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380–1395.

Farnsworth, G. L. 1998. Nesting success and seasonal fecundity of the Wood Thrush, *Hylocichla mustelina*, in Great Smoky Mountains National Park. Ph.D. dissertation, North Carolina State University, Raleigh.

Farnsworth, G. L., and T. R. Simons. 2000. Observations of Wood Thrush nest predators in a large contiguous forest. Wilson Bulletin 112: in press.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: Does choice of nest site matter? Condor 96:761–768.

Hoover, J. P, M. C. Brittingham, and L. J. Goodrich. 1995. Effects of forest patch size on nesting success of Wood Thrushes. Auk 112:146–155.

Howlett, J. S., and B. J. Stutchbury. 1996. Nest concealment and predation in Hooded Warblers: Experimental removal of nest cover. Auk 113: 1–9.

HUSCH, B., C. I. MILLER, AND T. W. BEERS. 1982. Forest mensuration. John Wiley and Sons, New York.

JOHNSON, D. H. 1979. Estimating nesting success: The Mayfield method and an alternative. Auk 96: 651–661.

JOHNSON, M. S. 1997. The effect of age on nest concealment and its complimentary effects on production of Wood Thrush. Wilson Bulletin 109: 68–73.

LINK, W. A., AND D. C. HAHN. 1996. Empirical Bayes estimation of proportions with application to cowbird parasitism rates. Ecology 77:2528–2537.

MARTIN, T. E. 1988. Habitat and area effects on forest bird assemblages: Is nest predation an influence? Ecology 69:74–84.

MARTIN, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455–473 *in* Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Eds). Smithsonian Institution Press, Washington, D.C.

MARTIN, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. Nature 380:338–340.

MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51–57.

MAYER, G. H., H. Q. P. CRICK, AND J. J. D. GREENWOOD. 1997. The effect of observers visiting the nests of passerines: An experimental study. Bird Study 44:53–65.

MAYFIELD, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

PERRINS, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. Journal of Animal Ecology 34:601–647.

PETERJOHN, B. G., J. R. SAUER, AND C. S. ROBBINS. 1995. Population trends from the North American Breeding Bird Survey and population trends of Neotropical migrant birds. Pages 3–39 *in* Ecology and management of Neotropical migratory birds (D. M. Finch and T. E. Martin, Eds). Oxford University Press, New York.

PULLIAM, H. R. 1988. Sources, sinks and population regulation. American Naturalist 132:652–661.

REDONDO, T., AND F. CASTRO. 1992. The increase in risk of predation with begging activity in broods of Magpies *Pica pica.* Ibis 134:180–187.

ROBBINS, C. S., J. R. SAUER, R. S. GREENBERG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences USA 86:7658–7662.

ROBINSON, S. K., S. I. ROTHSTEIN, M. C. BRITTINGHAM, L. J. PETIT, AND J. A. GRZYBOWSKI. 1995a. Ecology and behavior of cowbirds and their impact on host populations. Pages 428–460 *in* Ecology and management of Neotropical migratory birds (D. M. Finch and T. E. Martin, Eds). Oxford University Press, New York.

ROBINSON, S. K., F. R. THOMPSON, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995b. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

ROPER, J. R., AND R. R. GOLDSTEIN. 1997. A test of the Skutch hypothesis: Does activity at nests increase nest predation? Journal of Avian Biology 28:111–116.

ROTH, R. R., M. S. JOHNSON, AND T. J. UNDERWOOD. 1996. Wood Thrush (*Hylocichla mustelina*). *In* The birds of North America, no. 246 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

ROTH, R. R., AND R. K. JOHNSON. 1993. Long-term dynamics of a Wood Thrush population breeding in a forest fragment. Auk 110:37–48.

SAS INSTITUTE 1995. Logistic regression examples using the SAS system, version 6. SAS Institute, Inc., Cary, North Carolina.

SAS INSTITUTE 1996. SAS/STAT Software: Changes and enhancements through release 6. 11. SAS Institute, Inc., Cary, North Carolina.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

TERBORGH, J. W. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey.

TRINE, C. L. 1998. Wood Thrush population sinks and implications for the scale of regional conservation strategies. Conservation Biology 12: 576–585.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136–179 *in* Sexual selection and the descent of man (B. Campbell, Ed.). Aldine, Chicago.

WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

WILSON, G. R., M. C. BRITTINGHAM, AND L. J. GOODRICH. 1998. How well do artificial nests estimate success of real nests? Condor 100:357–364.

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