

NEST-SITE SELECTION AND NESTING SUCCESS OF WOOD THRUSHES

JEFFREY P. HOOVER^{1,2,3} AND MARGARET C. BRITTINGHAM¹

ABSTRACT.—We characterized nest sites and compared specific nest-site characteristics to nesting success for Wood Thrushes (*Hylocichla mustelina*) nesting in southeastern Pennsylvania in 1991. We determined if nests were placed in areas that differed from randomly selected points within a given tract of forest and compared specific nest-site characteristics for successful nests (those that produced at least one fledgling) and nests that failed because of predation. Wood Thrushes selected nest sites non-randomly within a tract of forest, and female Wood Thrushes built nests in areas that had a higher density of trees, higher canopy, higher density of shrubs, and higher average shrub height than randomly selected points. Specific nest-site characteristics had little effect on the ultimate success or failure of nests. The only specific nest-site characteristic included in a stepwise logistic regression model comparing successful and failed nesting attempts was the concealment of the nest from above and below. The average concealment of successful nests was greater than unsuccessful nests, but the model that included nest concealment did not give good fit to the data. Rather, a landscape-level feature, size of forest tract, had the greatest influence on the success and failure of nests for Wood Thrushes in this region. Received 10 Feb. 1997, accepted 20 April 1998.

The Wood Thrush (*Hylocichla mustelina*) is a neotropical migrant that has undergone significant population declines in recent decades (Sauer et al. 1996). Poor reproductive success, particularly as a result of high rates of nest predation, has been cited as one probable cause of the decline (Robinson 1992, Roth and Johnson 1993, Hoover et al. 1995). Identification of specific habitat features associated with nest sites and nesting success, and a calculation of the probability of success given certain characteristics are needed in order to develop long-term strategies for reversing declines in populations of Wood Thrushes and other neotropical migrants (Martin 1992). Also, information on nest-site selection may be applied to management of habitat for this and other species of neotropical migrants.

General characteristics of the forest habitat where Wood Thrushes are found during the breeding season have been described by other researchers (Bertin 1977, James et al. 1984, Roth 1987). In addition, other researchers have documented the influence of landscape features such as forest patch size and proximity to edge habitat on the probability of nest success (e.g., Robinson 1988, 1992; Hoover

et al. 1995). In this study, we looked at nest-site selection by Wood Thrushes in two different ways. We first determined whether or not Wood Thrushes, within the forest, used particular areas for nesting based on the structure of the vegetation. We then measured microhabitat characteristics of successful nests and nests that were lost to predators. Our specific objectives were to: (1) determine the characteristics of the vegetation that influenced the probability that a site would be used for nesting by a Wood Thrush, and (2) determine whether or not microhabitat characteristics at the nest site influenced the probability of nesting success.

METHODS

During the summer of 1991, data for this study were collected as part of a larger study of the nesting success of Wood Thrushes in a fragmented forest landscape in Berks County, Pennsylvania (see Hoover et al. 1995 for a general description of the study sites). Characteristics of the vegetation were measured on nine tracts of forest (study sites) ranging from 16.4 ha to more than 500 ha (Table 1). Nine randomly-selected points were established on each tract of forest by placing a 150 × 150 m scale grid over a map of each tract, assigning a number to each grid point, and using a random numbers table to select the points. Points were separated by a minimum of 150 m and, when possible, were located at least 60 m from the nearest forest edge.

We collected vegetation data from each study site during July. We measured characteristics of the vegetation within a 0.04 ha circle centered on each of the nine points by using a modification of the James and Shugart (1970) method. We recorded the number of

¹ School of Forest Resources, The Pennsylvania State Univ., University Park, PA 16802.

² Present address: Illinois Natural History Survey, 607 E. Peabody Drive, Champaign, IL 61820; E-mail: j-hoover@staff.uiuc.edu.

³ Corresponding author.

TABLE 1. Characteristics of the study sites in Berks County, Pennsylvania.

Study site	Forest area (ha)	Forest core area (ha) ^a	Distance to contiguous forest (km) ^b	Percentage forested area within a 2 km radius ^c
Owl's Head	>10,000 ^d	>10,000	0.0	96.5
River of Rocks	>10,000 ^d	>10,000	0.0	97.2
Spitzenberg	126.5	45.3	2.4	35.7
Gun Club	103.4	47.8	10.6	50.5
Snook	79.8	6.5	11.2	42.7
Kunkle	23.4	2.5	9.1	20.9
Kehl	19.4	0.04	3.3	27.4
Lilienthal	18.7	1.4	11.8	42.7
Dixon	16.4	2.3	7.0	22.9
Bauscher ^e	9.2	0.5	6.7	23.4

^a Area of forest that was >100 m from an edge (Temple 1986).

^b Nearest forest >10,000 ha.

^c Measured from the center of each study site.

^d Nest searching occurred primarily within a 40 ha plot.

^e Study site used only for analysis of nesting success related to nest-site characteristics.

trees (total number of trees greater than 5.1 cm dbh per 0.04 ha circle), basal area (total basal area per 0.04 ha circle), and canopy height (estimated average height of the trees within each 0.04 ha circle). We tallied the number of shrub stems along two arm-length perpendicular transects (approximately 2 m wide) that bisected the 0.04 ha circle, and recorded the mean height of the shrubs. We measured percent cover with an ocular tube in two height classes (ground cover between 0.0 and 0.5 m and canopy cover greater than 10 m) at 20 randomly-selected points within each 0.04 ha circle and calculated the mean percent cover for each height class.

Study grids (30 m × 30 m) were established on each study site. Territories of Wood Thrushes were spot-mapped in relation to the grid points and we found nearly all nests within these territories. We searched for Wood Thrush nests on 10 study sites between 1 May and 1 August, 1991. We included data collected from the additional study site (Bauscher) in the analysis of specific nest-site characteristics and nesting success but not in the nest-site selection analysis. We searched over the entire tract of forest on the smaller study sites (those less than 100 ha) and on a 40 ha portion of the larger study sites. After a nest was found, we recorded its status every four days until the nesting attempt either failed or young fledged from the nest. Nests were visited more frequently near the expected time of fledging to verify fledging. We used a pole with an attached mirror (Parker 1972) to monitor the contents of nests located up to 8 m from the ground. A nesting attempt was classified as successful if at least one Wood Thrush fledged (Harris et al. 1963).

The number of Wood Thrush nests found per study site ranged from 6–33. We randomly selected five Wood Thrush nests on each study site and measured the characteristics of the vegetation within a 0.04 ha circle centered at each nest, using the modified James

and Shugart (1970) method. If, on a given study site, we selected a nest that was located within 25 m of one of the nine randomly selected points, it was not used and another nest was selected in its place. We measured characteristics of the vegetation around the five nests on each study site in late July after all of the nests were no longer being used.

We also recorded seven nest-site characteristics for all Wood Thrush nests found. For each nest, specific nest-site characteristics were measured within two days of when the nest became inactive. We measured nest height, distance to forest edge [distance of the nest to the nearest external forest edge (with the exception of six nests on the Owl's Head site where the distances were measured to forest openings 0.4–0.8 ha)], dbh of supporting vegetation (diameter at breast height of the vegetation supporting the nest, averaged for vegetation with multiple stems), lateral distance of the nest from the main stem of the vegetation supporting the nest (measured from the center of the nest), and nest concealment indices (percentage of nest that was visible in a horizontal plane, a vertical plane, and combined horizontal and vertical planes).

We determined how well each nest was concealed by calculating an index of nest exposure both horizontally and vertically by using a modification of a white cover board (30 × 20 cm; Nudds 1977). On the cover board, we painted 10 yellow circles in two rows of 5. The circles were 5 cm in diameter, with centers spaced 6 cm apart. We placed the cover board directly on the north, south, east, west facing, top, and bottom sides of each nest. We recorded the number of circles completely visible from each direction at a lateral distance of 3 m from the cover board at the height of the nest, from 1 m above, and from ground level beneath the nest. Measurements were taken from ground-level beneath each nest to simulate concealment of nests from nest predators on the ground. Lateral and above-nest measurement distances were chosen to obtain a relative quantitative index of nest concealment

within close proximity to the nest. We defined the total number of circles completely visible from the four lateral directions as the horizontal exposure, and from above and below as the vertical exposure of the nest. We determined total exposure by summing values for horizontal and vertical exposure. We report all exposure measurements as percentage of circles visible (nest concealment is equal to percent exposure subtracted from 100).

In order to simultaneously evaluate the influence of multiple characteristics on the probability of a site being selected for nesting or on the probability of a nest being successful, we used stepwise logistic regression (SAS on a DOS computer; PROC LOGISTIC; SAS Institute Inc. 1990, 1995) with the nest-site variables (general vegetation or specific nest-site characteristics) included as independent variables and the possible responses (nest/no nest or success/failure) as the dependent variables. For the analysis of nest-site selection we used study site as a control variable to reduce the influence that differences in vegetation among study sites might have on the results. Similarly, we included size of forest tract as a control variable for the analysis of nesting success because we were aware of a significant positive correlation between forest area and nesting success (Hoover et al. 1995). In this way, we could determine whether or not any of the specific nest-site characteristics had a significant association with nesting success when controlling for forest area.

The best subset selection method (Hosmer and Lemeshow 1989) was used to find the best four models for all possible model sizes. These were then compared on the basis of the Hosmer-Lemeshow C ($H-L$) statistics, the Wald statistics for individual variables, the amount of change in the β coefficients between models (>20% considered important), and the size of the standard errors of the coefficients. Likelihood ratios were also compared between models with the same number of terms, and a χ^2 statistic using the likelihood ratios was used to compare models with different numbers of hierarchically arranged terms to select the best model for each analysis.

RESULTS

We found 127 Wood Thrush nests on 10 study sites in 1991. Most of the nests (>85%) were found during the nest building, egg laying, or early incubation (days one through three) stage of the nesting cycle. One nest lost during a storm was not used for the analysis of nest-site characteristics and nesting success. Of the 126 nests, 76 were successful (at least one Wood Thrush fledgling produced) and 50 failed because of predation. We attributed all nesting failures to predation, with the exception of the nest destroyed during a storm. Thirty-six nests were preyed upon during incubation, and 14 during the nestling phase. Based on the condition of the nests and

TABLE 2. Species of vegetation supporting 127 Wood Thrush nests found in Berks County, Pennsylvania, 1991.

Species	n	Percent of total
Spicebush (<i>Lindera benzoin</i>)	57	44.9
Witch hazel (<i>Hammamelis virginiana</i>)	21	16.5
Tartarian honeysuckle (<i>Lonicera tatarica</i>)	10	7.9
Black cherry (<i>Prunus serotina</i>)	8	6.3
Black tupelo (<i>Nyssa sylvatica</i>)	8	6.3
American beech (<i>Fagus grandifolia</i>)	3	2.4
Eastern hemlock (<i>Tsuga canadensis</i>)	3	2.4
Mapleleaf viburnum (<i>Viburnum acerifolium</i>)	3	2.4
Red maple (<i>Acer rubrum</i>)	3	2.4
Mountain laurel (<i>Kalmia latifolia</i>)	2	1.6
Rosebay rhododendron (<i>Rhododendron maximum</i>)	2	1.6
Sassafras (<i>Sassafras albidum</i>)	2	1.6
Sugar maple (<i>Acer saccharum</i>)	2	1.6
Multiflora rose (<i>Rosa multiflora</i>)	1	0.8
White ash (<i>Fraxinus americana</i>)	1	0.8
White mulberry (<i>Morus alba</i>)	1	0.8

their contents following predation events, approximately 80% of nest predation events were attributed to either avian, snake, or small mammalian nest predators, and the remaining 20% to large arboreal mammals.

Nests were built in 16 species of vegetation including 8 species of shrub and 8 species of tree (Table 2). Nearly 77% of all nests were built in shrubs with 70% built in spicebush (*Lindera benzoin*), witch hazel (*Hammamelis virginiana*), or tartarian honeysuckle (*Lonicera tatarica*; Table 2). Black cherry (*Prunus serotina*) and black tupelo (*Nyssa sylvatica*) were the species of tree most often used for nest sites. Several of the trees that were used for nesting were either saplings or small trees (less than 10 cm dbh). Mountain laurel (*Kal-*

TABLE 3. Mean values for seven nest-site selection and seven specific nest-site location variables for Wood Thrushes nesting on study sites in Berks County, Pennsylvania, 1991.

Variable ^a	Mean	SD	Range
Characteristics of nest-site selection (<i>n</i> = 45 nests)			
Number of trees per 0.4 ha	42.6	18.1	7-95
Basal area (m ²)	2.7	0.8	0.31-3.74
Canopy cover ^b (%)	93.5	10.1	25-100
Canopy height (m)	24.1	4.7	10-33
Number of shrub stems	79.5	53.7	3-234
Shrub height (m)	2.5	0.4	0.6-4.6
Ground cover ^b (%)	80.0	26.5	5-100
Characteristics of specific nest-site location (<i>n</i> = 126 nests)			
Nest height (m)	2.2	1.1	1.0-6.5
Distance to edge (m)	61.3	50.3	1-300
Dbh of supporting vegetation (cm)	4.8	6.8	0.8-55.9
Distance from nest to main stem (cm)	7.6	23.6	0.0-182.9
Horizontal exposure ^c (%)	13.8	13.8	0-65
Vertical exposure ^c (%)	17.5	14.6	0-70
Total exposure ^c (%)	15.0	12.0	0-60

^a See text for descriptions of variables.

^b Statistical analyses were conducted using number of sightings, but results are reported as percentage of sightings.

^c Statistical analyses were conducted using number of cover board circles completely visible, but results are reported as the percentage of circles visible.

mia latifolia), rosebay rhododendron (*Rhododendron maximum*), and eastern hemlock (*Tsuga canadensis*) were the only evergreens used by Wood Thrushes for nest sites. The means, standard deviations, and ranges of values for the nest site characteristics used for the nest site analysis and for the nesting success analysis are given in Table 3.

A four variable regression model best explained which sites were used for nesting when controlling for study site (Table 4). Wood Thrushes built nests in areas within the forest that had higher densities of trees, higher canopy heights, higher densities of shrub

stems, and higher average shrub heights than randomly-selected points (Table 4). There were no interaction terms that met the criterion for inclusion. The model gave good fit to the data (*H-L* statistic = 4.3, *df* = 8, *P* = 0.83). When testing for the fit of a model, a high *P*-value indicates that the expected values from the model are not different from the observed values, hence the model is a good fit. The odds ratios (Table 4) evaluate the strength or magnitude of the association of the variables to the outcome (nest or no nest). The conditional odds ratios (Table 4) represent the change in likelihood of a nest being present

TABLE 4. Results of stepwise logistic regression analysis of vegetational characteristics in the vicinity of 45 randomly chosen Wood Thrush nests and 81 randomly chosen non-nest points on study sites in Berks County, Pennsylvania, 1991.

Variable ^a	β	<i>P</i> ^b	Odds ratio	Conditional odds ratio	Units ^c
Intercept	-14.814	—	—	—	—
Site	-0.0643	—	—	—	—
Number of trees	0.0766	0.0001	1.080	1.467	5.0
Canopy height	0.3578	0.0001	1.430	2.045	2.0
Number of shrub stems	0.0168	0.0123	0.017	1.188	10.0
Average shrub height	1.1562	0.0007	3.178	1.783	0.5

^a See text for description of variables.

^b *P*-value for significance of Wald χ^2 .

^c Units for conditional odds ratio (e.g., within the range of values for average shrub height, with an increase of 0.5 m, the probability of a nest being present increases by 1.8 times).

TABLE 5. Results of stepwise logistic regression analysis comparing specific nest-site characteristics between 76 successful and 50 failed Wood Thrush nests on study sites in Berks County, Pennsylvania, 1991.

Variable ^a	β	P^b	Odds ratio	Units ^c
Intercept	0.3206	—	—	—
Forest area	0.0075	—	—	—
Vertical exposure ^d	-0.1852	0.011	0.831	5.0

^a See text for description of variables.

^b P -value for significance of Wald χ^2 .

^c Units for odds ratio (e.g., within the range of values for vertical exposure, with a 5% increase in exposure, the probability of nesting success decreased by 0.8 times).

^d Statistical analyses were conducted using number of cover board circles completely visible, but odds ratio units are reported as a percentage (one circle = 5%).

for every unit change of a variable within the range of values for that variable (Table 3). For example, within the range of average shrub heights (0.6–4.6 m), the probability of a nest being present in a particular area within the forest increases by 1.8 times with every 0.5 m increase in average shrub height (given that Wood Thrushes are present on the site).

All Wood Thrush nests were within 6.5 m of the ground and were built as close to a forest edge as 1 m and as far away as 300 m. Most forest edges were with adjacent agricultural fields (>90%), some with highways or residential areas, and a few with natural openings (0.4–0.8 ha) within the forest. Nests were usually built near the main stem of the shrub or tree supporting the nest, and the main stem of the shrub or tree usually had a relatively small dbh (Table 3). For all nests, mean concealment was 86% laterally and 82% from above and below (but note the large ranges of values in Table 3). When controlling for forest tract size, the only variable significant enough to enter the model was vertical exposure (amount the nest is exposed from above and below; Table 5). The average nest concealment (percent exposure subtracted from 100%) above and below nests was approximately 85% and 75% for successful and failed nests, respectively. The model, however, lacked good fit to the data ($H-L$ statistic = 16.5, $df = 8$, $P = 0.036$) and explained the variability in the nesting success poorly.

DISCUSSION

A variety of factors can potentially influence nest-site selection including availability

of song perches, floristic composition, moisture regimes, amounts and kinds of feeding substrata, amounts of food, structure of the plant community, and risks of nest predation (Bertin 1977, Holmes et al. 1979, James et al. 1984, Steele 1993, Martin 1993a). When considering factors related to characteristics of vegetation within the forest, Wood Thrushes selected areas that had taller trees and taller shrubs than randomly selected sites. Bertin (1977) suggested that Wood Thrushes prefer to establish breeding territories in areas within the forest where there are taller trees because taller trees provide better (higher) song perches for males and an increased amount of leaf litter as a substrate for foraging. If this is true, then nest-site selection by females would also show the same tendency because they are building nests within the territories of the males. Tall shrubs were frequently used as nest sites possibly because they provided larger branches and a more stable structure for nests than shorter shrubs, although we did not test for this.

Nest sites were selected in areas within the forest where the density of trees was greater than random sites and possibly in response to the amount of leaf litter created by the larger number of trees. In addition, areas within the forest with larger numbers of tree and shrub stems could be indicative of a favorable moisture regime that influences the use of an area by Wood Thrushes (Bertin 1977).

Other researchers have suggested that shrub-nesting birds should preferentially select nest sites with higher shrub densities to reduce the risk of predation (Joern and Jackson 1983, Martin 1993b). Wood Thrushes nested in areas that had a higher density of shrubs than expected based on availability. Shrub density did not differ among the seven smaller sites but was significantly greater than on the two largest study sites (Hoover 1992). Nesting success was highest on the two largest sites where shrubs were lowest in density, (Hoover et al. 1995). This result suggests that increased shrub density itself did not increase nesting success in these forests. Shrub cover was scattered throughout all of our sites, and the relationship between density of shrubs and risk of predation may be more important in more open habitats where shrubs form discrete patches.

Of the several specific nest-site characteristics that might influence nesting success (e.g., concealment, nest height, proximity to habitat edge; Martin 1993b, Filliater et al. 1994), only the vertical exposure of the nest (visibility of the nest from above and below) was deemed significant in our analysis. In 29 of 36 studies summarized by Martin (1992), predation rates were lower at nests with greater concealment. Nest concealment may be particularly important in areas where corvids are suspected of being the major nest predators because corvids use visual cues to locate nests (Morrow and Silvy 1982, Westmoreland and Best 1985, Angelstam 1986, Yahner and Scott 1988, Patnode and White 1992). Although we were usually unable to identify the specific nest predators responsible for nest predation events, Blue Jays (*Cyanocitta cristata*) and American Crows (*Corvus brachyrhynchos*) were present on all of our study sites and were most abundant on small sites where predation rates were highest (Hoover et al. 1995).

Angelstam (1986) found that visibility through the vegetation in the area around each nest was more important to nesting success than the visibility directly at the nest site. Bowman and Harris (1980) also found that increased levels of spatial heterogeneity around artificial ground nests increased predator search time and reduced the number of nests found by the nest predator. They concluded that spatial heterogeneity is more important than nest concealment. We did not measure spatial heterogeneity around the nest, but our method of measuring nest concealment did measure the visibility of the nest through the vegetation from a distance of 3 m laterally from four different directions. Also, by using a cover board, we eliminated the arbitrary estimation of nest concealment and obtained a quantitative value for nest concealment. We did not detect a difference in lateral concealment between successful and failed nests. It is possible that our measure of nest concealment was not at a spatial scale relevant to the particular nest predators in this region.

The lack of correlation between nest height and nest success may be due to the diverse predator community present in the study sites. The nest predator community consisted of a variety of birds, snakes, and small and large

arboreal mammals (Hoover et al. 1995). Because of the diversity of potential nest predators, the techniques used by the nest predators when searching for prey are also diverse and, as a group, they would not be expected to detect nests at any one height better than another (Filliater et al. 1994). If there were only a few species of potential nest predators, or one species that specialized on a particular layer of the vegetation while foraging, then specific nest placement would be favored to avoid the limited search area of those particular nest predators.

Selection of a nest site near the forest edge may increase the risk of nest failure because of elevated rates of nest predation associated with "edge effects" (e.g., Gates and Gysel 1978). However, other researchers have failed to detect differential nesting success with distance from the forest edge (Angelstam 1986, Small and Hunter 1988, Yahner and Scott 1988, Robinson 1990, Filliater et al. 1994; see Paton 1994 for a critique). Nest success increased with distance from an edge when combining all nests located on our study sites (Hoover et al. 1995), but we did not detect an edge effect when we controlled for forest tract size in the logistic regression analysis. On small sites, predation rates were high throughout the forest and nest success was low. On large sites, predation rates were low throughout and nest success was high (Hoover et al. 1995). However, because most nests on small sites were near edges and most nests on large sites were away from edges, it is difficult to clearly distinguish between area and edge effects.

Nest predation is a major cause of nest failure for passerines as a group (e.g., Lack 1954; Ricklefs 1969; Martin 1992, 1993a) and for Wood Thrush specifically (Robinson 1992, Roth and Johnson 1993, Hoover et al. 1995, Robinson et al. 1995, Trine et al., 1998). The pervasive nature of nest predation and the potential influence of nest-site location on predation risk suggest that there should be strong selective pressure favoring individuals that choose nest sites that minimize the risk of predation (Martin 1992, 1993b). For Wood Thrushes nesting in highly fragmented landscapes, nest-site selection at the landscape level may be more important than at the level of the micro-habitat surrounding the nest. We

found that nesting success of Wood Thrushes increased, and conversely, that nest predation decreased with increasing size of forest tracts (Hoover et al. 1995). Also, the abundance or activity level of potential nest predators decreased with increasing size of forest tracts (Hoover et al. 1995). It appears that nest predation was influenced more by features of the landscape (area of forest, percentage of forest within a certain area; Hoover et al. 1995) than by specific characteristics of a nest site.

A combination of lower abundances of nest predators and lower rates of nest predation on large tracts of forest should favor Wood Thrushes selecting large tracts for nesting. Site fidelity has been found to be related to nesting success (Greenwood and Harvey 1982); and Roth and Johnson (1993) and Trine (in press) have found return rates to be higher for reproductively successful Wood Thrushes than for those that are not successful. High rates of nest predation in small tracts of forest may provide a partial explanation for the Wood Thrush being classified as "area sensitive" (Robbins et al. 1989, Askins et al. 1990). If predation rates remain high in small tracts of forest, over time we would expect the absence or rarity of Wood Thrushes and perhaps other migrants to become more rather than less pronounced on small tracts of forest. However, we do not expect to see a shift in nest-site selection within a forest tract because predation pressure probably is not consistent by predator type or over time, and nest predation could be nearly random.

Wood Thrushes appear to select certain structural components of the vegetation in the forest when establishing a breeding territory and follow some general behavioral "rules" (e.g., Best 1978, Morton et al. 1993, Filliater et al. 1994) when selecting a specific nest site within a breeding territory. For Wood Thrushes, simple behavioral rules for placing nests were to: (1) provide some concealment for the nest, (2) build the nest against or near the main stem of the vegetation supporting the nest, and (3) build the nest in tall (>2 m) shrubs if they are available. These rules apply to the nests that were built in our study area but may change in forests with different vegetation structure and species composition or in forests with markedly different nest predator communities. In regions where the nest pred-

ator community is diverse and habitat for nesting is not rare, it is probable that specific nest-site selection to avoid nest predation will not be favored and will not be apparent in studies of nest sites and nest predation. However, nesting in small tracts of forest, where both the abundance of potential nest predators and the rate of nest predation are high, should be selected against. This would result in nest-site selection to avoid predation being apparent at the level of the selection of a tract of forest rather than at the level of selection of specific nest-site characteristics within a tract of forest. As has been concluded previously (Hoover et al. 1995), the long-term health of Wood Thrush populations will depend on the maintenance of large tracts of forest.

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