NESTING ECOLOGY OF WOOD THRUSH (TURDIDAE: PASSERIFORMES) IN HARDWOOD FORESTS OF SOUTH CAROLINA

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ARSTRACT We studied nesting success of the Wood Thrush (*Hylocichla mustelina*) in bottomland and upland hardwood forests in South Carolina. Twenty-one of 26 nests (80.8%) were located in bottomland sites, and 76.2% of these nests were in narrow (<150-m wide) bottomland corridors. No nests were found in upland sites enclosed by fields. The Mayfield success rate for 20 nests was 35.3%. All nest failures were attributed to predation; no nests were parasitized by Brown-headed Cowbirds (*Molothrus ater*). Nest sites were characterized by a dense overstory and a moderately developed understory. Bottomland hardwoods, especially relatively narrow corridors, appear to provide suitable nesting habitat for Wood Thrush in this region. Brood parasitism by Brown-headed Cowbirds does not appear to be a significant factor in the failure of Wood Thrush nests in these sites.

INTRODUCTION

Fragmentation of breeding habitats is considered a factor contributing lo the apparent decline in Wood Thrush abundance (Robbins 1979, Robinson 1992). Forest fragments can be ecological traps for this specks (Robinson 1992) since they attract high densities of nest predators and Brown-headed Cowbirds, a brood-parasite (Brittingham and Temple 1983). Most nesting studies of Wood Thrush have been conducted in hardwood forest fragments isolated by agriculture or suburbia (Donovan et al. 1995). Results from these studies may not be applicable to the southeastern United States, where hardwood forest fragments often exist in association with extensive pine forests.

We monitored nesting success of Wood Thrush in various-sized bottomland hardwood forests bordered by mature pine forest, and in small upland hardwood forests enclosed either by mature pine forest or by agricultural fields. We tested the hypothesis that nest predation and brood parasitism would be the principal factors limiting nesting success. Additionally, we assessed nest-site selection by quantifying nest-site vegetation.

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SITE DESCRIPTION

Study sites were on and adjacent (i.e., ≤ 33 km) to the U.S. Department of Energy's Savannah River Site (SRS), a 78,000-ha tract in Aiken, Barnwell, and Allendale Counties in the Upper Coastal Plain of South Carolina. The landscape of the SRS is predominantly forested, consisting of a mixture of planted pine, upland hardwood fragments, and bottomland hardwood forest. The surrounding privately-owned landscape is primarily large agricultural fields with scattered, small upland hardwood fragments. Bottomland sites ($n = 15$) on the SRS were corridors ranging from < SO m to > 1,000 m in width (i.e., area of these study sites ranged from approximately 2-50 ha), and were bordered by mature pine forest (*Pinus taeda* and *P. palustris*). Overstory species included water oak (*Quercus nigra*), laurel oak (Q. *laurifolia*), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), and swamp tupelo (*Nyssa sylvatica* var. *biflora*). The midstory included American holly (*Ilex opaca*), red bay (*Persea borbonia*), and ironwood (*Carpinus caroliniana*), with the understory consisting of switchcane (*Arundinaria gigantea*), dog-hobble (*Leucothoe axillaris*), and Christmas fern (*Polystichum acrostichoides*). Upland hardwood sites ($n = 18$) ranged from 0.5-40 ha, although the mean size was < 5.0 ha (i.e., only 2 sites were > 6 ha), and were characterized by various oaks, hickories (*Carya spp.*) and black cherry (*Prunus serotina*). Mid- and understory species included flowering dogwood (*Cornus florida*), American holly, *Rubus* spp. and *Vaccinium* spp. Upland sites on the SRS ($n = 10$) were surrounded by pine forest. Upland sites adjacent to the SRS ($n = 8$) were enclosed by agricultural fields.

METHODS

We thoroughly searched each site for nests every l-2 weeks during May-July 1993-94. Site search frequency was limited primarily because of the large amount of acreage that required searching, particularly in the bottomland sites. Nest search efforts typically involved spacing field technicians along the edge of a site, then walking compass transects through the site. Technicians were instructed to maintain visual contact with technicians on either side of them, thereby ensuring complete search coverage of each site. We monitored the status of each nest at 3–4-day intervals (Martin and Geupel 1993) and assessed the outcome of each nesting attempt according to Best and Stauffer (1980). We calculated daily survival rates of nests, and Mayficld nest success (Mayfield 1975), and tested for differences in nest survival rates between incubation and nestling intervals with Fisher's exact test.

To assess nest-site characteristics, we measured vegetative parameters at 10 nests located in bottomland sites in 1994, along with their associated nest patches. We recorded nest substrate species, nest height, height and dbh of nest substrate, nest distance from the main stem, nest

distance from the plant edge, nest distance from the habitat edge, and number and diameter of supporting branches (Ralph et al. 1993). We defined the nest patch as a 5-m-radius circle centered on the nest site (Martin and Roper 1988). Within the nest patch we recorded basal area of plants ≥ 3-cm dbh and the number of plants of the same species and dbh (± 3.0 cm) as the nest substrate (Martin and Roper 1988). At the four cardinal directions along the perimeter of the nest patch, we estimated canopy cover with a spherical densiometer and vegetation profile with a 3-m density board subdivided into 0.5-m intervals.

RESULTS

We located 26 nests, of which 21 (80.8%) were found in bottomland sites. Sixteen (76.2%) nests found in bottomlands were in stands < 150-m wide. We found no active nests in upland sites enclosed by agricultural habitats. In contrast, five nests were located in four of the 10 upland sites enclosed by pine forest. Three of these sites were ≤ 100 m from forested wetlands.

Sample sizes varied among nesting parameters because some nests could not be monitored, and because some nests were found after the eggs had hatched. Mean clutch size was 3.1 (range = 2-4; SE = 0.21; $n = 14$), and hatching success for 29 eggs was 96.6%. Mean hatch and fledge dates were 8 June (range = 10 May-l I July) and 18 June (range = 22 May-19 July), respectively. The mean number of young fledged per successful

Table 1. Microhabitat variables at 10 Wood Thrush nest sites and 10 5-m radius nest patches within bottomland hardwood forests, South Carolina, 1994.

Variable	Mean	SE
Nest		
Height (m)	2.3	0.3
Distance to main stem (cm)	14.6	13.5
Distance to substrate edge (cm)	69.8	11.9
Distance to habitat edge (m)	41.9	12.3
Number of supporting branches	3.4	0.5
Diameter of supporting branches (cm)	0.7	0.1
Nest Substrate		
height (m)	4.9	1.2
dbh (cm)	4.8	1.0
Basal area (m^2)[1]	2.6	0.6
Vegetation profile[2]		
0.0–0.5 m	1.9	0.3
0.5–1.0 m	1.8	0.3
1.0–1.5 m	1.7	0.3
1.5–2.0 m	1.8	0.3
2.0–2.5 m	1.7	0.4
2.5–3.0 m	1.9	0.3
Nest height[3]	1.9	0.4
Canopy cover (%)	98.0	0.5
Same substrate[4]	1.4	0.5

[1] All woody stems ≥ 3 cm dbh.
[2] Index of percent foliar coverage: 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100%.
[3] Vegetation profile at nest height for eight nests.
[4] Number of plants that were the same species and dbh (± 3.0 cm) as the nest substrate.

Wood Thrush nest attempt was 2.9 (SE = 0.2; n = 10). Nest survival did not differ (P = 0.22) between the incubation and nestling intervals, and data were pooled for the entire nest cycle. Mayfield success rate for 20 nests was 35.3% (247 exposure days), and the daily survival rate was 0.960 (SE = 0.013). All nest failures were attributed to predation. No nests were parasitized by Brown-headed Cowbirds. Most (n = 7) depredated nests were found empty and intact. In three cases nests were either dislodged from the substrate or contained large egg fragments.

Wood Thrushes nested in a diversity of plant species in our study sites. Mean nest height was 2.3 m, and nests usually were located in a fork near the main stem, or were mounted on horizontal branches or the main stem of bent-over trees. Nesting substrates in bottomland forests generally were midstory trees and saplings, particularly red bay (28%), sweetgum (17%), American holly (11%), and red maple (11%), and were located ≤ 75 m ($\overline{X}$ = 41.9 m) from habitat edges (Table 1). Mean basal area of woody stems ≥ 3.0 cm in the nest patches was 2.6 m^2. Nest patches were characterized by a dense overstory and moderately-developed understory.

DISCUSSION

Both seasonal and daily Mayfield nest success in this study (0.353 and 0.960, respectively) were within the ranges of those reported in other studies of the Wood Thrush in forested landscapes. For example, Roth et al. (1996) reviewed several Wood Thrush studies and found that nest success in forested landscapes ranged from 0.30–0.50. Reported daily nest survival rates from forested landscapes include 0.948 in Georgia (Powell et al. 1999) and 0.982 in Wisconsin and Minnesota (Donovan et al. 1995). However, these data do not provide a sufficient gauge for annual fecundity because Wood Thrush produce two broods per season (Pease and Grzybowski 1995; Roth et al. 1996).

Nest parasitism apparently does not limit Wood Thrush nesting success in this region; we observed no nests parasitized by cowbirds. In contrast, Wood Thrush nests commonly are parasitized by cowbirds in other regions, and in some cases 100% of nests may be parasitized (Robinson 1992). Post and Gauthreaux (1989) noted that cowbirds are uncommon in the upper Coastal Plain of South Carolina. Common hosts for cowbird parasitism in that region include Prairie Warbler (*Dendroica discolor*), Hooded Warbler (*Wilsonia citrina*), Yellow-breasted Chat (*Icteria virens*), and Indigo Bunting (*Passerina cyanea*), but not Wood Thrush (Sargent et al. 1997, J.C. Kilgo, unpubl. data). Similarly, Powell et al. (1999) reported very low parasitism rates (< 0.5%) for Wood Thrush nests in the Piedmont of Georgia.

Wood Thrush nesting habitat appears to be correlated with tree diversity and the availability of saplings (Bent 1949). Our measurements of these vegetative parameters suggest that suitable nesting sub-

strates may not be limiting in the bottomland sites we studied. Moreover, the lack of Wood Thrush nests found in upland sites versus bottomland sites is consistent with the assertion of Roth et al. (1996) that this species has an affinity for mesic sites. Interestingly, census data from our bottomland sites indicate that Wood Thrushes were more likely to be found in narrow than in wide bottomland corridors (Kilgo et al. 1998). This conclusion was supported by the discovery that three-fourths of the nests we found in bottomland sites were in corridors <150 m wide, although these narrow sites comprised just 6 of the 15 bottomland study sites. In fact, only 5 nests were found in wide (> 300 m) bottomland stands, such as those that typically occur on larger creeks and rivers (i.e., Savannah River and Upper Three Runs Creek in our study). When wide bottomland stands were used as nesting habitat, nests generally were located near the upland-bottomland interface. The scouring effect of flooding, which most commonly occurs in wide bottomland sites, may negatively impact the leaf litter in which Wood Thrushes forage, or it may diminish the survival of understory vegetation used as nesting substrates. Additionally, soil moisture levels at the time of arrival on the breeding grounds may be high enough to actually diminish Wood Thrush prey availability. Bertin (1977) believed that moist conditions were a better indicator of Wood Thrush presence than the availability of running water, possibly because adequate soil moisture is key to promoting abundant prey for the species. Others have emphasized the importance of a dense canopy and a moderately developed understory featuring scattered saplings, moist soil, and abundant leaf litter (James et al. 1984, Roth 1987). Thus, the value of soil moisture content in our bottomland study sites likely was important in contributing to an adequate prey base for nesting Wood Thrushes; however, very wet conditions likely were detrimental because they could have reduced the availability of nesting substrates and prey.

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