

# NEST PREDATION AND NEST-SITE SELECTION OF A WESTERN POPULATION OF THE HERMIT THRUSH<sup>1</sup>

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*Abstract.* Audubon's Hermit Thrushes (*Catharus guttatus auduboni*) in central Arizona have a low nesting success (7 to 20%) due almost exclusively to nest predation. We examine the sites chosen for nesting and compare them to nonuse sites randomly selected within the vegetation types associated with nests. Hermit Thrush nest sites differ from nonuse sites primarily in that nest sites have more small (1- to 3-m tall) white firs (*Abies concolor*) in the patch (5-m radius circle) surrounding the nest. Hermit Thrushes nest almost exclusively in small white firs and they do not forage in or near them. Hermit Thrushes may select nest sites that have a large number of other potential nest sites (i.e., small white firs) near the nest because predation risk is thereby reduced. Indeed, nests with a high probability of predation were surrounded by a lower density of small white firs than more successful nests. However, low predation nests also were more concealed than high predation nests. Nest-site selection appears to be a function of characteristics in the immediate vicinity of the nest (concealment, overhead cover, nest orientation), but also on a larger scale surrounding the nest. Consideration of nest-site selection on this larger scale may cast light on the question of whether nest sites limit territory and habitat selection by birds.

*Key words:* Daily mortality; nest concealment; nest orientation; nest predation; nest-site selection; nest-patch selection; nesting success.

## INTRODUCTION

Nest-site selection is closely tied to fitness because of the effects on offspring production (e.g., see Martin, in press a). Consequently, nest-site choice should be molded by nest-site characteristics that influence the number and quality of young that can be successfully fledged. Habitat characteristics that influence probability of nest predation may be particularly important because nest predation often is the primary source of nesting mortality for a wide range of bird species (Ricklefs 1969).

Nests may be affected by habitat at two spatial scales: (1) the nest site (characteristics within the immediate vicinity of the nest) and (2) the nest patch (characteristics of the habitat patch surrounding the nest). Previous work has focused on the nest site, examining effects of overhead cover on energy costs (e.g., Calder 1973, Walsberg and King 1978, Walsberg 1981), nest orientation relative to solar exposure (e.g., Giesen et al. 1980, Schafer 1980, Cannings and Threlfall 1981, Zerba and Morton 1983), and effects of nest concealment on probability of predation (e.g., Keppie and Herzog 1978, Nolan 1978, Best and

Best 1985). However, the nest patch may be equally important to selection of sites for nesting. Nonrandom selection of nest patches has only been examined a few times (i.e., MacKenzie and Sealy 1981, Clark et al. 1983, Petersen and Best 1985) and none of these studies attempted to relate vegetation characteristics of the nest patch to nesting success. Yet, studies in aquatic systems provide a basis for expecting foliage density to influence predation probability at a scale as large or larger than the nest patch; increases in vegetation density in foraging patches of aquatic predators often reduce predation risk by concealing prey or inhibiting predator search efficiency (e.g., Crowder and Cooper 1982, Anderson 1984, Cook and Streams 1984, Leber 1985). Indeed, Bowman and Harris (1980) found raccoon (*Procyon lotor*) foraging efficiency decreased, search time increased, and fewer clutches of bird eggs were found in enclosures where understory foliage density was artificially increased. Thus, foliage density in the nest patch may impede random and intentional nest discovery by inhibiting transmission of chemical, auditory, or visual cues. An alternative hypothesis that may operate simultaneously or independently is that predation probability may decrease with increases in density of the particular

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foliage types that are used as nest sites; such increases may reflect the number of potential nest sites that predators must examine which reduces their chances of finding the actual nest (Martin, unpubl.). These alternatives can be addressed by examining effects of the nest patch on probability of nest predation and by specifically examining predation probability as a function of numbers of potential nest sites surrounding nests.

In this paper, we present data on nesting success and nest-site and patch choice of Audubon's Hermit Thrush (*Catharus guttatus auduboni*) and then examine nesting success and predation probability relative to the numbers of potential nest sites and other habitat characteristics associated with actual nests. As we will show, Audubon's Hermit Thrush is particularly appropriate for this analysis because nest-tree selection in central Arizona is highly specific, which allows reasonable estimates of numbers of potential nest sites.

#### STUDY AREA AND METHODS

Study sites are drainages dominated by big tooth maple (*Acer grandidentatum*) in the understory and located on the Mogollon Rim in Central Arizona at 2,300 m elevation. These drainages vary in area and numbers of coexisting bird species with a total of 29 species recorded (Martin, in press b). These sites have a mixed overstory with ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), douglas-fir (*Pseudotsuga menziesii*), white pine (*Pinus strobiformis*), quaking aspen (*Populus tremuloides*), and Gambel oak (*Quercus gambelii*). Saplings of canopy trees, plus maple and New Mexican locust (*Robinia neomexicana*) are the dominant understory woody species (see Martin [in press b] for further description). These drainages contrast with surrounding forest which is primarily characterized by open ponderosa pine with Gambel oak in the subcanopy and little understory vegetation.

Red squirrels (*Tamiasciurus hudsonicus*), gray-neck chipmunks (*Eutamias cinereicollis*), long-tailed weasels (*Mustela frenata*), House Wrens (*Troglodytes aedon*), and Steller's Jays (*Cyanocitta stelleri*) are present as possible nest predators on Hermit Thrushes (Martin, unpubl. data).

From mid-May to early July in 1984 through 1986, 15 maple drainages were searched for Hermit Thrush nests. Nests were located by observing parents with nesting material or by simply searching the vegetation. Date and status (pres-

ence of parents, eggs, nestlings) of each nest were recorded every 3 to 5 days. Nests that fledged at least one young were considered successful. Observations of fledging, fledglings near the nest, or parents feeding new fledglings in the general area of the nest were taken as evidence of a successful nest. Depredation was assumed when the nest or eggs or nestlings (when too young to fledge) disappeared. Although most nests were found prior to onset of incubation, some nests were not and, so, nest success and mortality were calculated using the Mayfield method (Mayfield 1961, 1975) as modified by Johnson (1979) and Hensler and Nichols (1981). Half the number of days between subsequent visits over which a nest was depredated was added to the number of previous days the nest survived to obtain the total number of days a nest survived. Tests of differences in nesting success were conducted using the *z*-test described in Hensler and Nichols (1981).

Four nests in 1985 and nine nests in 1986 that were found by observing parents were never visited more closely than 10 m to check effects of human visitation on probability of predation because such effects can sometimes obscure the importance of nest concealment (Westmoreland and Best 1985). These nests were checked from 10 m or more using binoculars and observations of parental activity at the nest to determine whether or not the nest was active. When no activity was found, the nest was approached to verify predation.

Nest-site characteristics were measured after termination of nesting. Plant species used as the nesting substrate, height of the nest above the ground and height of the nest tree were measured by meter stick, or by ocular estimation in the three cases of large trees. Orientation of the nest relative to the main stem was recorded in 45° octants. Nest concealment was indexed by estimating percent foliage cover in a 25-cm circle centered on the nest from a distance of 1 m from above and from the side in each of the four cardinal directions. Minimum (MINSC) and average (AVESC) side cover were used for analyses.

Habitat characteristics within a 5-m radius circle around each nest were measured at all nests in 1985 and 1986 and for a few nests in 1984. Included within this sampling were a few nests that were found in the first 2 weeks of the breeding season but which never contained eggs. These nests were probably depredated before being found by human observers. However, these nests

were assigned a status of "unknown" and not included in analyses of habitat characteristics relative to nesting success. Habitat variables measured within the circles included numbers of white firs between 1 and 3 m tall (WFSM) because Hermit Thrushes almost always nest in such locations (see later). Numbers of all other conifer species between 1 and 3 m were also counted (CONSM). Numbers of trees taller than 3 m were counted for all conifer species (CONBIG). Numbers of maple stems were counted for all stems less than 5 cm dbh (MASM), between 5 and 15 cm (MAMED), and greater than 15 cm (MABIG). Numbers of locust stems were counted for all stems less than 5 cm (LOSM) and greater than 5 cm (LOMED). Locusts were always smaller than 15 cm dbh, so the large class was not necessary. All other deciduous woody stems were counted for all stems less than 5 cm (DECSM) and greater than 5 cm (DECBIG). A separate intermediate group was not included because this group included very few stems.

All habitat variables were also measured in nonuse plots in 1986. Nonuse plots were randomly located within the general vegetation type associated with nest sites of Hermit Thrush and other ground and understory nesting species. Nonuse sites for Hermit Thrushes (HTNU hereafter) and other species (OSNU hereafter) were located by pacing 50 m from the nest sites in a direction parallel to the drainage. In this way, the vertical position on the side slopes was maintained. Vegetation structure changes with increasing distance up the side slopes and, thus, HTNU sites represented randomly sampled vegetation within the same vegetation type selected by Hermit Thrushes. OSNU sites provided more complete coverage of the full range of habitat sites available because other species nested in other vegetation zones.

Habitat variables were compared between Hermit Thrush nest sites and the two types of nonuse sites. In addition, habitat variables and nest-site characteristics were compared between two groups of Hermit Thrush nests defined as high predation rate (HPHT) and low predation rate (LPHT) groups. These groups were defined as nests that were depredated during the egg stage (HPHT nests) vs. those that were depredated during the nestling stage or were successful (LPHT nests). Nests were grouped in this way because nesting success was extremely low (only three nests successfully fledged) and such grouping

provided more adequate sample sizes for analyses.

Analysis of variance was used to test univariate differences in habitat variables between groups. Variables that discriminated between groups were identified by stepwise discriminant function analysis. Covariance matrices were tested for homogeneity using Box's M criterion (SPSS X 1986). For each pair of groups tested, the matrices showed significant heteroscedasticity ( $P < 0.05$ ). Discriminant function analysis was then based on the pooled within-group covariance matrix and using the Mahalanobis distance (Minimum  $D^2$ ) between group centroids as the criterion for maximizing separation of groups. This method is most appropriate when covariance matrices are not homogeneous (Hand 1981, Williams 1983). Finally, original variables selected by DFA were correlated with the discriminant function to examine their importance.

## RESULTS

### GENERAL NESTING SUCCESS

Daily mortality rates did not differ between nests that were and were not visited by humans ( $z = 0.42$ ,  $P > 0.64$ ; Table 1a). Probability of nesting success varied between 7 and 20% (Table 1b). Only one of the nest losses over the 3 years could be attributed to some cause other than predation, so mortality reflects predation rates. Daily mortality rates were surprisingly similar among years; daily mortality for 1985 did not differ ( $z = 0.08$ ,  $P > 0.92$ ) from 1984, and 1986 did not differ ( $z = 0.08$ ,  $P > 0.92$ ) from 1985 (Table 1b). Consequently, all 3 years were pooled for subsequent analyses.

### NEST-SITE CHARACTERISTICS

Ninety-three percent of the nest trees ( $n = 57$ ) were white firs between 1 and 3 m tall. The rest were maples (5%) and white firs taller than 3 m (2%). Mean nest-tree height was  $172.0 \pm 16.28$  ( $\bar{x} \pm SE$ ) and nest height was  $107.8 \pm 9.16$  cm. Nests were most common in the southwest quadrant of the nest tree ( $\chi^2 = 17.00$ ,  $P < 0.025$ ) (Fig. 1).

### NEST-PATCH SELECTION

More small white firs occurred on Hermit Thrush nest patches than on HTNU patches (Table 2a). Numbers of small white firs also were most important in differentiating between Hermit Thrush and OSNU patches, but number of locust stems

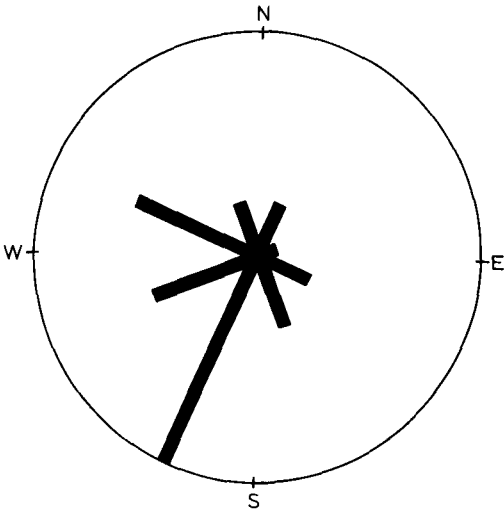


FIGURE 1. Nest orientation of Hermit Thrushes in trees used for nesting ( $n = 51$ ). Length of bars reflect number of nests that were found with an orientation in each octant: NNE (4), ENE (1), ESE (4), SSE (5), SSW (16), WSW (8), WNW (9), NNW (4).

greater than 5 cm dbh also was important (Table 2b). In both analyses, the number of correctly classified cases indicated that birds were selecting specific features in their nesting patches.

**NESTS WITH LOW VS. HIGH RATES OF NEST PREDATION**

Four variables discriminated between nests with high and low predation rates (Table 3a). Again, numbers of small white firs were most important in discriminating between the groups, with more firs associated with nests with lower predation

rates. The second most important discriminant was minimum side cover, with greater minimum side cover at nests with lower predation rates (Table 3a). Nests with lower predation rates were associated with more small maple stems and lower nesting heights, but the low correlations of these variables with the discriminant function show that their importance is weak (Table 3a). High predation nests were associated with fewer small firs than low predation nests, but high predation nests still had more small firs than nonuse sites (Table 3b).

**DISCUSSION**

Nest concealment, as indexed by minimum side cover, was significantly greater at low predation nests than at high predation nests. Similar results have been obtained by other woodland bird studies (e.g., Keppie and Herzog 1978, Nolan 1978, Murphy 1983, Westmoreland and Best 1985; but see Best and Stauffer 1980). On our sites, this result not only reflects positioning of the nest within a selected fir, but also reflects qualities of the fir selected. The density and fullness of boughs of small white firs are influenced by grazing herbivores to varying extents and birds appeared to select firs with high cover density (pers. observ.) General cover densities of firs was not measured but may be important to refining discriminations; firs with a particularly high cover density may not require as many surrounding firs to be a suitable nest site. The fact that discrimination between low and high predation nests was so highly accurate when both numbers of small firs and minimum side cover were incorporated into

TABLE 1. Numbers of successful and unsuccessful nests and the nesting success based on numbers of nests, plus numbers of days those nests were observed to survive and daily mortalities and predicted nest success under the Mayfield method for (a) nests that were visited and nests that were not visited by humans during the nesting attempt and (b) for all nests in each year.

Year	No. successful/ unsuccessful	% Nests successful	Days observed	Daily mortality	Predicted nest success (%)
(a) Visited vs. unvisited nests					
Visited	3/13	18.8	150.5	0.086 (0.0005) <sup>a</sup>	8.8
Unvisited	1/12	7.7	118.5	0.101 (0.0008)	5.6
(b) Nest success among years					
1984	3/13	18.8	139	0.094 (0.0006)	7.0
1985	2/8	20.0	88	0.091 (0.0009)	7.6
1986	2/17	10.5	181	0.094 (0.0005)	7.0
All	7/38	15.6	408	0.093 (0.0002)	7.2

<sup>a</sup> Variance as calculated under the methods of Hensler and Nichols (1981).

TABLE 2. Mean (SD) of habitat characteristics that are important in discriminating between Hermit Thrush (HT) nest sites vs. other (OSNU) and Hermit Thrush (HTNU) nonuse sites, plus the univariate ANOVA of differences in the means and results of stepwise, discriminant function analysis.

Variable	Univariate analyses				Discriminant function analyses			
	HT (46) <sup>a</sup>	OSNU (29)	F	P	Wilk's lambda	Minimum D <sup>2</sup>	P	Correlation coefficient
(a) Hermit Thrush vs. other species nonuse sites								
WFSM <sup>b</sup>	17.52 (15.76)	7.62 (7.38)	10.02	0.002	0.879	0.563	0.002	0.781**
LOMED <sup>c</sup>	6.00 (13.92)	18.86 (23.08)	9.09	0.004	0.816	0.923	0.001	-0.744**
Correctly classified	80.4%	69.0%						
(b) Hermit Thrush vs. Hermit Thrush nonuse sites								
	HT (46)	HTNU (22)						
WFSM <sup>b</sup>	17.52 (15.76)	7.59 (6.40)	8.05	0.006	0.893	0.541	0.006	1.000
Correctly classified	76.1%	81.8%						

<sup>a</sup> Sample size.  
<sup>b</sup> Numbers of white firs between 1 and 3 m in height.  
<sup>c</sup> Numbers of New Mexican locust stems greater than 5 cm in dbh.  
 \*\*P < 0.01.

the discriminating model suggests that both factors are important in discriminating nest sites from nonuse sites. Indeed, the significant correlation of minimum side cover with the discriminant function documents its interacting importance.

Moreover, quality of a fir as a nest site may also be influenced by the distribution of cover within the fir. Hermit Thrushes apparently position their nests to take advantage of the warm

afternoon sun at this cool, high elevation (Fig. 1). Thus, suitability of firs as nest sites may be further constrained by the availability of nest sites with dense cover and an opening for a nest with a southwest exposure.

NEST-PATCH SELECTION

Hermit Thrushes select their nesting sites with regard to surrounding habitat characteristics. Comparisons of Hermit Thrush nest patches with

TABLE 3. Results of univariate and discriminant function analyses of (a) high (HPHT) vs. low (LPHT) predation Hermit Thrush nest sites and (b) high predation sites (HPHT) vs. Hermit Thrush nonuse (HTNU) sites.

Variable	Univariate analyses				Discriminant function analyses			
	HPHT (27) <sup>a</sup>	LPHT (12)	F	P	Wilk's lambda	Minimum D <sup>2</sup>	P	Correlation coefficient
(a) High predation Hermit Thrush nest sites vs. low predation nest sites								
WFSM <sup>b</sup>	10.50 (4.31)	30.92 (15.58)	22.17	0.000	0.619	2.70	0.000	0.708**
MINSC <sup>c</sup>	52.88 (19.35)	68.75 (21.23)	5.20	0.029	0.500	4.38	0.000	0.343*
MASM <sup>d</sup>	49.38 (33.33)	48.08 (38.18)	0.01	0.916	0.473	4.89	0.000	0.015
NH <sup>e</sup>	112.96 (65.64)	79.91 (32.53)	2.70	0.109	0.449	5.39	0.000	-0.247
Correctly classified	96.2%	83.3%						
(b) High predation Hermit Thrush nests vs. Hermit Thrush nonuse sites								
	HPHT (27)	HTNU (22)						
WFSM <sup>b</sup>	10.78 (4.47)	7.59 (6.40)	4.19	0.046	0.918	0.346	0.046	1.000
Correctly classified	63.0%	68.2%						

<sup>a</sup> Sample size.  
<sup>b</sup> Numbers of white firs between 1 and 3 m in height.  
<sup>c</sup> Minimum side cover around nests.  
<sup>d</sup> Numbers of big tooth maple stems less than 5 cm in dbh.  
<sup>e</sup> Nest height in cm.  
 \*P < 0.05.  
 \*\*P < 0.01.

OSNU patches showed that Hermit Thrush patches had fewer locust stems. This result seems to reflect nest-patch selection on a moisture gradient rather than avoidance of locust; locust is most abundant on the upper sides of slopes where conditions are drier. Hermit Thrushes tend to select nest trees at or near the bottom of the drainages where conditions are more moist (pers. observ.). Thus, moisture conditions seem to be important in nesting microhabitat choice, as also found by Dilger (1956) in the northeastern United States.

The density of small white firs was clearly the most important factor discriminating Hermit Thrush nest patches from nonuse patches in both selected (HTNU) and other (OSNU) microhabitats. Food limitation is an unlikely cause of these nest-patch choices; small white firs do not provide food resources because all observations of Hermit Thrush foraging showed they were not associated with small white firs (Martin, unpubl. data; also see Dilger 1956). Given that the Hermit Thrush in central Arizona almost always selected small white firs for nesting, our results suggest that Hermit Thrushes select sites that are associated with a large number of other potential nest sites in the patch surrounding the actual nest site. Such choices cannot reflect availability of sites for reneating attempts because Hermit Thrushes always move to different nest patches for reneating (Martin, unpubl. data).

The most likely explanation is that such choices are associated with lower probability of nest predation. The high rates of nest predation found over the 3 years of this study suggest that it should exert strong selection on nest site and patch choice. Moreover, the fact that nests with low predation rates had considerably more small firs surrounding the nest than high predation nests documents that numbers of small white firs in the nest patch influence probability of nest predation. These results, then, support the hypothesis that the number of potential nest sites that predators must examine influences the probability of nest predation. Moreover, at least for Hermit Thrushes on our sites, these results indicate that the effects of foliage on numbers of potential nest sites may be more important to predation probability than the effects on such factors as impeding travel of the predator, concealing activity of the parents from predators, or simply inhibiting transmission of auditory or chemical cues. This latter conclusion derives from

the fact that small firs do not provide a dense thicket of foliage even when in a dense clump because of the spacing between the firs. Maple thickets, which dominate the sites, provide a much denser thicket of foliage. Consequently, if Hermit Thrushes were trying to select nest sites with dense foliage, they would do better by selecting maple or selecting firs surrounded by maple. Yet, they rarely select such sites. The significant effect of nest concealment suggests that foliage density could be important, but the low correlation of maple stems with the discriminant function suggests that general foliage density is not as important as numbers of potential nest sites on predation probability.

Territory (e.g., see Conner et al. 1986) and habitat (e.g., see Rosenzweig 1981, 1985) selection have historically been considered primarily in terms of availability of food and foraging opportunities, under the assumption that food is most limiting to reproductive success. Food is an important limit on reproductive success (see Martin 1987), but the availability of nest sites that minimize risk of nest predation may be just as important, given the amount of mortality attributable to predation (see Ricklefs 1969). Nest sites are conventionally thought to be abundant (Ricklefs 1969, Lack 1971, but see MacKenzie and Sealy 1981, Finch 1985), but if nest-site needs are considered at both the site and patch levels, then high quality nest sites may not be as abundant as conventionally assumed (Martin, unpubl.). Thus, future considerations of nest site, territory, and habitat selection need to pay closer attention to the availability and suitability of nest sites based on habitat attributes surrounding a nest at multiple scales.

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