Wilson Bull., 108(1), 1996, pp. 53–60

NEST-SITE SELECTION BY HOODED WARBLERS IN BOTTOMLAND HARDWOODS OF SOUTH CAROLINA

JOHN C. KILGO, ROBERT A. SARGENT,
BRIAN R. CHAPMAN, AND KARL V. MILLER

ABSTRACT.—We measured habitat features at 45 nests of Hooded Warblers (*Wilsonia citrina*) and 45 non-use sites in bottomland hardwood habitats in the coastal plain of South Carolina during the breeding seasons 1993–1994 to determine features that affect nesting success. Hooded Warblers nested in switchcane (*Arundinaria gigantea*) and hardwood saplings or shrubs that averaged 1.76 ± 0.10 m (*SE*) in height. Nests were more concealed from above ($P = 0.001$) and from the side ($P = 0.002$) than surrogate nests placed at non-use sites but were less concealed from below ($P = 0.002$). Nest sites also had a greater number of potential substrates ($P = 0.014$) in the nest patch (5-m radius) and greater measures of vegetation density ($P < 0.05$) in the nest patch than non-use sites. Successful nests differed from unsuccessful nests only in the amount of fern cover in the nest patch (greater for successful nests, $P = 0.012$). Fern cover may influence nesting success through an effect on behavioral defense strategies. Nesting success of Hooded Warblers may largely be unrelated to fine-scale differences in vegetative characteristics of the nest site. *Received 28 Mar. 1995, accepted 20 Sept. 1995.*

Because availability of suitable nest sites may be the most critical determinant of habitat selection (and thus perceived habitat quality) by some birds (Steele 1993), knowledge of what constitutes a suitable nest site, or more importantly a successful nest site, is necessary (Martin 1993a). For example, Martin and Roper (1988) found that successful Hermit Thrush (*Catharus guttatus*) nests were characterized by a greater density of white fir (*Abies concolor*) saplings in the 5-m radius circle surrounding the nest. Such specific habitat features that affect nest fate should be identified for other species.

Hooded Warblers (*Wilsonia citrina*) have been classified by the Partners In Flight prioritization scheme as a species of "very high concern" in the Southeast (Hunter et al. 1993a, b). We examined nest-site selection patterns of Hooded Warblers to determine habitat differences between successful and unsuccessful nests. We measured variables at two scales, the nest site and the nest patch. Hooded Warblers inhabit moist mature deciduous forests of eastern North America (Bent 1953, Powell and Rappole 1986, Evans Ogden and Stutchbury 1994). In the coastal plain of the southeastern United States, Hooded Warblers occur almost exclusively in forested wetlands (Bent 1953) and reach their greatest abundance in bottomland hardwood forests (Oak-Gum-Cypress [*Quercus-Nyssa-Taxodium*] association).

Daniel B. Warnell School of Forest Resources, The Univ. of Georgia, Athens, Georgia 30602-2152.

STUDY AREA AND METHODS

We conducted this study at the U.S. Dept. of Energy's Savannah River Site (SRS), a 78,000-ha tract in Aiken, Barnwell, and Allendale counties, South Carolina. These counties lie in the Upper Coastal Plain physiographic province. Elevation ranges from <25 m at the Savannah River to 80 m at headwater streams (Workman and McLeod 1990). Bottomland hardwood forests are found along stream courses and may be seasonally flooded, usually during late winter–early spring. Dominant canopy species include sweetgum (*Liquidambar styraciflua*), swamp tupelo (*Nyssa sylvatica* var. *biflora*), red maple (*Acer rubrum*), water oak (*Quercus nigra*), and diamond-leaf oak (*Q. laurifolia*). Dominants in the mid-story include American holly, (*Ilex opaca*), sweet bay (*Magnolia virginiana*), red bay (*Persea borbonia*), and ironwood (*Carpinus carolina*). Switchcane (*Arundinaria gigantea*) and dog hobble (*Leucothoe axillaris*) dominate the shrub layer, and ferns, primarily netted chain fern (*Woodwardia areolata*) and Christmas fern (*Polystichum acrostichoides*), are the dominant ground cover (Workman and McLeod 1990). Bottomland study sites ranged in width from <50–>1000 m and were adjacent to closed-canopy pine (*Pinus elliottii* and *P. palustris*) forest.

We located Hooded Warbler nests in 11 bottomland hardwood strips during May–June 1993 and 1994 by observing adult behavior and by searching potential nesting habitat. We found most nests during the incubation stage. We were unable to determine whether nests were first or second attempts because individual birds were not marked and territories were not mapped. We monitored nests at 3–4 day intervals (Ralph et al. 1993) to determine nest fate. Nests containing nestlings on the last visit before the expected fledging date were assumed to have fledged. We defined successful nests as those that fledged at least one nestling. Vegetation measurements were made following termination of the nesting attempt. We made measurements at the nest plant and in the nest patch, defined as the 5-m radius circle centered on the nest plant (Martin and Roper 1988). Vegetation measurements then were repeated at an unused site. We located non-use sites by pacing 35 m (Ralph et al. 1993) upstream or downstream (determined by coin toss) in a direction parallel to the general bearing of the bottomland strip. This procedure located non-use sites outside of the nest patch but within the bottomland habitat. Non-use sites were centered on the plant stem nearest to the 35-m point that was of the same species and approximate size as the substrate plant (Ralph et al. 1993). Thus, equal numbers of nest sites and non-use sites were sampled. Success data were obtained from 36 nests, 15 nests in 1993 (8 successful, 7 unsuccessful) and from 21 nests in 1994 (10 successful, 11 unsuccessful). Eight additional nests in 1993 and one nest in 1994 that were empty when found were sampled and included in the comparison of nest sites versus non-use sites but not in the analyses relating to nest success (Martin and Roper 1988).

Measurements taken at the nest site included plant species used as the nesting substrate, nest height, plant height, and percentage of nest concealment. Concealment indices (0–4: 0 = 0% concealed, 1 = 1–25% concealed, 2 = 26–50% concealed, etc.) were estimated by viewing the nest from above and below and at nest level from a distance of 1 m in each of the four cardinal directions (Martin and Roper 1988, Holway 1991). For concealment estimates at non-use sites, an empty Hooded Warbler nest was placed at nest-height (i.e., the height of the nest corresponding to the non-use site) in the surrogate substrate plant (Holway 1991).

Measurements taken in the nest patch included overstory canopy cover, stem density of potential nest substrates and trees, fern cover, other herbaceous ground cover, and vegetation profile. Canopy cover above the patch was estimated by five hit-miss readings through an ocular tube (James and Shugart 1970), one at the nest plant and one in each of the cardinal

directions from the perimeter of the patch. Potential substrate and tree (woody stems > 3 m tall) densities were measured in five 1-m^2 quadrats located randomly along the four cardinal directions (transect and position on transect were randomized). Potential substrates were defined as switchcane >1 m tall and other woody species 1–3 m tall. Percent foliage cover of ferns and of other herbaceous ground cover also was estimated (0–4) within the quadrats. Vegetation profile of the patch, which may be viewed as an index of concealment at the scale of the patch, was determined using a 3-m tall vegetation profile board (Nudds 1977, Noon 1981) against which percentage cover was estimated (0–4) for each 0.5-m interval. The profile board was located at the nest plant and was read from a distance of 5 m in each of the cardinal directions.

For comparisons involving potential substrate density, nests were classified as either "switchcane" or "other", depending on the species of their actual substrate. Stem density of switchcane then was determined for switchcane nests and of other for other nests. Thus, the potential substrate variable was a nest-specific measurement which circumvented the problem, e.g., of comparing average switchcane density across all nests when only a portion of nests were in switchcane. Similarly, one vegetation profile measurement (nest level) was nest-specific. The profile readings for the 0.5-m interval corresponding to the height of each nest were compiled for the variable vegetation profile at nest level.

Univariate comparisons were made between Hooded Warbler nest sites and non-use sites and between successful and unsuccessful nest sites for each habitat variable. Variables estimated with the 0–4 index were compared with a Wilcoxon rank-sum test. All other comparisons were made with a two-sample *t*-test. Variances were assumed to be equal for comparisons in which the sample sizes were the same. When sample sizes differed, the *F*-test for equality of variance was used to test the equal variance assumption. Equal variance tests always were appropriate. Because no differences ($P > 0.05$) were found between years for any variables, data from both years were pooled.

RESULTS

Hooded Warblers selected saplings of nine different species as nest substrates: switchcane, 20 (44%); red bay, 7 (16%); common gallberry, 5 (11%); American holly, 5 (11%); water oak, 2 (4%); diamond leaf oak, 2 (4%); blueberry (*Vaccinium* spp.), 2 (4%); wax myrtle (*Myrica cerifera*), 1 (2%); and black oak (*Quercus velutina*), 1 (2%). Mean height of the nest plant was 1.76 ± 0.10 m (*SE*). With one exception, in which the nest was located in an upright branch of an American holly, nests were placed in crotches of the main stem and primary branches of the substrate plant. Nest height averaged 0.98 ± 0.36 m.

Hooded Warbler nest sites differed from non-use sites in several ways. Concealment of nests from above and from the side was greater ($P < 0.005$) at nest sites than at non-use sites, but from below was lower ($P = 0.002$) at nest sites than at non-use sites (Table 1). Potential substrate density was greater ($P = 0.014$) at nest sites (3.79 ± 3.37 stems/m^2) than at non-use sites (2.08 ± 1.88 stems/m^2). Vegetation profile measures for all heights and at nest level were greater ($P < 0.05$) at nests sites than at non-use sites (Table 1). Conversely, only one difference was determined

TABLE 1

COMPARISON OF MICROHABITAT VARIABLES ($\bar{x} \pm$ SE) AT HOODED WARBLER NEST SITES (N = 45) WITH THOSE AT RANDOM SITES (N = 45) WITHIN BOTTOMLAND HARDWOODS, SAVANNAH RIVER SITE, SOUTH CAROLINA 1994–1994

Parameter	Nest site	Random site	*P*
Nest site			
Nest height (m)	0.98 ± 0.05	1.01 ± 0.05	
Plant height (m)	1.76 ± 0.10	1.78 ± 0.14	
Concealment[a]			
Side	1.93 ± 0.10	1.50 ± 0.08	0.002
Above	3.36 ± 0.13	2.40 ± 0.21	0.001
Below	1.58 ± 0.16	2.09 ± 0.14	0.002
Nest patch			
Canopy cover[b]	4.36 ± 0.10	4.49 ± 0.10	0.360
Potential substrate density[c]	3.79 ± 0.60	2.08 ± 0.33	0.014
Fern cover[a]	1.19 ± 0.12	1.31 ± 0.16	0.842
Ground cover[a]	1.48 ± 0.10	1.69 ± 0.12	0.268
Vegetation profile[a]			
0.0–0.5 m	3.07 ± 0.10	2.68 ± 0.13	0.025
0.5–1.0 m	3.39 ± 0.10	2.83 ± 0.14	0.000
1.0–1.5 m	3.12 ± 0.09	2.36 ± 0.14	0.000
1.5–2.0 m	2.94 ± 0.13	2.14 ± 0.14	0.000
2.0–2.5 m	2.53 ± 0.14	2.02 ± 0.22	0.002
2.5–3.0 m	2.30 ± 0.14	1.79 ± 0.13	0.007
Mean	2.88 ± 0.08	2.31 ± 0.10	0.000
Nest level	3.47 ± 0.08	2.86 ± 0.11	0.000

[a] Index of percent coverage: 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%. Index values were compared with the Wilcoxon rank-sum test; all other comparisons were made with a two-sample *t*-test.

[b] Estimated as the sum of five hit-miss readings taken within the patch (5 = total canopy closure).

[c] Stem density (# stems/m^2) of the plant species used as substrate. Substrates were categorized as switchcane or other (woody stems 1.0–3.0 m). Sample includes switchcane nests from 1993 and 1994 (N = 20) and other nests from 1994 (N = 12; total sample = 32).

for the comparison between successful and unsuccessful nests: fern cover was greater ($P = 0.012$) around successful nests.

DISCUSSION

Nest-site characteristics.—Switchcane best provides the structural features of a nest substrate sought by Hooded Warblers of all plant species occurring in bottomland hardwood habitats at SRS. It apparently is the preferred substrate species throughout much of the southeastern United States (Sprunt and Chamberlain 1949, Burleigh 1958). Switchcane is a woody grass (Poaceae) that may grow to 10 m (Radford et al. 1964) but normally ranges from 1–3 m. It commonly forms extensive thickets, or canebrakes, in southeastern swamps. In addition to the nests that were in

switchcane, many of the other nests were in saplings growing in canebrakes (i.e., switchcane provided most of the cover for most nests).

A variety of other plant species also were used as nest substrates. Hooded Warblers reportedly prefer mountain laurel (*Kalmia latifolia*), American holly, and fetterbush (*Lyonia* spp.) in other parts of their range (Bent 1953). All of these species are thicket-forming shrubs (during the sapling stage for American holly). Thus, Hooded Warblers may select shrubs, regardless of species, not only for their microsite characteristics but also for their thicket-forming properties, as evidenced by the greater density of potential substrates within the nest patch than at non-use sites. Holway (1991) found that species preference by another shrub-nesting warbler, the Black-throated Blue Warbler (*Dendroica caerulescens*), also was site-specific; they selected the understory shrub that offered the best protection from weather and predators.

Hooded Warblers selected nest sites that were less concealed from below than nests at non-use sites. Bent (1953, p. 613) quotes one author who said that "the easiest way to locate a [Hooded Warbler] nest was to place [his] head close to the ground, scan the low open spaces and look for a clump of leaves, which sooner or later proved to be a nest." The adaptive advantage of an opening immediately below the nest is unclear, though it may be related to escape strategies. Although Hooded Warblers normally do not approach or leave the nest near the ground (Odum 1931), when flushed, the female often drops from the nest straight to the ground before flying away just above the ground for a short distance (J. C. Kilgo, pers. obs.; Evans Ogden and Stutchbury 1994). Alternatively, such openings may result simply from the greater shading provided by the understory.

Murphy (1983) and Martin (1992, 1993a) have suggested that predation, because it is the primary cause of nest failure, should be the key factor influencing nest-site selection. Selection of nest sites with dense vegetation theoretically can inhibit predator efficiency by visually screening the nest and parent activity, by providing too many potential nest sites for the predator to search, and by physically impeding predators (Holway 1991). Our results indicate that Hooded Warblers may utilize each of these strategies in their selection of nest sites. Hooded Warblers selected nest sites that were better concealed from the side and from above than non-use sites. Furthermore, nest patches contained a greater density of potential substrates and denser vegetation profiles at all heights than non-use patches.

Effect of nest-site characteristics on success.—We detected no difference in concealment from any angle between successful and unsuccessful nests. Similarly, Howlett and Stutchberry (in press) detected no effect of

nest concealment on predation of Hooded Warbler nests in Pennsylvania, and Holway (1991) was unable to detect a relationship between concealment and the nest success of Black-throated Blue Warblers. We also failed to detect a difference in the number of potential substrates between successful and failed nests, as predicted by Martin and Roper (1988) and Martin (1993a). Several factors may make statistical distinction of these subtle habitat features difficult. First, Holway (1991) suggested that predators using olfactory cues would be less inhibited by visual concealment. Furthermore, nest predation sometimes can be random, with some nests being found by chance alone. Second, human visitation of nest sites during monitoring may have increased the likelihood of predation, and thus masked any effects of habitat on predation (Westmoreland and Best 1985, Martin 1992). Finally, all nests of shrub-nesting woodland birds should be concealed because selection of poorly concealed sites should be eliminated by natural selection (Wray and Whitmore 1979). The latter prediction is contradicted by several authors who have detected differences in concealment between successful and failed nests (e.g., Nolan 1978, Wray and Whitmore 1979, Martin and Roper 1988). However, Wray and Whitmore (1979), suggest that the apparently nonadaptive trait to select poorly concealed nest sites may be maintained in Vesper Sparrows (*Pooecetes gramineus*) because annual variation in their environment may permit the occupancy of a variety of nest sites to be adaptive over time. Although such temporal variation is probably great in the early successional habitats of Vesper Sparrows, the environments of mature forests are relatively stable. In addition, nest predation generally is higher in shrub and grassland habitats than in mature forests (Martin 1993b). Thus, a relationship between concealment and success should not be as evident in forested habitat. Studies of woodland shrub-nesting passerines support this contention (Best and Stauffer 1980, Conner et al. 1986, Holway 1991, Howlett and Stutchbury, in press; but see Martin and Roper 1988), whereas results of studies of birds in earlier successional habitats are more variable (Caccamise 1977, Best 1978, Nolan 1978, Wray and Whitmore 1979). Much of the predation on shrub-nesting woodland birds may largely be unrelated to fine-scale differences in concealment (Holway 1991).

The difference in fern cover between successful and failed nests is intriguing. This finding may be related to nest-defense strategies. Female Hooded Warblers almost invariably drop to the ground when flushed from the nest, and rather than flying away, they often engage in a distraction display, which consists of running through the underbrush with wings drooped and tail spread (J. C. Kilgo, pers. obs.; Evans Ogden and Stutchbury 1994). This behavior likely is their primary (if not only) means of nest defense. If insufficient ground cover exists in the patch to make this

technique effective (i.e., if the bird must itself escape and is not able to risk distracting the predator) the nest may be rendered more susceptible to predation. Ferns may provide structure that conceals the displaying female yet is sufficiently open to allow the predator to detect her. Thus, degree of fern cover may be one of the subtle habitat features that determines nest fate of Hooded Warblers. This may also explain why the more obvious measures of concealment and vegetation density did not differ between successful and failed nests.

ACKNOWLEDGMENTS

This study was funded by the United States Dept. of Energy, Savannah River Site, the United States Forest Service, Savannah River Forest Station Biodiversity Program, the Univ. of Georgia, and McIntire-Stennis Project No. GEO-0074-MS. J. Blake provided logistical support. We thank the many field assistants who helped in locating and monitoring nests and measuring vegetation. We thank G. W. Ware for providing statistical advice and A. S. Johnson, K. C. Parker, R. J. Warren, and D. H. White for reviewing the manuscript. L. B. Best and B. J. Stutchbury also provided valuable editorial comments.

LITERATURE CITED

BENT, A. C. 1953. Life histories of North American wood warblers. Bull. 203, U. S. National Museum, Washington, D.C.

BEST, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95:9–22.

——— AND D. F. STAUFFER. 1980. Factors affecting nesting success in riparian bird communities. Condor 82:149–158.

BURLEIGH, T. D. 1958. Georgia birds. Univ. of Oklahoma Press, Norman, Oklahoma.

CACCAMISE, D. F. 1977. Nesting success and nest site characteristics in the Red-winged Blackbird. Wilson Bull. 89:396–403.

CONNER, R. N., M. E. ANDERSON, AND J. G. DICKSON. 1986. Relationships among territory size, habitat, song, and nesting success of Northern Cardinals. Auk 103:23–31.

EVANS OGDEN, L. J. AND B. J. STUTCHBURY. 1994. Hooded Warbler (*Wilsonia citrina*). *In* The birds of North America, No. 110 (A. Poole and F. Gill, eds.). The Acad. Nat. Sci. of Philadelphia, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.

HOLWAY, D. A. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. Condor 93:575–581.

HOWLETT, J. S. AND B. J. STUTCHBURY. Nest concealment and predation in Hooded Warblers: experimental removal of nest cover. Auk (in press).

HUNTER, W. C., M. F. CARTER, D. N. PASHLEY, AND K. BARKER. 1993a. The Partners in Flight prioritization scheme. Pp. 109–119 *in* Status and management of Neotropical migratory birds (D. M. Finch and P. W. Stangel, eds.). U.S.D.A. For. Ser. Gen. Tech. Rep. RM-229.

HUNTER, W. C., D. N. PASHLEY, AND R. E. F. ESCANO. 1993b. Neotropical migratory landbird species and their habitats of special concern within the southeast region. Pp. 159–171 *in* Status and management of Neotropical migratory birds (D. M. Finch and P. W. Stangel, eds.). U.S.D.A. For. Ser. Gen. Tech. Rep. RM-229.

JAMES, F. C. AND H. H. SHUGART. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

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

———. 1993a. Nest predation, nest sites, and birds: new perspectives on old patterns. BioScience 43:523–532.

———. 1993b. Nest predation among vegetation layers and habitat types: revising the dogmas. Am. Nat. 141:897–913.

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

MURPHY, M. T. 1983. Nest success and nesting habits of Eastern Kingbirds and other flycatchers. Condor 85:208–219.

NOLAN, V. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor.* Ornithol. Monogr. 26.

NOON, B. R. 1981. Techniques for sampling avian habitats. Pp. 42–51 *in* The use of multivariate statistics in studies of wildlife habitat (D. E. Capen, ed.). USDA For. Serv. Gen. Tech. Rep. RM-87.

NUDDS, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildl. Soc. Bull. 5:113–117.

ODUM, E. P. 1931. Notes on the nesting habits of the Hooded Warbler. Wilson Bull. 43: 316–317.

POWELL, G. V. N. AND J. H. RAPPOLE. 1986. The Hooded Warbler. Pp. 827–853 *in* Audubon wildlife report 1986 (R. L. Di Silvestro, ed.). National Audubon Society, New York, New York.

RADFORD, A. E., H. E. AHLES, AND C. R. BELL. 1964. Manual of the vascular flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill, North Carolina.

RALPH, C. J., G. R. GUEPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook of field methods for monitoring landbirds. USDA For. Serv. Gen. Tech. Rep. PSW-144.

SPRUNT, A. AND E. B. CHAMBERLAIN. 1949. South Carolina bird life. Univ. of South Carolina Press, Columbia, South Carolina.

STEELE, B. B. 1993. Selection of foraging and nesting sites by Black-throated Blue Warblers: their relative influence on habitat choice. Condor 95:568–579.

WESTMORELAND, D. AND L. B. BEST. 1985. The effect of disturbance on Mourning Dove nesting success. Auk 102:774–780.

WORKMAN, S. W. AND K. W. MCLEOD. 1990. Vegetation of the Savannah River Site: major community types. Publication SRO-NERP-19, National Environmental Research Park Program. Savannah River Ecology Laboratory, Aiken, South Carolina.

WRAY, T. AND R. C. WHITMORE. 1979. Effects of vegetation on nesting success of Vesper Sparrows. Auk 96:802–805.