

NESTING HABITAT AND NESTING SUCCESS OF EASTERN WILD TURKEYS IN THE ARKANSAS OZARK HIGHLANDS¹

ALEXANDER V. BADYAEV²

Arkansas Cooperative Fish and Wildlife Research Unit, Department of Biological Sciences,
University of Arkansas, Fayetteville, AR 72701

Abstract. I studied nesting habitat of the eastern Wild Turkey (*Meleagris gallopavo silvestris*) in the Arkansas Ozarks during the breeding seasons of 1992 and 1993. Hens selected cover with greater complexity and variability in habitat structure than was generally available. Vegetation in preferred cover types provided substantial concealment at 0–1 m height. Hens selected large patches of habitat (about 80 m in diameter) for nesting. Areas adjacent to nests had characteristics intermediate between nest and non-use sites. Open overstory at nest site and dense understory adjacent to the nest-site areas were apparently used as cues in nest habitat selection early in spring. Parameters correlated with enhanced lateral and overhead concealment of the nest site contributed the most to discrimination between used and non-used sites. Successful and depredated nests were best discriminated when data were considered on a larger spatial scale. Visual obstruction of the nest at 0–1 m height and variable nesting habitat appearance contributed the most to avoiding nest predation. Vegetation characteristics at re-nest sites were more variable, resulting in habitat appearance more diverse than that of first nest sites. I suggest that nest predation influences habitat selection here and availability of suitable nesting habitat may be a limiting factor for Wild Turkey populations in the Arkansas Ozarks.

Key words: Nest concealment; nest site selection; nest patch selection; nest success; eastern Wild Turkey; *Meleagris gallopavo silvestris*; Arkansas.

INTRODUCTION

Nest predation is the primary source of nesting mortality across many bird species and habitats (Ricklefs 1969; Martin 1991, 1992, 1993a). Study of habitat features associated with successful nesting in areas with substantial nest predation may be useful in understanding the process of nest habitat selection (e.g., Martin and Roper 1988; Li and Martin 1991; Martin 1992, 1993b; Kelly 1993). It is necessary to consider different spatial scales in investigation of habitat selection (e.g., Wiens et al. 1987, Martin and Roper 1988, Orians and Wittenberger 1991, Bergin 1992, Knopf and Sedgwick 1992, Sedgwick and Knopf 1992, Kelly 1993) as structure and vegetation characteristics of areas adjacent to the nest site influence the probability of nest predation (Martin and Roper 1988). Dense vegetation and high structural heterogeneity of habitats may reduce predation rates of nests by providing both nest concealment and an increased number of potential nest sites, thereby decreasing predator success (e.g., Bowman and Harris 1980; Martin and

Roper 1988; Martin 1988a, 1993a; Clark and Nudds 1991; Knopf and Sedgwick 1992; Riley et al. 1992; Steele 1993; Gregg et al. 1994). High heterogeneity of nest habitats may prevent common predators from developing search images, and may therefore further reduce predation (Storaas and Wegge 1987, Martin 1988b).

High nest predation and nest habitat limitation are important factors causing early nest initiation (e.g., Orians and Wittenberger 1991). In seasonal environments, selection of early nest sites is based on incomplete information about the future resources of the selected area. Therefore, temporal scale is important in studies of habitat selection (Orians and Wittenberger 1991).

Here I examine nesting habitat selection by eastern Wild Turkeys (*Meleagris gallopavo silvestris*) in the Arkansas Ozark Mountains. Nest predation is the major source of breeding failure in Wild Turkeys in these mountains (Badyaev 1994) and the rate of 83% is among the highest reported for the southeastern portion of the species range (see review in Vangilder 1992). The influence of predation on habitat selection in Wild Turkeys is relatively unstudied (Lewis 1992), but might be expected to exert strong selection for nest predation avoidance in populations experiencing high predation pressure (e.g., Martin and

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² Present address: Department of Biological Sciences, University of Montana, Missoula, MT 59812.

Roper 1988; Martin 1992, 1993b). I examine four questions. (1) Does habitat of nesting sites differ from habitat in non-used areas? (2) What is the appropriate spatial scale (e.g., cover type, nest patch, and nest site), to study nesting habitat selection? (3) What (if any) features of nesting habitat contribute to avoidance of nest predation at the nest patch and nest site scales? (4) Do female turkeys make any changes in habitat selection within a season following unsuccessful nesting attempts?

STUDY AREA

This study was conducted in two areas in the Ozark Mountains, northwestern Arkansas. Both White Rock and Piney Creeks Wildlife Management Areas are characterized by flat-topped mountains (elevation up to 746 m) with numerous narrow valleys. White oak-red oak-hickory and shortleaf pine-oak-hickory forest types cover most of both areas. Dominant species include white oak (*Quercus alba*), northern red oak (*Q. rubra*), post oak (*Q. stellata*), shagbark hickory (*Carya ovata*), and shortleaf pine (*Pinus echinata*). The understory is dominated by saplings of the canopy species, as well as maple (*Acer* spp.), elm (*Ulmus* spp.), black gum (*Nyssa sylvatica*), flowering dogwood (*Cornus florida*), eastern hophornbeam (*Ostrya virginiana*), Carolina buckthorn (*Rhamnus caroliniana*), and eastern red cedar (*Juniperus virginiana*). Sassafras (*Sassafras albidum*), downy serviceberry (*Amelanchier arborea*), blackberry (*Rubus* spp.), devil's walkingstick (*Aralia spinosa*), and persimmon (*Diospyros virginiana*) are common on clearcuts and old fields. Common vines include poison ivy (*Rhus radicans*), Virginia creeper (*Parthenocissus quinquefolia*), and grapes (*Vitis* spp.).

Principal nest predators include raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), bobcats (*Felis rufus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), and domestic dogs (*Canis familiaris*) (Badyaev, unpubl. data).

METHODS

Capture sites were evenly distributed throughout the study area and among available cover types to ensure unbiased and thorough sampling of the turkey population. Thirty-two female Wild Turkeys were captured with cannon nets in White Rock area during February–March 1992. In addition, 72 females were captured in both study sites during February–March 1993. All birds were

banded and fitted with 110 g backpack-style radio transmitters (Telonics, Mesa, AZ). Twenty-four and 81 radio-marked females survived to the beginning of each nesting season (April–June) in 1992 and 1993. Hens were radiolocated once every two days during the nesting season (see Badyaev 1994 for description of telemetry methods). Nest sites were marked by circling incubating hens at 40–50 m distance, and flagging vegetation. I also used five nest sites of untagged hens in vegetation sampling. These nests were used only in nest vs. non-use site analyses. I considered nests to be successful when at least one egg hatched. Seven nests that were abandoned as a result of disturbance by observers were excluded from nest success analyses. I calculated nest initiation dates for most nests either by analyzing hen movement data from telemetry, or by subtracting the number of days of the egg-laying period (based on clutch size) from the first date of incubation. Only nests with known initiation date and nesting attempt number were used in first nest vs. re-nest sites analyses.

HABITAT MEASUREMENTS

Cover types (forest types) were classified using the system of U.S. Forest Service forest types, stand conditions and management types (U.S. Forest Service Silvicultural Examination and Prescription Field Book). White oak-red oak-hickory, shortleaf pine-oak, shortleaf pine, clearcuts (in regeneration), and old fields were the principal cover types in both study areas. After nest attempts were completed, I sampled vegetation structure and composition on 20-m diameter nest-centered plots (hereafter nest plots) and adjacent to the nest plots (adjacent plots) (see below, Fig. 1) as well as randomly located (non-use) sites. Six randomly located plots were sampled in each of available cover types. Habitat measurements of nest, adjacent and corresponding non-use plots were conducted on the same day. I measured understory height and overstory density at the center of each plot and at four perimeter points. Litter depth and the number of shrub and tree stems were measured along two perpendicular diameters within a plot. I counted stems in the following categories: small tree (<25 cm in diameter at breast height, (DBH)), medium tree (25–45 cm DBH), large tree (>45 cm), small shrub (<3 cm in diameter at 0.1 m height), and large shrub (>3 cm). A vegetation profile board (Nudds 1977) was used to evaluate understory

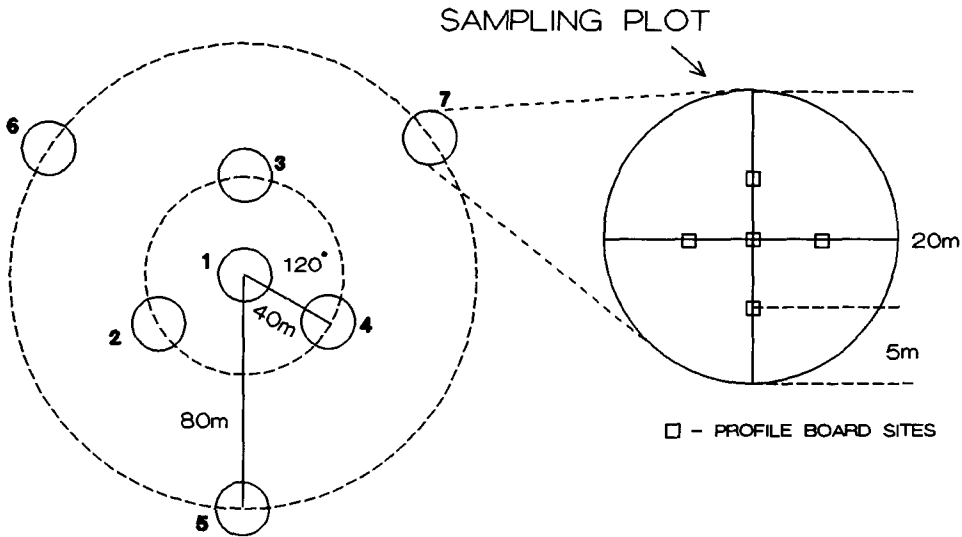


FIGURE 1. Habitat sampling plots. No. 1 is the center plot (either nest or non-use site). No. 2, No. 3, and No. 4 are adjacent plots. Plots No. 5, No. 6, and No. 7 were used only during 1992 season (see text for explanation). The center plot and one of adjacent plots (No. 2-4) were used in 1993.

cover at three height classes (0-50 cm, 51-100, and 101-200 cm). I used six categories to estimate percentage of cover (after Schmutz et al. 1989): (1) <2.5%, (2) 2.5-25%, (3) 26-50%, (4) 51-75%, (5) 76-95%, and (6) >95%. The profile board was placed at the center of the plot and read from four points at the plot perimeter. It was then placed at four intermediate points 5 m from the center of the plot and read from corresponding points in the plot perimeter at 10 m distance. I also measured distance to edge—an average radius of the most homogeneous patch of cover type around the nest. All variables measured are listed in Table 1.

In 1992, I established a system of concentric plots around nests to estimate the size of the area selected by nesting birds. All plots were 20 m in diameter, centered on the nest (or non-used site), and on points at distances of 40 and 80 m from the nest (Fig. 1). In 1993, I established three types of plots: a nest plot centered on the nest site, an adjacent plot located 40 m from the nest at a randomly selected direction, and a non-use plot randomly located in the study area within the same cover type as the nest. For 1992 nests, visual obstruction in all three height levels and overstory densities were remeasured at 16 nest and 12 corresponding adjacent plots during spring of 1993. Sixteen non-use and adjacent to non-use plots were also remeasured at the same time.

Nest sites of females that survived to the next spring were mostly used for this analysis. I followed reproductive behavior of these females during spring of 1993 and remeasured their 1992 nest sites at the time of nest initiation during 1993 to control for meteorological variation between years.

STATISTICAL ANALYSES

All analyses were performed with the Statistical Analysis System software (SAS Institute 1989). I used non-parametric tests (Kruskal-Wallis and Mann-Whitney tests) for univariate comparisons. The log-likelihood ratio and chi-square goodness-of-fit tests were employed to test use-availability patterns between cover types (Neu et al. 1974, Zar 1984). I used Rao's spacing test and the Watson-Williams test for statistical analyses of nest orientation data (Batschelet 1981). Principal component and discriminant function analyses (DFA) were used for multivariate analysis of data. I employed the broken-stick model (Jackson 1993) to determine the number of interpretable eigenvalues. Multivariate analysis of variance, stepwise discriminant analysis and canonical discriminant analysis (PROC DISCRIM, CANDISC, and STEPDISC) were used to distinguish characteristics of nest, adjacent, and non-use sites, successful vs. depredated nests, and first nests vs. re-nests by using linear and

TABLE 1. Means (and range) of habitat variables at 58 Wild Turkey nests, 58 adjacent plots, and 56 non-use plots in the Arkansas Ozarks, 1992–1993.

Variable	Nest ^{a,d}	Adjacent ^e	Non-use
Understory height (center), cm	57.4 (210.0) ^{ns,***}	53.9 (210.0) ^{***}	23.9 (180.0)
Understory height (medium), ^a cm	60.6 (175.0) ^{ns,ns}	57.5 (205.0)	53.6 (172.5)
Overstory density (center), %	86.4 (100.0) ^{ns,ns}	80.4 (100.0)	82.3 (100.0)
Overstory density (medium), %	77.9 (98.0) ^{ns,ns}	82.2 (94.7)	81.5 (100.0)
Small shrubs, no.	69.7 (326.0) ^{***}	50.2 (325.0)	46.8 (158.0)
Large shrubs, no.	46.7 (203.0) ^{*,***}	36.3 (196.0) [*]	32.1 (167.0)
Small trees, no.	57.9 (181.0) ^{ns,*}	53.0 (196.0)	45.7 (116.0)
Medium trees, no.	6.0 (23.0) ^{ns,ns}	6.3 (26.0)	6.8 (25.0)
Large trees, no.	12.1 (31.0) ^{ns,*}	12.0 (28.0) [*]	14.4 (33.0)
Litter depth, cm	4.0 (6.6) ^{ns,**}	3.9 (6.0)	3.4 (8.6)
Distance to large tree, m	2.3 (25.0) ^{f,***}	—	5.2 (44.8)
Distance to road, m	31.5 (298.0) ^{f,***}	—	112.2 (430.0)
Distance to water, m	122.3 (396.0) ^{f,*}	—	205.8 (543.0)
Slope, %	27.2 (75.0) ^{ns,**}	24.7 (55.0)	19.3 (50.0)
Aspect, mean angle	142.9 (74.5) ^{e,f,***h}	—	69.4 (73.9*)
Distance to edge, m	69.1 (83.7) ^{f,ns}	—	66.3 (77.7)
Visual obstruction, category ^b			
0–50 cm (center)	5.0 ^{***,***}	4.0 ^{**}	3.5
0–50 cm (medium) ^a	4.5 ^{***,***}	4.0 ^{**}	3.5
51–100 cm (center)	4.0 ^{***,***}	3.5 ^{**}	3.0
51–100 cm (medium) ^a	3.5 ^{***,***}	3.0 ^{**}	3.0

Significance indicated by: ^{ns} = nonsignificant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

^a 10 m from the center of the plot.

^b Median category.

^c Kruskal-Wallis test for nest vs. adjacent plots.

^d Kruskal-Wallis tests for nest vs. non-use plots.

^e Kruskal-Wallis test for adjacent vs. non-use plots.

^f Comparison is not applicable.

^g Angular deviation, significant directionality ($P < 0.05$).

^h Watson-Williams test.

All multiple comparisons were conducted with correction for multiple tests.

quadratic combinations of original habitat variables and variables accounting for the most variance in the model. When model assumptions were met, I used cross-validation techniques to evaluate model classification efficacy (Williams et al. 1990). Cohen's *Kappa* and its *Z* value was calculated to test model performance (Titus et al. 1984). I used correlations between canonical variable(s) and original variables to interpret their importance in the model. Most of the variables were log or arcsin transformed (Zar 1984) to improve the normality of data. Percentage of understory cover was used instead of ranks when DFA was performed. DFA sample size requirements and the assumption of equality of covariance matrices were considered (Morrison 1969, Williams et al. 1990). The determinant of the group covariance matrix ($|\Sigma|$) which is the measure of generalized variance (Morrison 1969) was used to compare variability between groups. Samples sizes varied among tests because some data were missing. Individual habitat variables did not differ either between years or study sites

(all $P > 0.1$). Multivariate models describing habitat also failed to differentiate among years or study sites (both Wilks' Lambda $F P > 0.1$). Thus, unless otherwise indicated, data were pooled for both years and study sites.

RESULTS

COVER TYPE SELECTION

Nests were distributed proportionally among available cover types in Piney Creeks site ($G = 2.45$, $P > 0.1$), but not in White Rock site ($G = 7.82$, $P = 0.05$). In White Rock site, Wild Turkeys preferentially nested in clearcuts/forest openings, and pine stands with a hardwood understory ($G = 6.02$, $P < 0.05$ and $G = 3.83$, $P = 0.05$, respectively). Cover type preference did not differ between early and late first nests. Selection of cover types for first and re-nesting attempts for individual birds was independent ($P > 0.05$). I did not perform preference analyses for re-nests because of the small sample size.

Preferred (over-utilized) cover types had great-

er understory cover, as determined by both visual obstruction at the 0–1 m level, and by the number of shrub stems (structure correlations = |0.66| and |0.55|, respectively). Preferred cover types had lower overstory density (|0.62|), fewer trees of all classes (approximately |0.50|), and lesser amounts of litter debris on the ground (0.60) (all univariate test $P < 0.05$, Wilks' Λ $F = 3.80$, $P = 0.001$, Cohen's $Kappa = 97\%$, $Z = 25.6$, $P < 0.0001$). Preferred cover types also had more complex vegetation structure, as determined by smaller patches of homogeneous vegetation (|0.43|) and larger generalized variances than other cover types ($|\Sigma| = 0.02 \cdot 10^{-6}$ vs. $0.09 \cdot 10^{-13}$, $P < 0.001$). Accordingly, the within covariance matrices were used in DFA.

NEST PATCH SELECTION

Multiple comparisons of visual obstruction among plots situated at different distances from the center of the set (Fig. 1) and between nest and non-use sites yielded the results below. Understory cover at 1–2 m height level neither differed among nest, adjacent, and non-use plots nor within set of plots ($\chi^2 = 0.61$, $P = 0.73$). Understory vegetation cover in sites located >50 m from the nest (10 m radius plots centered 40 m from the nest) did not differ from non-use plots ($\chi^2 = 1.12$, $P = 0.87$), but did differ from sites located ≤ 50 m of the nest ($\chi^2 = 12.77$, $P < 0.001$). Visual obstruction in nest plots differed from plots within nest setup but situated farther away ($\chi^2 = 6.42$, $P < 0.002$, Fig. 1). There were no differences among plots within sets of plots centered on non-use sites, except that understory (0.5–1 m height) density consisted of patches of about 40 m in radius ($\chi^2 = 4.90$, $P < 0.03$). Thus, Wild Turkeys selected patches of about 40 m in radius (hereafter referred to as the nest patch) for nesting based on visual concealment.

NEST SITE SELECTION

I retained the first two principal components of 14 original variables in accordance with the broken-stick model and sphericity test. The first principal axis ordered plots according to their openness as determined by overstory density and understory height. The second principal axis arranged plots according to their visual concealment at understory level, distance to road, and slope (Tables 1 and 2, Fig. 2). Univariate and principal component analyses revealed that nest plots had higher understory and overstory cover

TABLE 2. Eigenvectors for the principal component analyses of habitat variables measured at Wild Turkey nests, adjacent to nest, and non-use sites^a.

Variable	PCI	PCII
Understory height (center)	0.45	
Overstory density	0.49	
Large shrubs		0.40
Small shrubs		0.56
Large trees	0.40	
Medium trees	0.37	
Small trees		0.58
Distance to road ^b		-0.33
Slope ^b		0.33
Explained variation (%)	33.6	25.4

^a Only eigenvectors ≥ 0.3 are reported.
^b For nest and non-use plots.

than non-use plots (Table 2, Fig. 2). Nests were also located closer to water sources than non-use sites ($P < 0.03$). Nest orientation distribution ($U = 301.5$, $P < 0.001$) was bimodal with nests oriented along an east-west axis. Mean orientation of nests (south-east) differed from non-use sites (north-east) ($F = 6.93$, $P < 0.01$).

Visual obstruction at 0–1 m, understory height, and number of stems in small and large shrubs contributed the most to discrimination among adjacent, nest, and non-use sites (structure correlations with canonical variable = 0.77, 0.56, 0.35, 0.37 respectively, approx. $F = 4.1$, $P < 0.001$; Wilks' $\Lambda = 0.67$, $P < 0.001$, Cohen's $Kappa = 0.80$, $Z = 14.58$, $P < 0.0001$). Covariance matrices were marginally different between groups ($P = 0.054$), so the pooled covariance matrix was used in DFA. The intermediate position of adjacent plots in relation to nest and non-use plots (Fig. 2) was suggested by univariate analyses (Table 1).

Some vegetation parameters changed over the course of the nesting period. Nest, adjacent, and non-use plots did not differ at the time of nest initiation in terms of visual concealment (all $P > 0.05$). Nest plots tended to be more open than other plots at the 0–100 cm level ($P = 0.1$). At the time of nest initiation, nest plots had less overstory cover around the center (27.5%) than did adjacent (32.3%) and non-use (44.9%) plots (all $P < 0.0005$). Overstory density directly above the center of the plot did not differ between plots ($P = 0.18$). At the time of nest initiation, nest plots had less understory cover at 0–1 m and less overstory density than at hatching time (all $P < 0.01$). Understory cover at the 1–2 m level was

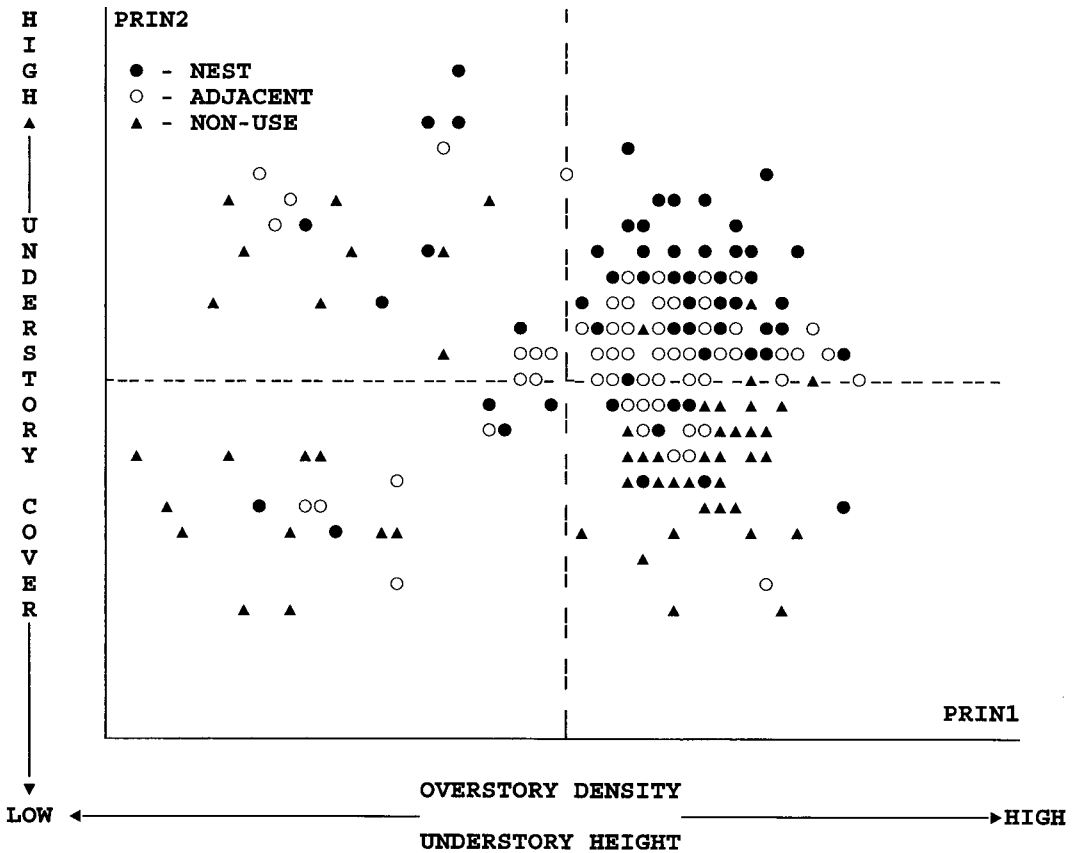


FIGURE 2. Principal component scores of 14 original variables measured at Wild Turkey nests, adjacent, and non-use sites in the Arkansas Ozarks. Understory cover is an interpretation of understory foliage density and visual obstruction (see text).

similar between initiation and hatching time ($P = 0.58$). Visual concealment in adjacent plots was similar at nest initiation and egg hatching ($P > 0.1$), whereas overstory density had changed ($P < 0.001$).

Nest patches during the nest initiation period had more understory cover at 0–1 m (all $P \leq 0.05$) than did non-use patches (non-use site and its adjacent plot). Again, there were no differences at the 1–2 m level ($P = 0.34$), but nest patches had less overstory cover than non-use sites (29.8% vs. 52.3%, $P < 0.0001$). Thus, understory cover at plots adjacent to the nest site and overstory density at the nest site contributed the most to distinguishing between used and non-use sites at nest initiation.

Nest sites of adult females ($n = 36$) differed in several ways from subadult females ($n = 13$). Nest sites of adult females had shorter understory

(46.4 vs. 109.5 cm, $P < 0.001$) and more small shrubs (77.2 vs. 40.0, $P < 0.05$). Nest patches selected by adults also had more large and medium trees than those selected by subadult females (12.47 vs. 8.58, $P < 0.05$ and 6.41 vs. 4.17, $P < 0.05$, respectively).

SUCCESSFUL VS. DEPREDATED NESTS

Successful nests were best discriminated from depredated nests by having higher concealment at the 0.5–1 m level at the nest (structure correlation = 0.42), and 5 m from the nest (0.45). Successful nests were also located farther from roads (0.57) and had fewer large trees around them (−0.30) (Table 3, Fig. 3).

Density of large trees contributed more (−0.50) to discrimination between successful and unsuccessful nests at the patch level. Understory height (0.41), small shrub density (−0.30), and over-

TABLE 3. Means (and range) of habitat variables at Wild Turkey nests in the Arkansas Ozarks, 1992–1993.

Variable	Successful ^c (n = 11)	Depredated (n = 29)	First nest ^e (n = 11)	Renest (n = 13)
Understory height (center), cm	58.2 (210.0)	45.6 (200.0)	47.2 (135.0)	38.1 (90.0)
Understory height (medium) ^a , cm	67.0 (172.5)	54.3 (152.5)	50.0 (76.2)	57.0 (126.2)
Overstory density (center), %	86.5 (80.0)	81.6 (100.0)	95.9 (13.0)*	82.3 (99.0)
Overstory density (medium), %	76.2 (69.0)	72.4 (98.0)	92.5 (15.0)	65.6 (97.5)
Small shrubs, no.	63.7 (201.0)	79.8 (323.0)	49.8 (111.0)*	82.2 (134.0)
Large shrubs, no.	56.3 (137.0)	50.9 (195.0)	28.8 (48.0)**	51.5 (101.0)
Small trees, no.	64.6 (159.0)	58.8 (112.0)	61.8 (148.0)	63.9 (126.0)
Medium trees, no.	5.3 (10.0)	5.7 (19.0)	6.1 (10.0)	7.5 (20.0)
Large trees, no.	9.3 (22.0)	12.9 (31.0)	13.2 (15.0)	10.6 (21.0)
Litter depth, cm	3.9 (3.5)	3.9 (6.6)	4.3 (4.9)	4.0 (5.5)
Distance to large tree, m	3.4 (20.0)	2.7 (25.0)	1.0 (2.5)	2.5 (15.0)
Distance to road, m	51.6 (298.0)	25.7 (147.0)	47.1 (140.0)*	16.4 (35.0)
Distance to water, m	228.9 (374.0)*	87.9 (320.0)	83.0 (120.0)	135.0 (260.0)
Slope, %	23.6 (63.0)	27.5 (75.0)	36.6 (66.0)*	21.2 (46.0)
Aspect, mean angle	— ^d	— ^d	140.0 (70.5) ^f	— ^d
Distance to edge, m	60.0 (83.7)	64.7 (80.5)	86.4 (32.5)**	57.2 (50.5)
Visual obstruction, category ^b				
0–50 cm (center)	5.0	5.0	4.5**	5.5
0–50 cm (medium) ^a	5.0***	4.5	4.0***	5.0
51–100 cm (center)	4.5**	4.0	3.5**	4.5
51–100 cm (medium) ^a	4.5***	3.5	3.0***	4.0

Significance indicated by: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

^a 10 m from the center of the plot.

^b Median category.

^c Kruskal-Wallis test for successful vs. depredated nests.

^d Directionality is not significant (Rao spacing test, $P > 0.1$).

^e Kruskal-Wallis test for first vs. second attempts.

^f Angular deviation, directionality is significant ($P < 0.05$).

story density (0.24) also entered the discriminant model. The DFA model performed better when the patch scale was considered for analysis. DFA correctly distinguished successful from depredated nests 62% better than by chance alone (Wilk's $\Lambda F = 2.73$, $P < 0.01$, Cohen's $Kappa Z = 3.95$, $P < 0.0001$). At the nest site scale, the model correctly classified nests 55% better than by chance alone and was marginally significant (Wilk's $\Lambda F = 3.24$, $P = 0.08$, Cohen's $Kappa Z = 2.20$, $P < 0.015$). Covariance matrices did not differ between groups when the nest site scale was used for analysis ($P = 0.39$). However, successful nests were more variable than depredated nests when the analysis was performed on nest patch scale ($|\Sigma| = 0.012$ vs. 0.004, $P = 0.002$). Within-covariance matrices were used for DFA in the latter case.

Nest plots were more distinct from corresponding adjacent plots for successful nests than for unsuccessful nests (Cohen's $Kappa = 0.80$, $Z = 3.78$, $P < 0.001$ and Cohen's $Kappa = 0.54$, $Z = 3.96$, $P < 0.001$, respectively). In the case of unsuccessful nests, most of this difference was contributed by reduced understory cover (struc-

ture correlation = $|0.59|$), and a lower small shrub density in adjacent plots ($|0.43|$). In the case of successful nests, the difference between nest and adjacent sites was mostly due to a smaller number of large shrubs ($|0.63|$) and greater understory cover ($|0.35|$) in adjacent plots. Covariance matrices did not differ ($P = 0.48$) between types of plots in this data subset, therefore pooled covariance matrices were used in DFA. Plots adjacent to successful and depredated nests did not differ in respect to variables measured.

FIRST NESTS VS. RENEST ATTEMPTS

Renest attempts were located closer to roads ($P < 0.05$) and on less steep slopes ($P < 0.05$) than first nests. Turkeys selected sites with greater understory cover (all $P < 0.005$), lesser overstory density ($P = 0.05$), and more shrubs ($P < 0.05$) for renests compared to first nests. Bimodal east-west orientation of first nests ($U = 228$, $P < 0.01$) was not repeated in reneating attempts (Table 2).

Distance to the nearest edge (radius of most homogeneous area around the nest) and density of small shrubs contributed the most to the discrimination between first and renest attempts

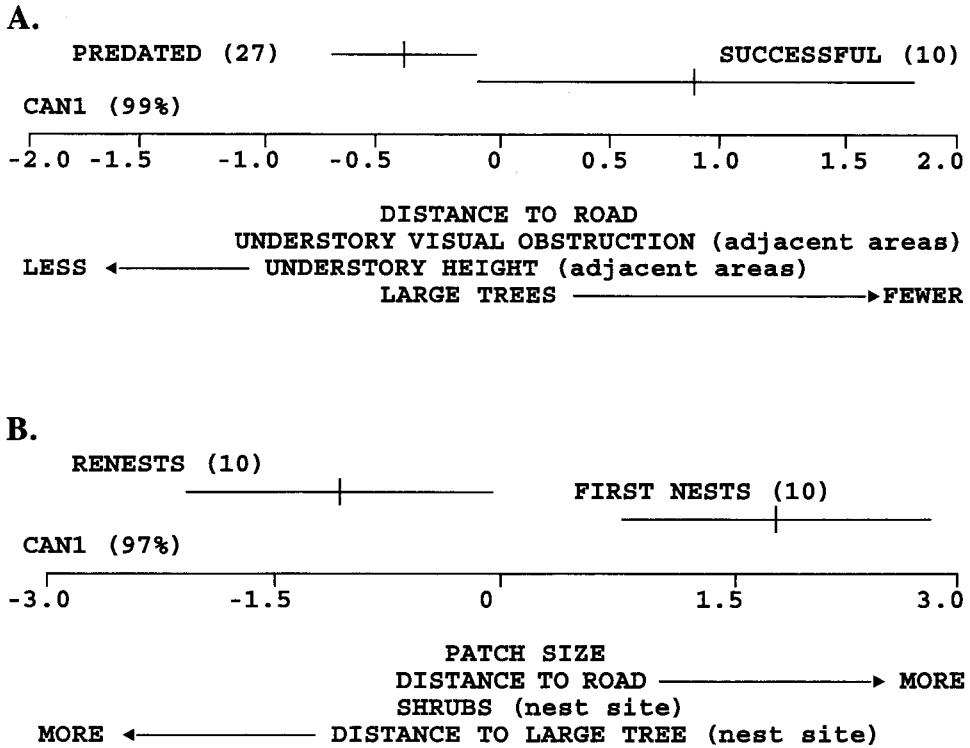


FIGURE 3. Means and 95% confidence intervals of the first canonical variable for discrimination of (A) successful vs. depredated nests and (B) first nest attempts and re-nests of Wild Turkeys in the Arkansas Ozarks.

(structure correlation = 0.79 and 0.53, respectively). Renest locations were farther from bases of trees and closer to roads or trails than first nests ($|0.30|$ and $|0.54|$, respectively). Understory cover at the 0–1 m level (-0.81) and overstory density at 10 m (0.53) entered the discriminant model when nest patch scale was considered for analysis. The DFA model classified observations 80% better than by chance (Wilks' $\Lambda F = 2.61$, $P < 0.05$, Cohen's $Kappa Z = 4.14$, $P < 0.0001$). The model performed slightly better when the patch scale was used (Cohen's $Kappa = 0.86$). Habitats chosen for re-nesting were far more variable than for first nests ($|\Sigma| = 0.016$ vs. $0.018 \cdot 10^{-3}$, $P = 0.003$). Accordingly, within-covariance matrices were used for DFA.

DISCUSSION

COVER TYPE SELECTION

Female turkeys preferred cover types of greater complexity and variability in habitat structure. Day et al. (1991) also found that Wild Turkeys

in South Dakota selected habitats with a higher interspersion index than in non-use areas. Clearcuts, overgrown old fields, and pine stands with dense herbaceous understory attracted more females, possibly because of greater nest concealment in these habitats and increased availability of suitable nest sites. Most heavily used cover types had dense understory cover and a more open midstory. Similar preferences for stand regeneration areas and mixed forest types have been observed throughout the Wild Turkey's range (Speake et al. 1975, Healy 1981, Lutz and Crawford 1987, Seiss et al. 1990, Still and Baumann 1990, Lewis 1992).

NEST PATCH AND NEST SITE SELECTION

Females selected patches at least 80 m in diameter for nesting. Plots at 40 m from the nest site (Fig. 1) had vegetation characteristics that were intermediate between nest and non-use sites. The size of patches selected by turkeys varies across the species' range and may be dependent upon the general heterogeneity of available hab-

itats. In lowland areas of South Dakota, the percentage of visual obstruction in a 0.5 ha area around nests was significantly higher than at non-use sites in both woodland and grassland communities (Day et al. 1991). However, hens selected patches ≤ 5 m in diameter in the Black Hills of South Dakota (Rumble and Hodorff 1993). In Minnesota, Lazarus and Porter (1985) found that the areas located at 40 m from the nest differed from non-use patches of the same size and occupied an intermediate position between nest and non-use sites, as found in this study. Vegetation within a radius of at least 13.3 m was found necessary to conceal incubating hens on the nest in Arizona (Mollohan and Patton 1991, unpublished report cited by Shaw and Mollohan 1992).

Wild Turkeys select nest sites with greater understory density (shrubs, grasses) and visual obstruction (logs, rocks, accumulation of slash) at or near the nest than at unoccupied sites (e.g., Healy 1981, Ransom et al. 1987, Lutz and Crawford 1987, Schmutz et al. 1989, Day et al. 1991, Rumble and Hodorff 1993). Nests are commonly located near roads or forest edges, presumably because of the availability of a variety of resources for incubating females and increased understory density (Speake et al. 1975, Holbrook et al. 1987, Wertz and Flake 1988). Females in the present study actively used roads for traveling to and from nests during the incubation period, thereby possibly reducing noise associated with movements through understory.

Visual obstruction at the 0–1 m level was the most important characteristic in nest area selection (this study, Wertz and Flake 1988). Understory vegetation density at levels higher than 1 m from the ground did not influence nest site selection (*see also* Lutz and Crawford 1987). Only 6% of non-use plots were reclassified by DFA as potential nest sites and none of these non-use plots was classified as a potentially successful nest site. This observation and the large patch size selected for nesting indicated that the number of suitable nest sites could be limited. Although the resulting concealment was much higher in nest than in non-use sites, habitat structure around the nests was as diverse as in non-use sites.

In first nests, vegetation cover differed substantially between the time of nest-site selection and hatching time (this study, Wertz and Flake 1988, Schmutz et al. 1989, Day et al. 1991).

Open overstory cover around the nest site (10 m from the nest) was the only characteristic that differed between nest and non-use sites at the time of the nest initiation. This characteristic may be used by Wild Turkey hens as a cue for nest site selection, as a predictor of early greening-up in these areas and dense grass cover around the nest site. In this study hens that initiated nests early in the season had a much better chance of success than females that nested later (Badyaev 1994). Thus, it is important for females to be able to recognize sites that will have suitable habitat features by the time of incubation (Orians and Wittenberger 1991). Understory density (mostly shrubs) on plots adjacent to the nest site provided most of the cover in the patch at the time of nest initiation. Vegetation in these areas may also make predator presence more conspicuous, as predators will make more noise moving through dense vegetation and also conceal the female's movements near the nest (e.g., Martin 1993b). Vegetation in the immediate vicinity of nest sites provided surrounding and overhead concealment, but nevertheless did not impede visibility or multiple routes of escape from the nest (Logan 1973, Williams and Austin 1988, A. Badyaev, pers. observ.).

SUCCESSFUL VS. DEPREDATED NESTS

In this study, successful nests were best distinguished from depredated nests when corresponding adjacent plots were included in the analyses, emphasizing the importance of characteristics of adjacent areas to avoidance of nest predation (e.g., Martin and Roper 1988, Knopf and Sedgwick 1992). It has been proposed that selection of nest areas with a large number of potential nest sites could enhance avoidance of nest predation, as it increases predator search time and that predation risk would decrease as total vegetation in the nest patch increases (e.g., Martin and Roper 1988, Martin 1993b). I found that variables which best separate nest and non-use sites (Table 1), also contribute the most to the difference between successful and depredated nest patches, suggesting that nest predation influences habitat selection in these populations (*see also* Martin and Roper 1988, Martin 1993b). For example, understory height and shrub density increase in nest sites as compared to non-use sites and in successful nest patches as compared to depredated patches (Fig. 2 and 3, Tables 1, 2, and 3). This may indicate that successful nest

patches contain more potential nest sites than patches ultimately depredated. However, plots adjacent to successful nests did not seem to contain more potential nest sites than plots adjacent to depredated nests, further stressing the importance of characteristics of entire nest patch (nest plus adjacent plots) to nest predation avoidance. Nest plots were more distinct from corresponding adjacent areas in cases of successful nesting than in depredated nests and dense vegetation on plots adjacent to successful nests contributed the most to this difference.

Macro- and microhabitat parameters were more variable in successful than in depredated nests, which resulted in a highly variable appearance of successful nesting habitats. Such diversity may prevent the development of a search image for nesting habitat by predators (Storaas and Wegge 1987, Martin 1988b, Brittas and Willebrand 1991). This diversity in nest habitat appearance could be especially effective considering the high heterogeneity of cover types in the study area. Dense understory vegetation around nests contributed the most to discrimination between successful and depredated nests (*see also* Schmutz et al. 1989, Seiss et al. 1990). Dense vegetation provides visual, auditory, and olfactory obstruction at nest sites, thereby preventing nest detection on smaller spatial scales (Bergerud and Gratson 1988, Martin 1993a).

FIRST NESTS VS. RENESTS

There were pronounced differences in habitats used for first nesting attempts and reneests. First-nest habitats showed much less variability and complexity compared to sites chosen for reneests. These differences in nesting habitats between nest attempts may correspond to an increase in suitable habitat availability as the season progresses (Williams and Austin 1988, Schmutz et al. 1989, Day et al. 1991) or could result from predation of a preceding nest (Martin 1992, Badyaev 1994). Undeveloped grass cover early in the season may have forced birds to nest much closer to the bases of trees than later in the season. Strong selection of east and west facing slopes for first nest attempts may indicate specific patterns of vegetation development on these slopes early in the spring. Hens also switched from nesting in large patches of homogeneous vegetation in first attempts to small patches for reneests. Selection of areas with enhanced spatial heterogeneity (smaller cover type patch sizes) later in the season pos-

sibly allows birds to choose better concealed nest sites. Changes in cover types for reneests and increased variability at reneest sites may contribute to nest predation avoidance (e.g., Storaas and Wegge 1987, Brittas and Willebrand 1991).

High nest predation (83%) in our study area may be caused by limitation of suitable nest habitats (Badyaev 1994). Long-distance dispersal movements of Wild Turkey females are caused by suitable nest habitat limitation and social interactions among birds (Badyaev 1994). Thus, it is possible that hens which have dispersed to sites from other areas were unable to correctly assess specific vegetation characteristics associated with successful nesting in the new area. Wild Turkey relocation programs should take into consideration the highly specialized requirements of Wild Turkey hens for suitable nest habitats in the source population. Relocation of hens to areas with different habitat structure precludes hens recognizing the suitable habitat features and leads to decreased reproductive performance and survival of relocated birds (e.g., Hopkins et al. 1982, McGuinness et al. 1990).

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LITERATURE CITED

- BADYAEV, A. V. 1994. Spring and breeding dispersal in an Arkansas population of Wild Turkeys: causes of and consequences for reproductive performance. M.Sc.thesis, Univ. of Arkansas, Fayetteville, AR.
- BATSCHLET, E. 1981. Circular statistics in biology. Academic Press, London.
- BERGERUD, A. T., AND M. W. GRATSON. 1988. Survival and breeding strategies of grouse, p. 473-577. *In* A. T. Bergerud and M. W. Gratson [eds.], Adaptive strategies and population ecology of northern grouse. Univ. of Minnesota Press, Minneapolis, MN.
- BERGIN, T. M. 1992. Habitat selection by the Western Kingbird in western Nebraska: a hierarchical analysis. *Condor* 94:903-911.
- BOWMAN, G. B., AND L. D. HARRIS. 1980. Effect of

- spatial heterogeneity on ground nest depredation. *J. Wildl. Manage.* 44:806-813.
- BRITTAS, R., AND T. WILLEBRAND. 1991. Nesting habitat and egg predation in Swedish Black Grouse. *Ornis Scand.* 22:261-263.
- CLARK, R. G., AND T. D. NUDDS. 1991. Habitat patch size and duck nesting success: the critical experiments have not been performed. *Wildl. Soc. Bull.* 19:534-543.
- DAY, K. S., L. D. FLAKE, AND W. L. TUCKER. 1991. Characteristics of Wild Turkey nest sites in a mixed-grass prairie-oak-woodland mosaic in the northern Great Plains, South Dakota. *Can. J. Zool.* 69: 2840-2845.
- GREGG, M. A., J. A. CRAWFORD, M. S. DRUT, AND A. K. DELONG. 1994. Vegetation cover and predation of Sage Grouse nests in Oregon. *J. Wildl. Manage.* 58:162-166.
- HEALY, W. M. 1981. Habitat requirements and habitat management for the Wild Turkey in the southeast. Virginia Wild Turkey Foundation, Ellison, VA.
- HOLBROOK, H. T., M. R. VAUGHAN, AND P. T. BROMLEY. 1987. Wild Turkey habitat preferences and recruitment in intensively managed Piedmont forests. *J. Wildl. Manage.* 51:182-187.
- HOPKINS, C. R., J. J. CAMPO, W. G. SWANK, AND D. J. MARTIN. 1982. Dispersal of restocked eastern Wild Turkeys in East Texas. *Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies* 36: 578-585.
- JACKSON, D. A. 1993. Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. *Ecology* 74:2204-2214.
- KELLY, J. P. 1993. The effect of nest predation on habitat selection by Dusky Flycatcher in limber pine-juniper woodland. *Condor* 95:83-93.
- KNOFF, F. L., AND J. A. SEDGWICK. 1992. An experimental study of nest-site selection by Yellow Warblers. *Condor* 94:734-742.
- LAZARUS, J. E., AND W. F. PORTER. 1985. Nest habitat selection by Wild Turkeys in Minnesota. *Proc. Natl. Wild Turkey Symp.* 5:67-81.
- LEWIS, J. B. 1992. Eastern turkey in midwestern oak-hickory forests, p. 286-305. *In* J. G. Dickson [ed.], *The Wild Turkey: biology and management*. Stackpole Books, Harrisburg, PA.
- LI, P., AND T. E. MARTIN. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. *Auk* 108:405-418.
- LOGAN, T. H. 1973. Seasonal behavior of Rio Grande Wild Turkeys in western Oklahoma. *Proc. Ann. Conf. Southeast. Assoc. Game and Fish Comm.* 27:74-91.
- LUTZ, R. S., AND J. A. CRAWFORD. 1987. Reproductive success and nesting habitat of Merriam's Wild Turkeys in Oregon. *J. Wildl. Manage.* 51:783-787.
- MARTIN, T. E. 1988a. Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology* 69:74-84.
- MARTIN, T. E. 1988b. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evol. Ecol.* 2:37-50.
- MARTIN, T. E. 1991. Food limitation in terrestrial breeding birds: is that all there is? *Acta Congressus Internationalis Ornithologici* 20:1595-1602.
- MARTIN, T. E. 1992. Breeding season productivity: what are the appropriate habitat features for management? p. 455-473. *In* J. M. Hagan and D. W. Johnston [eds.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- MARTIN, T. E. 1993a. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am. Nat.* 141:897-913.
- MARTIN, T. E. 1993b. Nest predation and nest sites: new perspectives on old patterns. *BioScience* 43: 523-532.
- 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.
- MCGUINNESS, J. H., J. M. BENNER, AND W. P. SMITH. 1990. Survival and nesting success of late winter Wild Turkey introductions. *Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies* 44: 171-181.
- MORRISON, D. F. 1969. *Multivariate statistical methods*. McGraw Hill, New York.
- NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541-545.
- NUDDS, T. D. 1977. Quantifying the vegetation structure of wildlife cover. *Wildl. Soc. Bull.* 5:113-117.
- ORIAN, G. H., AND J. F. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* 137:S29-S49.
- RANSOM, D., JR., O. J. RONGSTAD, AND D. H. RUSCH. 1987. Nesting ecology of Rio Grande turkeys. *J. Wildl. Manage.* 51:435-439.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contrib. Zool.* 9:1-48.
- RILEY, T. Z., C. A. DAVIS, M. ORTIZ, AND M. J. WISDOM. 1992. Vegetative characteristics of successful and unsuccessful nests of Lesser Prairie Chicken. *J. Wildl. Manage.* 56:383-387.
- RUMBLE, M. A., AND R. A. HODORFF. 1993. Nesting ecology of Merriam's turkeys in the Black Hills, South Dakota. *J. Wildl. Manage.* 57:789-801.
- SAS INSTITUTE, INC. 1989. *SAS/STAT user's guide*, version 6, 4th ed. Cary, NC.
- SCHIECK, J. O., AND S. J. HANNON. 1993. Clutch predation, cover, and the overdispersion of nests of the Willow Ptarmigan. *Ecology* 74:743-750.
- SCHMUTZ, J. A., C. E. BRAUN, AND W. F. ANDELT. 1989. Nesting habitat use of Rio Grande Wild Turkeys. *Wilson Bull.* 101:591-598.
- SEDGWICK, J. A., AND F. L. KNOFF. 1992. Describing Willow Flycatcher habitats: scale perspectives and gender differences. *Condor* 94:720-733.
- SEISS, R. S., P. S. PHALEN, AND G. A. HURST. 1990. Wild Turkey habitat and success rates. *Proc. Natl. Wild Turkey Symp.* 6:18-24.
- SHAW, H. G., AND C. MOLLOHAN. 1992. Merriam's turkey, p. 331-349. *In* J. G. Dickson [ed.], *The Wild Turkey: biology and management*. Stackpole Books, Harrisburg, PA.
- SPEAKE, D. W., T. E. LYNCH, W. J. FLEMING, G. A. WRIGHT, AND W. J. HAMRICK. 1975. Habitat use

- and seasonal movements of Wild Turkeys in the Southeast. *Proc. Natl. Wild Turkey Symp.* 3:122-130.
- STEELE, B. B. 1993. Selection of foraging and nesting sites by Black-throated Warblers: their relative influence on habitat choice. *Condor* 95:568-579.
- STILL, H. R., JR., AND D. P. BAUMAN, JR. 1990. Wild Turkey nesting ecology on the Francis Marion National Forest. *Proc. Natl. Wild Turkey Symp.* 6:13-18.
- STORAAS, T., AND P. WEGGE. 1987. Nesting habitats and nest predation in sympatric populations of Capercaillie and Black Grouse. *J. Wildl. Manage.* 51:167-172.
- TITUS, K., J. A. MOSHER, AND B. K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *Am. Midl. Nat.* 111:1-7.
- VANGILDER, L. D. 1992. Population dynamics, p. 144-164. *In* J. G. Dickson [ed.], *The Wild Turkey: biology and management*. Stackpole Books, Harrisburg, PA.
- WERTZ, T. L., AND L. D. FLAKE. 1988. Wild Turkey nesting ecology in south central South Dakota. *Prairie Nat.* 20:29-37.
- WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spacial scale. *Oikos* 48:132-147.
- WILLIAMS, B. K., K. TITUS, AND J. E. HINES. 1990. Stability and bias of classification in biological application of discriminant analysis. *J. Wildl. Manage.* 54:331-341.
- WILLIAMS, L. E., JR., AND D. H. AUSTIN. 1988. *The Wild Turkey in Florida*. Technical Bulletin # 10. Univ. of Florida Press, Gainesville, FL.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.