

LANDSCAPE ATTRIBUTES AND NEST-SITE SELECTION IN WILD TURKEYS

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ABSTRACT.—Rates of nesting participation, renesting, and nesting success for Wild Turkeys (*Meleagris gallopavo*) in the Ouachita Mountains, Arkansas, are among the lowest recorded in the eastern United States. I studied spatial attributes of 113 Wild Turkey nests to determine landscape-scale habitat characteristics that were important for nest placement and survival. Hens generally nested close to roads in large pine patches that occurred on southeast-facing slopes. Hens selected shortleaf pine (*Pinus echinata*; 68.1%) over mixed hardwood (23.9%), hardwood (0.9%), and open areas (7.1%). Most of the hens (57.5%) placed their nests in edge habitat, but placement in these areas did not influence nesting success. Rather, female turkeys appeared to respond to a high risk of predation by placing nests in large patches, away from areas of high edge density favored by nest predators. Mean patch size chosen by nesting females ($6,912.6 \pm \text{SE of } 634.5 \text{ ha}$) was considerably larger than the mean patch size for the study area ($31.4 \pm 7.8 \text{ ha}$). Although most hens nested close to roads, this association appeared to be detrimental to nesting success because all nests close to roads were unsuccessful. In general, habitat characteristics examined at the level of patch and stand were good predictors of nest location but poor predictors of nesting success, possibly due to a high abundance of edge habitat in the landscape. This large amount of edge apparently sustained predator populations that made even the largest patches hazardous for nesting by Wild Turkeys. Therefore, the lack of suitable nest sites may limit population size of Wild Turkeys in the Ouachita Mountains. Received 10 July 1998, accepted 25 January 1999.

POPULATIONS OF WILD TURKEYS (*Meleagris gallopavo*) in some southern pine forests are declining (Palmer et al. 1993), including that within the Ouachita Mountains of west-central Arkansas and eastern Oklahoma (Nicholson et al. 1995, Thogmartin 1998). The most important demographic parameter affecting Wild Turkey population size is nesting success (Roberts and Porter 1996), making quality of nesting habitat particularly important to Wild Turkeys (Hillestad and Speake 1970). If factors affecting nesting success can be identified and properly managed, populations of Wild Turkeys may stabilize or even increase in areas where they are now declining.

Microhabitats selected by nesting Wild Turkeys are well described (Lazarus and Porter 1985, Seiss et al. 1990, Badyaev 1995). For instance, shrub patches chosen for nesting often provide tall, dense vegetative cover (Lazarus and Porter 1985, Still and Baumann 1990). Vegetative concealment may reduce transmission

of olfactory and visual cues and impede movement of potential nest predators (Bowman and Harris 1980, Redmond et al. 1982, Crabtree et al. 1989). Numerous studies of artificial nests and of ground-nesting birds have demonstrated the importance of nest concealment to reproductive success (e.g. Keppie and Herzog 1978, Picman 1988, Gregg et al. 1994, Badyaev 1995).

Wild Turkey hens may use different proximate cues to select breeding-season habitat than to select actual nest sites (Orians and Wittenberger 1991, Bergin 1992). Lazarus and Porter (1985) reported nest-site characteristics at two scales, the immediate nest area (0.5 ha) and the surrounding nest patch (65 ha), that suggested Wild Turkeys in Minnesota were selecting nesting habitat in a hierarchical fashion. Badyaev (1995) suggested similar processes in the Arkansas Ozarks. Few studies, however, have identified variables at patch, stand, or landscape levels that are important to reproductive success (Burk et al. 1990, Badyaev 1995). Habitat selection at scales larger than the immediate area around the nest should affect predation risk (Martin and Roper 1988). Nest-site selection with consideration at both the

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landscape and the microhabitat level should provide a fitness benefit (Orians and Wittenberger 1991) and, therefore, should be readily identifiable.

In the Ouachita Mountains of west-central Arkansas, 87% of Wild Turkey nests fail, mostly due to predation (Thogmartin 1998). Consequently, Wild Turkeys in this area should be under intense selective pressure to choose habitat components that are linked to reproductive success. Successful decisions by hens at each level of nest-site selection are necessary if hens are to avoid detection by nest predators. I examined nest-site selection in Wild Turkeys at the patch and landscape levels (1) to determine whether females choose features of the environment at scales higher than the area immediately around the nest bowl; and (2) if so, to examine whether these habitat features are associated with reproductive success.

STUDY AREA AND METHODS

Study area.—I conducted this study on Muddy Creek Wildlife Management Area (Muddy Creek), a 39,000-ha reserve within the Ouachita National Forest cooperatively managed by the Arkansas Game and Fish Commission and U.S. Forest Service. This area lies within Scott, Yell, and Montgomery counties, west-central Arkansas. East-west trending ridges and stream valleys dominate the topography, and elevations range from 200 to 750 m (\bar{x} = 331 m). Terrain was hilly, with an average slope of approximately 5°. Cover types consisted chiefly of a patchy mosaic of shortleaf pine (*Pinus echinata*; 45%); mixed pine/hardwood (35%); hardwood (5%); and hayfields, food plots, and recently harvested forest openings (15%). Mean patch size was $31.4 \pm \text{SE of } 7.8$ ha; shortleaf pine patches were larger and more numerous than hardwood (oak/hickory) patches (Thogmartin 1998). Drier south-facing slopes were dominated by shortleaf pine and some oak, principally post oak (*Quercus stellata*). Mesic north-facing slopes and shaded, moist ravines were occupied by hardwoods, including northern red oak (*Q. rubra*), white oak (*Q. alba*), black oak (*Q. velutina*), mocker-nut hickory (*Carya tomentosa*), sweetgum (*Liquidambar styraciflua*), and blackgum (*Nyssa sylvatica*). Tree density varied from 490 to 620 trees per ha, with a mean diameter at breast height (dbh) of 23 cm (Kreiter 1995). Areas of recent timber harvest were dominated by blackberry (*Rubus* spp.), greenbriar (*Smilax* spp.), poison ivy (*Toxicodendron radicans*), bluestem and panic grasses (*Andropogon* spp. and *Panicum* spp.), grape (*Vitis* spp.), pine and oak seedlings, and sumac (*Rhus* spp.).

Capture and radio-telemetry protocols are provid-

ed in Thogmartin (1998). Briefly, turkeys were captured in rocket nets from January to March, 1993 to 1996 (see Bailey et al. 1980). This period is prior to the breakup of winter flocks, whereupon hens may disperse several km to suitable nesting areas. Capture sites were distributed in all habitat types to insure representative coverage of the study area. Feather characteristics were used to determine sex and age of captured turkeys. Backpack-style radio transmitters weighing approximately 110 g were attached to captured hens. Transmitters were equipped with a 4-h delay motion switch that modulated emitted pulse rate to determine whether a hen was active (signal unsteady and infrequent), inactive (signal steady and infrequent), or stationary ("mortality"; signal steady and frequent). All hens were released at their capture sites.

Initiation of incubation was determined when a hen remained at the same location for two consecutive days of radio contact, or a consistent inactive or mortality signal was received. Because of the high rate of nest predation in the study area, nests were flagged in a circle at least 30 m from the nest site two to four days into incubation. Incubating hens were monitored daily from a distance using radio telemetry until increased activity or dispersal indicated the hen had left the nest area. Nest sites were then located and nest fate, number of eggs laid, and number of eggs hatched were recorded. Nests were classified as successful if there were no signs of predator disturbance and at least one egg hatched, and unsuccessful if only unhatched eggs remained or if the nest exhibited obvious signs of disturbance or destruction.

Nest locations were marked on 1:24,000 U.S. Forest Service quadrangle maps, based upon distance from road, stream bed, and other topographical features. Universal Transverse Mercator coordinates of marked nest sites were recorded using a global positioning system in two of the four years of study. Nests located in areas that were not mapped in the geographic information system (GIS; data were unavailable for some stands) were not analyzed. Between 1993 and 1996, I located 113 nests suitable for analysis.

Habitat sampling.—Habitat analysis was conducted in Geographic Resource Analysis Support System 4.1 (GRASS; Army Corps of Engineers, Champaign, Illinois), a raster-based GIS. Overstory vegetation cover types, streams, roads, and elevation were obtained from the Gap analysis project for Arkansas (Dzur et al. 1996, 1998). Vector-based GIS (ARC/INFO) coverages of forest stand condition, stand age, and forest structure were obtained from the U.S. Forest Service and imported into GRASS raster coverages; these data were derived from the Continuous Inventory of Stand Condition management system (CISC; USDA 1993). Seventeen (15 even-aged and 2 uneven-aged) available stand-condition classes

within the CISC database were combined into three categories: (1) young (characterized by small and newly planted trees); (2) pole timber (characterized by trees <24.4 cm dbh); (3) and saw timber (characterized by trees >24.4 cm dbh). Unlike Gap-derived data sets, which were scaled to 900 m² pixels, CISC data were available only at the stand level.

To define habitat available to sampled Wild Turkeys, the study area was circumscribed by 3-km buffers around nests. This distance was chosen because it was approximately equal to annual hen dispersal from winter flocks and to the distance between annual nest sites (Thogmartin 1998). Comparison points were randomly generated within GRASS to locate 2,250 random sites in the study area. Because I compared used with available habitat as opposed to used versus unused habitat (design II.1; Manly et al. 1993), I allowed random points to occur anywhere in suitable nesting habitat (i.e. water and dry crop agriculture cover types were excluded).

A habitat patch was defined as a discrete, contiguous "surface area differing from its surroundings" (Kotliar and Wiens 1990). Edge habitat was defined as the area 60 m into a patch from any boundary between overstory cover-type polygons, whereas the inner portion of a patch farther than 60 m from the edge was defined as the core. This distance was chosen because Paton (1994) suggested that edge effects related to nest predation extended 50 m into forest patches, or nearly twice the 30-m pixel width. Using this definition of edge, edge habitat was not necessarily the sole product of roads, timber harvest, or other linear features of the environment, and included habitat (e.g. boundaries between pine and mixed pine/hardwood cover-types) that may be more properly defined as ecotones or "soft edges". Patch, core, and edge size were estimated for cover-type patches surrounding each nest using landscape ecology programs within GRASS (Baker and Cai 1992). An index of patch shape, the ratio of corrected perimeter:area (CP/A), was calculated for each nest patch using the formula: $(0.282 \times \text{perimeter}) / (\text{area})^{1/2}$ (Baker 1994). This index was chosen because it controls for variation attributed to increases in patch size, thus allowing for comparison of patches of different sizes.

Statistical analyses.—I used various univariate and multivariate procedures to examine relationships among patch- and stand-level characteristics of nests sites and associated hen age, nesting attempt order, and nest survival. I employed principal components analysis (PCA) to reduce the dimensionality of the habitat data set by creating orthogonal (i.e. independent) linear combinations of the original data set, which reduces the number of highly intercorrelated habitat variables (Rencher 1995). Selection functions (used sample proportion divided by available sample proportion) were employed to test use-availability patterns between cover types, understory com-

ponents, and slope classes (Manly et al. 1993). I estimated the likelihood that hens differed in their use of each category and that this use was independent of category abundance. For comparisons between nest sites and random locations, frequencies of habitats derived from random locations were used as expected habitat frequencies.

I compared habitat composition around Wild Turkey nests and random points at multiple spatial scales. Badyaev (1995) indicated that understory components in the Ozark Mountains differed between nest patches and random patches. Therefore, overstory cover-type interspersions, measured as the percentage of cells differing from the center or focal cell, was evaluated at two scales: (1) the nest patch (0.81 ha; 9-pixel area) and (2) the approximate mean habitat patch size (56.25 ha; 625-pixel area). This approach allowed examination of overstory cover-type variegation and its potential influence on nest-site selection at multiple scales.

To examine the effect of streams and roads on nest predation, I created 40 distance classes in 30-m increments. I used the nest as the observational unit and regressed nest fate, hen age, and nest-attempt order against $\log_{10}(\text{area})$, $\log_{10}(\text{area})^2$, and distance to habitat variable in maximum-likelihood, multiple logistic regression models. PCA scores were used in simple linear regression models as well to control for collinearity among habitat variables. Multiple linear and logistic regressions of reproductive parameters against habitat variables were rejected when models or effects were either nonsignificant ($P > 0.05$) or possessed Mallows' C_p far from $2p' - t$, where p' is the number of variables in a subset model and t is the number of variables in the full model. Only significant models are presented here.

Because of the generally poor performance of regression analyses in discriminating between successful and unsuccessful nests, I conducted stepwise linear discriminant function analysis (DFA) in SAS 6.12. I used PROC STEPDISC to select a subset of variables from all available habitat variables; significance levels were 0.25 to enter and 0.10 to stay. To provide better separation between successful and unsuccessful nests, optimal scores and transformations were provided by PROC TRANSREG. For consistency, I also conducted DFA to discriminate between random and nest locations. Statistical hypotheses were rejected if probability of committing a Type I error was ≤ 0.05 ; variation around means is presented as ± 1 SE.

RESULTS

HABITAT INFLUENCING NEST LOCATION

Patch size.—Principal components analysis identified five components (eigenvalues ≥ 1)

TABLE 1. Habitat variables and associated PCA scores measured at 113 Wild Turkey nest sites at Muddy Creek Wildlife Management Area, Arkansas, 1993 to 1996. Only PCA scores $\geq |0.40|$ are shown.

Variable	Scale	PC1	PC2	PC3	PC4	PC5
Elevation	Nest		-0.59	0.42		
Slope	Nest		-0.56			
Dist. to stream	Nest				0.58	0.68
Dist. to road	Nest				-0.71	
Interspersion (0.81 ha)	Nest			0.43		
Interspersion (56.25 ha)	Patch					-0.47
Patch size	Patch	0.47				
Core size	Patch	0.47				
Edge size	Patch	0.47				
Corrected perimeter: area	Patch	0.46				
Stand age	Stand			0.54		

describing 83.5% of the variance in nest location (Table 1). Following Stevens (1996), only component loadings $\geq |0.40|$ were considered. Significant component loadings for the first principal component axis were weighted on patch characteristics.

Four habitat variables and two interactions described habitat differences between turkey nests and random sites, with patch size exerting the largest influence on nest-site selection (Table 2). Habitat patches chosen by nesting females ($\bar{x} = 6,912.6 \pm 634.5$ ha) were significantly larger than typical habitat patches available in Muddy Creek ($\bar{x} = 31.4 \pm 7.8$ ha; $\chi^2 = 255.9$, $df = 1$, $P < 0.001$; Table 3, Fig. 1). To examine whether a few very large patches in Muddy Creek may have biased this result, I examined the proportion of area within Muddy Creek occupied by large patches versus the proportion of sampled nests within these large patches. Twelve habitat patches in Muddy Creek exceeded 500 ha and accounted for 49.8% of the area; 67.3% of nests (76/113) were found in these large patches, a larger propor-

tion than expected ($\chi^2 = 51.9$, $df = 1$, $P < 0.001$). The single largest patch (13,795 ha; 22.9%) in Muddy Creek accounted for 52 (46%) nesting attempts, again proportionately larger than expected ($\chi^2 = 115.0$, $df = 1$, $P < 0.001$).

Mean patch size for each cover type was positively related to the number of nests placed in each cover type (Fig. 2). Hens chose cover type nonrandomly (Fig. 3), selecting shortleaf pine (68.1%, $n = 77$) over mixed hardwood (23.9%, $n = 27$), hardwood (0.9%, $n = 1$), and open areas (7.1%, $n = 8$). No difference was observed in cover types between successful and unsuccessful nests ($\chi^2 = 1.33$, $df = 2$ and 100, $P > 0.5$), but successful nests were in habitat patches that were approximately 1,400 ha larger than were unsuccessful nests.

Forty-eight of 113 hens (42.5%) placed nests in core habitat (>60 m from an edge). The mean ratio of edge:core habitat for random sites was 1.80, indicating that nearly two-thirds of the typical patch in Muddy Creek consisted of edge habitat. Conversely, nests typically were placed in patches with an edge:core ratio <1.00 (unsuccessful nests, $\bar{x} = 0.96$; successful nests, $\bar{x} = 0.92$), areas with nearly equal edge and core habitat. Adult hens, probably a more experienced group of nesters, generally chose nest sites in core habitat ($\chi^2 = 4.66$, $df = 1$, $P = 0.03$), whereas novice subadults placed their nests in edge and core habitat at random ($\chi^2 = 0.95$, $df = 1$, $P = 0.33$). Patch shape, as measured by the CP/A ratio, did not appear to influence nest location except that CP/A was higher for nests placed in core habitat than for nests placed in edge habitat (28.9 ± 2.0 vs. 20.0 ± 1.9 ; $t = 3.21$, $df = 111$, $P < 0.01$).

The first principal component loaded on

TABLE 2. Multiple logistic regression of habitat variables chosen by nesting female Wild Turkeys at Muddy Creek Wildlife Management Area, Arkansas.

Effect	Like- lihood ratio χ^2	df	P
Patch size	12.24	1	0.0005
Slope	11.27	1	0.0008
Patch size \times slope	8.30	1	0.0040
Interspersion (56.25 ha)	8.17	1	0.0043
Aspect class	18.14	8	0.0202
Patch size \times aspect class	41.32	8	<0.0001
Entire model	514.26	20	<0.0001

TABLE 3. Summaries of habitat variables surrounding Wild Turkey nests and random sites in Muddy Creek, Arkansas, 1993 to 1996. Values are $\bar{x} \pm SE$, with coefficient of variation in parentheses. Within rows, different superscripts indicate significant pairwise differences.

Variable	Successful nests			Unsuccessful nests			Random sites			DFA ^a	
	n	$\bar{x} \pm SE$	<i>n</i>	$\bar{x} \pm SE$	<i>n</i>	$\bar{x} \pm SE$	<i>n</i>	$\bar{x} \pm SE$	<i>P</i>	U vs. A	S vs. F
Patch size (ha)	17	8,290 ± 1,647 (0.82) ^A	87	6,643 ± 687 (0.97) ^A	1,922	31.4 ± 7.8 (10.91) ^B	***	—	—	—	
Core size (ha)	17	4,323 ± 866 (0.83) ^A	87	3,389 ± 366 (1.01) ^A	1,922	11.2 ± 4.0 (15.51) ^B	***	0.86	—	—	
Edge size (ha)	17	3,968 ± 782 (0.81) ^A	87	3,254 ± 323 (0.92) ^A	1,922	20.2 ± 3.9 (8.46) ^B	***	0.81	—	—	
Interspersion (%; 0.81 ha) ^b	17	11.2 ± 3.6 (1.31)	87	13.4 ± 2.1 (1.48)	2,247	15.2 ± 0.5 (1.40)	ns	—	—	—	
Interspersion (%; 56.25 ha) ^b	17	43.6 ± 6.3 (0.95) ^{AB}	87	41.8 ± 2.2 (0.50) ^A	2,245	48.1 ± 0.5 (0.45) ^B	*	—	—	—	
Stand age (years)	17	58.6 ± 5.4 (0.38)	72	64.1 ± 3.3 (0.43)	1,550	59.3 ± 0.7 (0.46)	ns	—	—	0.27	
Basal area (m ² per ha)											
Pine pole timber	5	7.1 ± 1.7 (0.54)	44	4.5 ± 0.5 (0.72)	77	5.5 ± 0.4 (0.66)	ns	—	—	—	
Pine saw timber	5	12.3 ± 2.4 (0.44)	44	10.7 ± 1.0 (0.59)	77	10.2 ± 0.7 (0.56)	ns	—	—	—	
Hardwood pole timber	5	3.0 ± 0.7 (0.50)	44	4.8 ± 0.5 (0.72)	77	4.6 ± 0.3 (0.67)	ns	—	—	—	
Hardwood saw timber	5	1.6 ± 0.9 (1.22)	44	2.2 ± 0.3 (1.00)	77	2.7 ± 0.3 (0.93)	ns	—	—	—	
Hardwood mast	5	3.0 ± 1.6 (1.16)	44	4.5 ± 0.5 (0.69)	77	4.9 ± 0.4 (0.71)	ns	—	—	—	
DBH (cm)											
Pine pole timber	4	18.4 ± 0.6 (0.07)	27	17.9 ± 0.4 (0.11)	60	16.2 ± 0.7 (0.32)	ns	—	—	—	
Pine saw timber	4	23.5 ± 8.0 (0.68)	27	31.5 ± 0.6 (0.10)	60	31.8 ± 0.4 (0.09)	ns	—	—	—	
Hardwood pole timber	4	19.7 ± 1.2 (0.12)	27	20.8 ± 0.5 (0.12)	60	19.5 ± 0.6 (0.25)	ns	—	—	—	
Hardwood saw timber	4	34.9 ± 0.6 (0.04)	27	28.4 ± 2.7 (0.49)	60	29.4 ± 1.7 (0.43)	ns	—	—	—	
Elevation (m)	17	320.7 ± 16.8 (0.22)	87	329.7 ± 7.2 (0.20)	2,250	331.1 ± 1.9 (0.28)	ns	—	—	-0.24	
Slope (%)	17	5.9 ± 1.2 (0.82)	87	4.2 ± 0.4 (0.96)	2,248	5.2 ± 0.1 (1.01)	ns	-0.04	—	0.19	
Distance to stream (m)	17	248.8 ± 41.5 (0.69)	87	273.5 ± 24.6 (0.84)	1,898	300.4 ± 5.6 (0.81)	ns	—	—	0.20	
Distance to road (m)	17	368.8 ± 94.4 (1.06) ^{AB}	87	340.0 ± 36.6 (1.00) ^A	2,231	413.9 ± 6.6 (0.75) ^B	**	—	—	-0.35	

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.0001$; ns, $P > 0.05$.

^a Values are correlation coefficients from stepwise discriminant function analysis. Coefficient for discriminating used (U) vs. available (A) aspect was 0.08 for east-southeastern aspect and -0.04 for south-southeastern aspect and for discriminating successful (S) vs. unsuccessful (F) nests was 0.41 for transformed aspect.

^b Interspersion is the percentage of cells (8 for 0.81 ha, 624 for 56.25 ha) surrounding the focal cell that differ from the focal cell, i.e. highest interspersion occurs when most cells differ from the focal cell, lowest occurs when few cells differ.

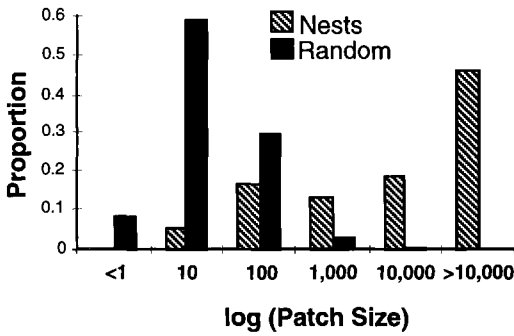


FIG. 1. Proportional distribution of Wild Turkey nests and random sites by log₁₀ of habitat patch size (ha) at the Muddy Creek study area, Arkansas.

patch characteristics (Table 1) and was positively correlated with the date incubation began ($r = 0.31, n = 72, P < 0.01$). Hens nesting in intermediate-sized patches began incubation about 10 days earlier than those nesting in larger patches ($t = 2.00, df = 83, P = 0.049$), perhaps because of the lower amount of edge habitat in intermediate-sized patches. Understory cover also influenced the date incubation began ($F = 4.16, df = 6 \text{ and } 69, P = 0.004, \text{ adjusted } R^2 = 0.15$); incubation at nests in blackgum and hickory understories started at least 10 days earlier than nests in grass or oak-dominated understories.

Patch structure.—Grass and oak understories were avoided by nesting hens (Fig. 3), and grassy understories were occupied only after the second week in June. Hens that nested in

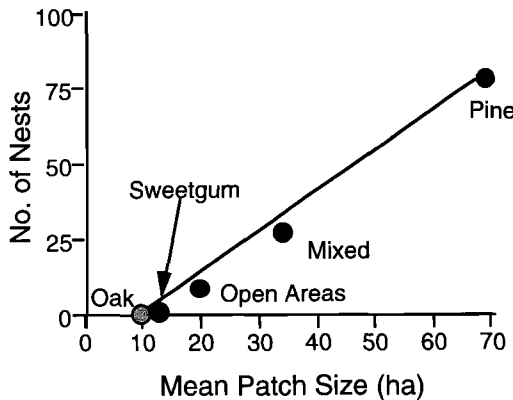


FIG. 2. Linear regression of the number of Wild Turkey nests in each cover type as a function of mean patch size. Number of nests = $-14.32 + 1.33 \text{ mean patch size}$ (adjusted $R^2 = 0.992, F = 495.1, P = 0.002$).

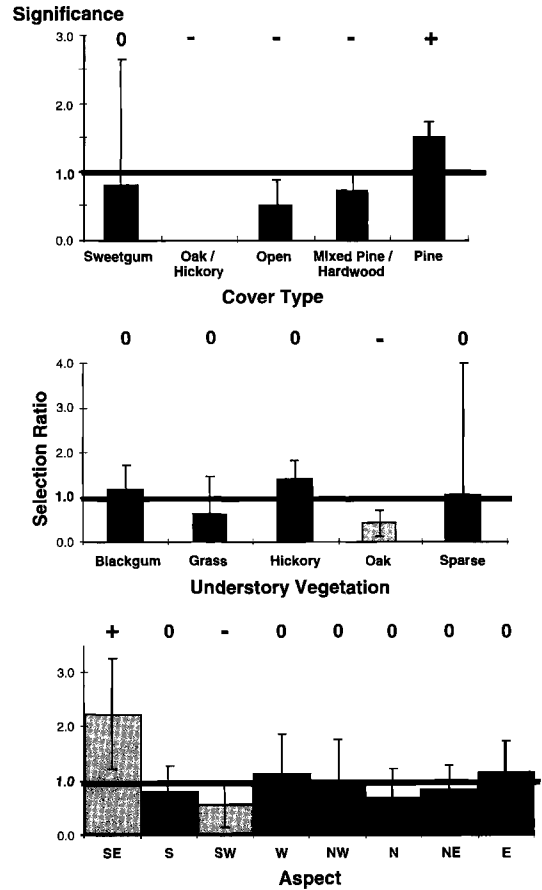


FIG. 3. Selection indices for overstory cover type, understory vegetation, and aspect class by nesting Wild Turkeys in Muddy Creek, Arkansas. 0 = no selection, + = selection for habitat characteristic, - = avoidance of characteristic. A negative lower limit for the confidence interval was replaced by 0 because negative values for selection indices are not possible.

core habitats avoided blackgum and selected hickory understories, although the opposite occurred for nests placed in edge habitats ($\chi^2 = 10.69, df = 4 \text{ and } 84, P = 0.03$). The basal area of mature hardwood saw timber was 50% higher in these core habitats chosen by nesting hens compared with edge habitats ($\chi^2 = 5.63, df = 1, P < 0.02$).

Stand age did not appear to strongly influence nest-site selection ($t = -1.64, df = 274, P = 0.10$) or nesting success ($\chi^2 = 1.42, df = 1, P = 0.23$), except that hens nesting early selected sites in stands with smaller hardwood pole timber (younger stands; Fig. 4). Stands occupied by adult hens were approximately 15

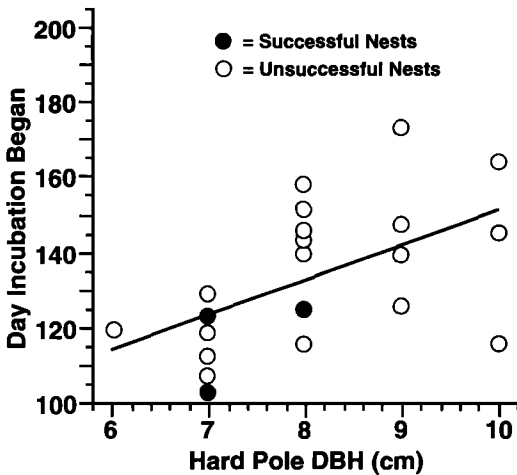


FIG. 4. Linear regression of day of year incubation began (DIB) for Wild Turkey nests in Muddy Creek versus diameter at breast height of hard pole timber. $DIB = 59.20 + 9.23 \text{ hard pole dbh}$ (adjusted $R^2 = 0.26$, $F = 8.01$, $P = 0.01$). Only nests ($n = 21$) with sufficient data on DBH were evaluated (see Methods).

years younger than stands occupied by subadult hens (59.9 ± 2.9 years vs. 75.5 ± 5.8 years; $t = -2.39$, $df = 93$, $P = 0.02$). Based on logistic regression, adult hens occupied higher-elevation sites in younger stands than did subadult hens ($\chi^2 = 12.37$, $df = 2$, $n = 95$, $P = 0.002$, pseudo $R^2 (U) = 0.13$).

Topography.—Loadings on the second principal component axis were weighted on topographic features (Table 1). Elevation was chosen in proportion to availability ($\chi^2 = 0.001$, $df = 1$, $P > 0.9$), and hens chose southeast aspects and avoided southwest aspects (Fig. 3). Nest placement was influenced by slope and aspect and their interaction with patch size (Table 2). Nests in large patches were on steeper slopes than nests in smaller patches ($\chi^2 = 8.61$, $df = 1$, $P = 0.01$). Nests in small and intermediate-sized patches also were farther from streams than those in large patches ($\chi^2 = 6.28$, $df = 1$, $P = 0.04$).

HABITAT INFLUENCING NESTING SUCCESS

Only 13% of nests successfully hatched eggs during the study (Thogmartin 1998). Data were available for all successful nests ($n = 17$) and 87 of 112 unsuccessful nests. Six of 25 habitat variables entered into the forward stepwise DFA,

with lower elevation and southwestern aspect being the best predictors of successful nesting. Successful nests were also on steeper slopes in older stands and were farther from roads and streams. Patch features important in nest-site selection did not enter into the linear DFA model that discriminated between successful and unsuccessful nests. Discriminant function analysis successfully classified 82% of nests based upon habitat features. Successful nests were correctly classified in 87% of cases, whereas unsuccessful nests were classified correctly in 77% of cases. Misclassified nests differed from correctly classified nests in aspect ($\chi^2 = 16.94$, $df = 8$ and 97, $P = 0.03$). Finally, hens nested closer to roads than expected based on random locations (332.7 ± 32.2 m; $\chi^2 = 13.46$, $df = 1$, $P < 0.001$), but this association was detrimental to nesting success because only unsuccessful hens nested significantly closer to roads ($\chi^2 = 8.79$, $df = 1$, $P < 0.01$).

DISCUSSION

Nest-site characteristics.—The most important reproductive decision a Wild Turkey hen must make is where to locate her nest site. At the scales I examined, nest-site selection by Wild Turkeys in Muddy Creek was influenced primarily by patch size, slope, aspect, cover type, cover type interspersions, and to a lesser extent proximity to roads. A wide spectrum of characteristics within these variables was chosen, however, as evidenced by high coefficients of variation for many selected habitat features (Table 3). Wild Turkeys generally nested in large patches of pine and avoided patches containing oak, including mixed pine/hardwood. Seiss et al. (1990) reported similar findings for habitat selection by nesting Wild Turkeys in Mississippi.

Wild Turkeys also avoided nesting in patches with oak understories. Occupation of grassy understories only after mid-June, and selection for larger hardwood mid-story trees later in the season, suggested that nesting activity shifted in response to increased availability of suitable habitat as the nesting season progressed. Grassy understories were used in late spring only after *Panicum* and *Andropogon* grasses developed sufficient cover for nesting (Williams et al. 1968). Occupation of grassy understories may also have been an attempt by late-nesting

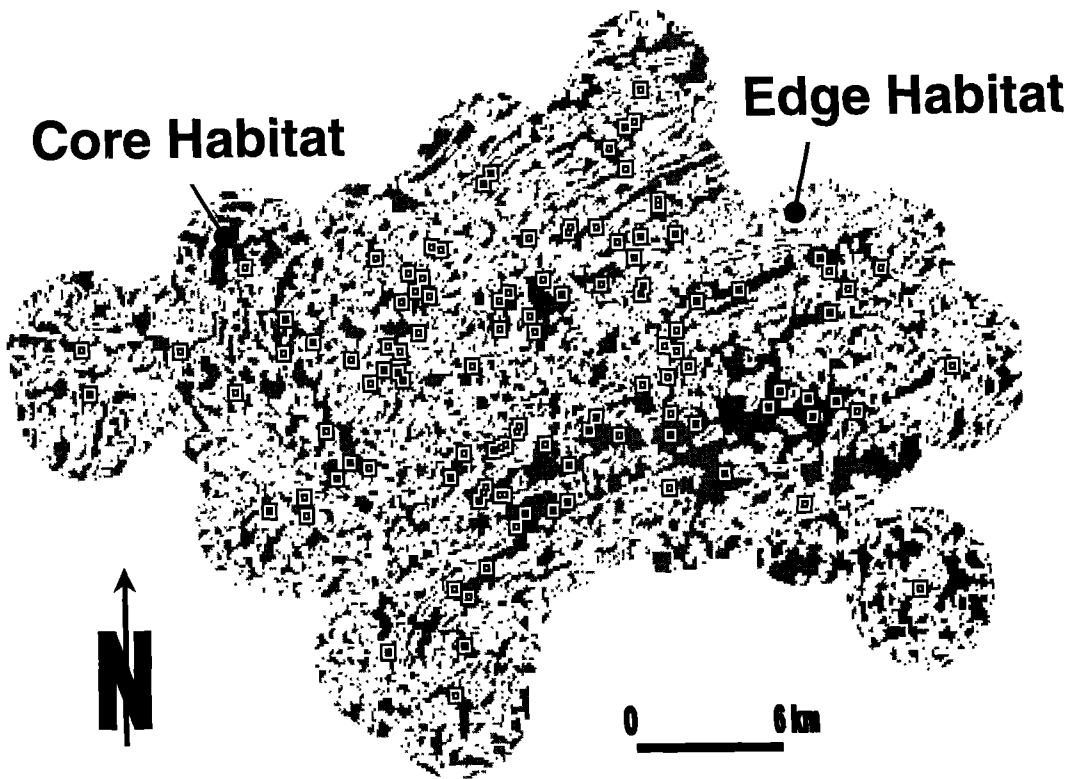


FIG. 5. Edge/core contrast map (with Wild Turkey nest locations) illustrating the extent of edge habitat at Muddy Creek. White area is edge habitat, gray area is core habitat, boxes are approximate locations of nests (not to scale).

hens to place their nests closer to suitable brood-rearing habitat (Lazarus and Porter 1985).

Influence of habitat on risk of nest predation.—The probability of nest predation is a function of nest placement relative to predator activity centers (Gates and Gysel 1978, Boag et al. 1984). The two most common nest predators in the Ouachita Mountains, raccoons (*Procyon lotor*) and black rat snakes (*Elaphe o. obsoleta*), favor hard forest edges for hunting (Durner and Gates 1993, Pedlar et al. 1997). In Muddy Creek, timber harvest has reduced patch size so that 50% of habitat patches were <6 ha in size, 75% were <17 ha, and 90% were <52 ha, resulting in most of Muddy Creek consisting of edge habitat (Fig. 5). Nearly 9% (163 patches) of patches consisted entirely of edge. Open areas resulting from timber harvest and food plot creation comprised up to 15% of the study area but averaged only 20 ha in size. This has resulted in a large proportion of edge habitat in

Muddy Creek consisting of hard discontinuities rather than gradual transitions between cover types.

Higher densities of nest predators are found in smaller patches (Wilcove 1985, Heske 1995), at forest edges (Gates and Gysel 1978, Wilcove 1985), and in landscapes such as Muddy Creek that have a complex and heterogeneous structure (Angelstam 1986, Martin 1993, Donovan et al. 1997). Raccoon and coyotes (*Canis latrans*) are more abundant in diverse landscapes (Oehler and Litvaitis 1996) and were very common in my study area (Thogmartin 1998). These factors lead to elevated rates of nest predation in edge habitat (Paton 1994, Niemuth and Boyce 1997) and probably explain the very low rate of nesting success that I observed, even in the highly dispersed core areas.

In general, though, female Wild Turkeys throughout their range select forest edges for nesting. For instance, in Mississippi (Seiss et al. 1990) and West Virginia (Swanson et al. 1996),

most nests were within 60 m of a habitat edge. In Alabama (Speake et al. 1975) and Minnesota (Porter 1978), approximately 75% of nests were found in edge habitats. Conversely, although the majority of nests at Muddy Creek were placed in edge habitat (58%), adult hens chose edge habitat less than expected. In Muddy Creek, increased predator activity in edges may be responsible for a shift in selection away from "preferred" edge habitat toward nesting in core areas of large patches, which are less susceptible to edge-related nest loss (Burger et al. 1994, Niemuth and Boyce 1997). Nests in core areas survived 19% (2.7 days) longer than nests placed in edge habitat ($t = 1.66, P = 0.10$).

In addition, although female Wild Turkeys chose nest sites that were closer to roads than were random sites, another measure of edge, distance of nests from maintained roads ($\bar{x} = 333$ m), was considerably farther at Muddy Creek than for Wild Turkey nests in other studies (Speake et al. 1975, Everett et al. 1985, Still and Baumann 1990), suggesting avoidance rather than selection for nesting near edges. Moore (1995) reported an increase in nest survival of 1/2 day for each 100 m a nest was placed from a well-traveled road at Muddy Creek. Nests far from edges may be safer because more potential nest sites are offered in large core areas (Martin 1993), potentially reducing the foraging efficiency of predators (Bowman and Harris 1980).

Predator avoidance.—If hens cue on habitat features that are correlated with patch size, such as the type of overstory and understory cover, steepness of slope, stream distance, and size of hardwood timber, then core areas within large patches may be selected. Therefore, nest-site selection may not be a function of overstory cover type per se (e.g. Williams et al. 1968, Burk et al. 1990, Seiss et al. 1990, Still and Baumann 1990), but rather may depend on whether the nest is placed within large or small patches.

As suitable nesting patches at Muddy Creek decrease in number and size, the foraging efficiency of nest predators may increase (Bowman and Harris 1980), leading to increased risk of predation despite development of predator-avoidance behaviors (Martin 1992). An "ecological trap" may form as the landscape becomes increasingly unsuitable (Gates and Gysel 1978). Heske (1995) suggested that a high

level of habitat fragmentation (such as at Muddy Creek) may preclude persistence of true core habitat despite the few large tracts that remain. Willson and Comet (1998) suggested that deciduous patches in their study area were not large enough to prevent conifer-based predators from preying on nests in these patches. The abundance of predators at Muddy Creek apparently made even the largest patches hazardous for nesting. If this hypothesis is correct, suitable nest-sites may be limited at Muddy Creek, and their rarity may account for low rates of nesting participation and nesting success. Rates of nesting participation (62%), re-nesting (35%), and nesting success (13%) in my study area are among the lowest known for Wild Turkeys in the eastern United States (Thogmartin 1998).

Conservation and management implications.—Placement of nests in edge habitat has been linked to both successful (Speake et al. 1975, Seiss et al. 1990) and unsuccessful (Moore 1995) nesting by Wild Turkeys. Other studies of nest predation in forested environments have shown little or no increase in predation along forest edges (Storch 1991, Rudnický and Hunter 1993, Hanski et al. 1996). I suggest that this inconsistency is a function of the amount of edge per patch and landscape, rather than simply the distance from edge. Negative effects of patch-size reduction may not occur until 70 to 90% of original habitat has been lost or altered (Andrén 1994). Studies suggesting that nesting success increases with edge proximity may have been conducted in landscapes with greater original habitat, larger mean patch size, or lower road density. In studies evaluating the influence of edge on nesting success, landscape context should be considered.

In landscapes with multiple habitat types, further evaluation of the relationship of Wild Turkey nest-site selection to patch size is warranted. If high rates of nest predation have altered Wild Turkey nest-site selection behavior in Muddy Creek by requiring hens to nest away from edge habitats, then turkeys in less-fragmented landscapes may not select large patch sizes. Much of the edge habitat at Muddy Creek was created by fragmentation of contiguous forest by logging roads and logging activity. Suitability of nesting habitat at Muddy Creek may increase with expansion in size of timber cuts, thereby enlarging mean patch size and re-

ducing edge habitat in the landscape (Li et al. 1993, Niemuth and Boyce 1997).

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LITERATURE CITED

- ANDRÉN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos* 71:355–366.
- ANGELSTAM, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47:365–373.
- BADYAEV, A. V. 1995. Nesting habitat and nesting success of Eastern Wild Turkey in the Arkansas Ozark Highlands. *Condor* 97:221–232.
- BAILEY, W., D. BENNETT, JR., H. GORE, J. PACK, R. SIMPSON, AND G. WRIGHT. 1980. Basic considerations and general recommendations for trapping the Wild Turkey. *Proceedings of the National Wild Turkey Symposium* 4:10–23.
- BAKER, W. L. 1994. The r.le programs, a set of GRASS programs for the quantitative analysis of landscape structure, version 2.1. Published by author, Bozeman, Montana.
- BAKER, W. L., AND Y. CAI. 1992. The r.le programs for multiscale analysis of landscape structure using the GRASS geographical information system. *Landscape Ecology* 7:291–302.
- BERGIN, T. M. 1992. Habitat selection by the Western Kingbird in western Nebraska: A hierarchical analysis. *Condor* 94:903–911.
- BOAG, D. A., S. G. REEBS, AND M. A. SCHROEDER. 1984. Egg loss among Spruce Grouse inhabiting lodgepole pine forests. *Canadian Journal of Zoology* 62:1034–1037.
- BOWMAN, G. B., AND L. D. HARRIS. 1980. Effect of spatial heterogeneity on ground nest depredation. *Journal of Wildlife Management* 44:807–813.
- BURGER, L. D., L. W. BURGER, AND J. FAABORG. 1994. Effects of prairie fragmentation on artificial nests. *Journal of Wildlife Management* 58:249–254.
- BURK, J. D., G. A. HURST, D. R. SMITH, B. D. LEOPOLD, AND M. A. MELCHORS. 1990. Wild Turkey use of loblolly pine plantations for nesting and brood rearing. *Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies* 44:163–170.
- CRABTREE, R. L., L. S. BROOME, AND M. L. WOLFE. 1989. Effects of habitat characteristics on Gadwall nest predators and nest-site selection. *Journal of Wildlife Management* 53:129–137.
- DONOVAN, T. M., P. W. JONES, E. M. ANNAND, AND F. R. THOMPSON III. 1997. Variation in local-scale edge effects: Mechanisms and landscape context. *Ecology* 78:2064–2075.
- DURNER, G. M., AND J. E. GATES. 1993. Spatial ecology of black rat snakes on Remington Farms, Maryland. *Journal of Wildlife Management* 57:812–826.
- DZUR, R. S., M. E. GARNER, D. G. CATANZARO, K. G. SMITH, AND W. F. LIMP. 1998. Landcover of Arkansas: Gap analysis. University of Arkansas, Fayetteville.
- DZUR, R. S., M. E. GARNER, K. G. SMITH, AND W. F. LIMP. 1996. Gap analysis partnerships for mapping the vegetation of Arkansas. Pages 179–186 in *GAP analysis: A landscape approach to biodiversity planning* (J. M. Scott, T. H. Tear, and F. W. Davis, Eds.). American Society of Photogrammetry and Remote Sensing, Bethesda, Maryland.
- EVERETT, D. D., D. W. SPEAKE, AND W. K. MADDOX. 1985. Habitat use by Wild Turkeys in northwest Alabama. *Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners* 39:479–488.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–883.
- GREGG, M. A., J. A. CRAWFORD, M. S. DRUT, AND A. K. DELONG. 1994. Vegetational cover and predation of Sage Grouse nests in Oregon. *Journal of Wildlife Management* 58:162–166.
- HANSKI, I. K., T. J. FENSKE, AND G. J. NIEMI. 1996. Lack of edge effect on nesting success of breeding birds in managed forest landscapes. *Auk* 113:578–585.
- HESKE, E. J. 1995. Mammalian abundances on forest-

- farm edges versus forest interiors in southern Illinois: Is there an edge effect? *Journal of Mammalogy* 76:562–568.
- HILLESTAD, H. O., AND D. W. SPEAKE. 1970. Activities of Wild Turkey hens and poults as influenced by habitat. *Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners* 24:244–251.
- KEPPIE, D. M., AND P. W. HERZOG. 1978. Nest site characteristics and nest success of Spruce Grouse. *Journal of Wildlife Management* 42:628–632.
- KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. *Oikos* 59:253–260.
- KREITER, S. D. 1995. Dynamics and spatial pattern of a virgin old-growth hardwood-pine forest in the Ouachita Mountains, Oklahoma, from 1896 to 1994. M.S. thesis, Oklahoma State University, Stillwater.
- Proceedings of the National Wild Turkey Symposium 5:67–82.
- LI, H., J. F. FRANKLIN, F. J. SWANSON, AND T. A. SPIES. 1993. Developing alternative forest cutting patterns: A simulation approach. *Landscape Ecology* 8:63–75.
- MANLY, B. F. J., L. L. McDONALD, AND D. L. THOMAS. 1993. Resource selection by animals, statistical design and analysis for field studies. Chapman and Hall, London.
- MARTIN, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455–473 in *Ecology and conservation of Neotropical migrant land birds* (J. M. Hagan III and D. W. Johnson, Eds.). Smithsonian Institution Press, Washington, D.C.
- MARTIN, T. E. 1993. 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.
- MOORE, L. A. 1995. Factors influencing reproductive success of Wild Turkeys (*Meleagris gallopavo*) in the Ouachita Mountains of Arkansas. M.S. thesis, University of Arkansas, Fayetteville.
- NICHOLSON, D. S., M. D. STEWART, R. L. LOCHMILLER, D. M. LESLIE, JR., R. E. MASTERS, AND T. G. BIDWELL. 1995. Factors influencing Eastern Wild Turkey nesting success. Oklahoma Department of Wildlife Conservation, Performance Report, W-145-R-1, Oklahoma City.
- NIEMUTH, N. D., AND M. S. BOYCE. 1997. Edge-related nest losses in Wisconsin pine barrens. *Journal of Wildlife Management* 61:1234–1239.
- OEHLER, J. D., AND J. A. LITVAITIS. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology* 74:2070–2079.
- ORIAN, G. H., AND J. F. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29–S49.
- PALMER, W. E., S. R. PRIEST, R. S. SEISS, P. S. PHALEN, AND G. A. HURST. 1993. Reproductive effort and success in a declining Wild Turkey population. *Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies* 47:138–147.
- PATON, P. W. C. 1994. The effect of edge on avian nesting success: How strong is the evidence? *Conservation Biology* 8:17–26.
- PEDLAR, J. H., L. FAHRIG, AND H. G. MERRIAM. 1997. Raccoon habitat use at 2 spatial scales. *Journal of Wildlife Management* 61:102–112.
- PICMAN, J. 1988. Experimental study of predation on eggs of ground-nesting birds: Effects of habitat and nest distribution. *Condor* 90:124–131.
- PORTER, W. F. 1978. The ecology and behavior of the Wild Turkey (*Meleagris gallopavo*) in southeastern Minnesota. Ph.D. dissertation, University of Minnesota, Minneapolis.
- REDMOND, G. W., D. M. KEPPIE, AND P. W. HERZOG. 1982. Vegetative structure, concealment, and success at nests of two races of Spruce Grouse. *Canadian Journal of Zoology* 60:670–675.
- RENCHER, A. C. 1995. *Methods of multivariate analysis*. John Wiley and Sons, New York.
- ROBERTS, S. D., AND W. F. PORTER. 1996. Importance of demographic parameters to annual changes in Wild Turkey abundance. *Proceedings of the National Wild Turkey Symposium* 7:15–20.
- RUDNICKY, T. C., AND M. L. HUNTER, JR. 1993. Avian nest predation in clearcuts, forests, edges in a forest-dominated landscape. *Journal of Wildlife Management* 57:358–364.
- SEISS, R. S., P. S. PHALEN, AND G. A. HURST. 1990. Wild Turkey nesting habitat and success rates. *Proceedings of the National Wild Turkey Symposium* 6:18–24.
- SPEAKE, D. W., T. E. LYNCH, W. J. FLEMING, G. A. WRITE, AND W. J. HAMRICK. 1975. Habitat use and seasonal movements of Wild Turkeys in the southeast. *Proceedings of the National Wild Turkey Symposium* 3:122–130.
- STEVENS, J. 1996. *Applied multivariate statistics for the social sciences*, 3rd ed. Lawrence Erlbaum Publishers, Mahwah, New Jersey.
- STILL, H. R., JR., AND D. P. BAUMANN, JR. 1990. Wild Turkey nesting ecology on the Francis Marion National Forest. *Proceedings of the National Wild Turkey Symposium* 6:13–17.
- STORCH, I. 1991. Habitat fragmentation, nest-site selection, and nest predation in Capercaillie. *Ornis Scandinavica* 22:213–217.
- SWANSON, D. A., J. C. PACK, C. I. TAYLOR, D. E. SAM-

- UEL, AND P. W. BROWN. 1996. Selective timber harvesting and Wild Turkey reproduction in West Virginia. *Proceedings of the National Wild Turkey Symposium* 7:81-88.
- THOGMARTIN, W. E. 1998. Factors influencing the decline of an Eastern Wild Turkey (*Meleagris gallopavo silvestris*) population in the Ouachita Mountains of Arkansas. M.S. thesis, University of Arkansas, Fayetteville.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- WILLIAMS, L. E., JR., D. H. AUSTIN, N. F. EICHOLZ, T. E. PEOPLES, AND R. W. PHILLIPS. 1968. A study of nesting turkeys in southern Florida. *Proceedings of the Annual Conference of Southeastern Association of Game and Fish Commissioners* 27: 602-622.
- WILLSON, M. F., AND T. A. COMET. 1998. Bird communities of northern forests: Ecological correlates of diversity and abundance in the understory. *Condor* 98:350-362.
- UNITED STATES DEPARTMENT OF AGRICULTURE. 1993. Continuous inventory of stand condition database, version 3.1. United States Department of Agriculture Forest Service, Atlanta, Georgia.

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