NESTING ECOLOGY OF MERRIAM'S TURKEYS IN THE BLACK HILLS, SOUTH DAKOTA

MARK A. RUMBLE, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, 501 East St. Joe, Rapid City, SD 57701
ROBERT A. HODORFF, USDA Forest Service, Nebraska National Forest, 209 N. River, Hot Springs, SD 57747

Abstract: Merriam's wild turkeys *(Meleagris gallopavo merriami)* were introduced to the Black Hills approximately 40 years ago, and recent population estimates show a large and stable population. Until now, few studies have evaluated nesting ecology of Merriam's turkeys, and none occurred in predominantly pure ponderosa pine *(Pinus ponderosa)* forests. Thus, we studied nesting and nest habitat factors that influence population productivity using a hierarchical approach in the Black Hills, South Dakota. In contrast to other studies, yearling Merriam's turkey hens showed a high propensity to nest. Nest survival for adult hens did not differ ($P = 0.18$) from yearlings, but adult hen success was higher ($P = 0.03$). April- June precipitation was positively related ($R^2 = 0.93$, $P < 0.01$) to the number of nest attempts. Primary nest predators were mammals and American crows *(Corvus brachyrhynchos;* hereafter referred to as crows). Among macrohabitats (third-order habitats), there were no ($P = 0.45$) patterns of nest site selection. Among microhabitats (fourth-order habitats), hens selected small sites (<5 m across) with obstructed view of the nest and vegetation averaging 2.3 dm tall. Few microhabitat differences occurred between successful and unsuccessful nests, and those that did were related to higher ($P = 0.02$) survival of third nest attempts. Our data indicate that availability of nest habitat was not limiting turkey populations in this area.

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Merriam's wild turkeys were released in the Black Hills in 1948, 1950, and 1951, and populations expanded rapidly (Petersen and Richardson 1975). The Black Hills encompass approximately 866,000 ha with an estimated annual harvest >3,100 birds (R. Hauk, Game Rep. No. 90-18, S.D. Game, Fish, and Parks, Pierre; B. Lanka, Wyo. Game and Fish Dep., pers. commun.). This density of harvest exceeds other areas within historic Merriam's turkey distribution (Kennamer et al. 1992).

The quality of nesting habitat and net predation can affect wild turkey populations (Hillestad and Speake 1970, Speake 1980, Ransom et al. 1987). Before our study, little information existed on the nesting ecology of Merriam's turkeys in ecosystems dominated by pur ponderosa pine. No studies have been conducted on populations of Merriam's turkeys with densities as high as those occurring in the Black Hills.

Our objectives were to evaluate nesting variables that affect population productivity and to determine nest habitat selection patterns for Merriam's wild turkeys in an area of stable, high population density, outside historic range. Further, we provide managers with information regarding the effects of forest management on turkey nesting habitats. We tested hypotheses that nesting productivity did not differ between adult and yearling hens, macrohabitats selected for nests did not differ from random availability, and microhabitats selected for nests did not differ between yearling and adult hens, among nest attempts, and from random sites.

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STUDY AREA AND METHODS

We studied nesting Merriam's turkeys during 1986-91 in the central Black Hills of Pennington County, South Dakota. Elevation ranges from 1,300 to 1,800 m. The Black Hills National Forest manages most of the land. Vegetative and study area descriptions, and methods for trapping turkeys appear in Rumble (1992). We radiomarked 63 individual hens during our study, of which 11, 14, 21, 12, 21, and 17 were alive at the beginning of each nesting season in 1986-91, respectively. During nesting, hens were located ≥ 3 times/week. We recorded nest attempts based on criteria from Williams et al. (1974) and Little and Varland (1981). Nests were flagged in several locations approximatel 50 m away. We monitored incubating hens until they left the nest and recorded nest fate, number of eggs laid, and number of eggs hatched.

We estimated nest initiation dates by back-dating I.5 days from the start of incubation for each egg laid (E. Keinholz, Colo. State Univ., pers. commun.). If the inception of incubation was not accurately known from telemetry data, incubation date was back-dated 28 days from the hatch date. We estimated nest survival (Mayfield 1975) as the product of survival during 5 periods: nest initiation and 4 I-week periods of incubation. Hen success was defined as the proportion of hens alive on 21 April that hatched ≥ 1 egg irrespective of nesting attempt (Cowardin et al. 1985).

Habitat Descriptions

Macrohabitats. -We evaluated nesting habitat for Merriam's turkeys at 2 scales of resolution. Macrohabitats (third-order habitat [Johnson 1980]) were, with few exceptions, land units of 4-32 ha described by vegetation type and overstory canopy cover (Buttery an Gillam 1983, Rumble and Anderson 1992) Macrohabitat categories for vegetation type wer ponderosa pine, aspen-birch, oak, white spruce, and meadows; overstory canopy cover categories were 0-40%, 41-70%, and 71-100%.

Microhabitats. -We characterized microhabitats (fourth-order habitats [Johnson 1980]) with vegetation measurements centered at each nest. We estimated percent slope with a clinometer and recorded aspect as the downhill compass bearing at the nest. Nest overstory cover (%) was estimated with a spherical densiometer (Griffing 1985) from the nest bowl. We estimated percent overstory canopy cover, tree basal area (BA), average diameter at breast height (dbh), and density of trees from 3 plots at the nest and 30 m away from the nest along the contour in 2 directions. We used a spherical densiometer to estimate percent overstory canopy cover and a 10-factor prism (Sharpe et al. 1976) to determine trees included in measurements of BA, average dbh, and density of trees at each point. Data for overstory canopy cover, BA, dbh, and tree density were averaged across plots (n = 3) for each nest. Presence or absence of a guard object (e.g., log, rock, or tree protecting the nest frorn 1 direction) also was recorded at each nest.

We estimated percent canopy cover of herbaceous and shrub vegetation from 8 0.1-m^2 quadrats (Daubenmire 1959) along each of 8 transects radiating from the nest at 45° intervals. Percent canopy cover was estimated at 0.5-m intervals along these transects. After completing preliminary analyses, we reduced the number of transects to 4, at 90° intervals in 1989. Horizontal cover surrounding nests was estimated as the height of visual obstruction (VOR) of a pole viewed from 4 m away and 1 m from the ground (Robel et al. 1970). VOR's were read at the nest and at l-m intervals out to 5 m, and 5-m intervals out to 30 m along 2 transects extending from the nest on the contour. Based on preliminary analyses, we modified this procedure in 1989 and VOR's were read along 4 transects radiating from the nest at 90° intervals at l-m intervals to 5 m.

We expanded microhabitat data in 1989 to include silvicultural prescription, time since cut, stand structure, and fuels. Silvicultural prescriptions included no cut (no evidence of past timber harvest), clearcut, commercial thin (harvest of some or most mature trees), shelterwood seed cut (≤ 9 m^2/ha BA mature seed producing trees remaining), and precommercial thinning (small dbh trees cut). Categories for time since cut included <2 years, 2-5 years, and >5 years. We considered forest stands with 2 or more layers in the canopy to be multistory stands. We used pictorial guides to estimate small (2.5-7.6 cm) and large (>7.6 cm) diameter wood residue (fuels) (Photo series for quantifying forest residues in the Black Hills, AMF 831, USDA For. Serv., Rocky Mt. Reg., Denver, Colo., 1982 unpubl. document).

We sampled random microhabitats (n = 570) at approximately 10 sites/year from each macrohabitat category (ponderosa pine macrohabitats were further stratified by dbh [Buttery and Gillam 19831]). Data collection procedures at random sites were similar to procedures at nests. Nest cover and presence of guard objects were not applicable at random sites. VOR at random sites was estimated at 5-m intervals along a 60-m transect and discontinued in 1989. Percent canopy cover of herbaceous and shrub vegetation was estimated from 30 0. 1-m^2 quadrats (Daubenmire 1959) along a 60-m transect.

Statistical Analyses

Nest Survival.-We used Chi-square tests for independence to evaluate hypotheses that nest survival and hen success were similar between age categories of hens, and nest survival was similar among nest attempts; we used analysis of many proportions (Fleiss 1981) to determine nest attempts that differed. We used analysis of variance to test the hypotheses of no differences in clutch size and hatch rates between adult and yearling hens, among nest attempts, and among years. We used a Monte Carlo estimated Chi-square contingency table program, STATXACT, (Mehra and Pate1 1991) to test the hypothesis that causes of nest mortality were similar among years. This test eliminates the influence of low cell counts on the Chi-square statistic (Agresti et al. 1990). We evaluated standardized Chi-square residuals to determine significant differences among categories of nest mortality (Mosteller and Parunak 1985). Because of the large number of cells (30), we did not apply the Bonferroni correction to the critical α recommended by Mosteller and Parunak (1985), and standardized Chi-square residuals were evaluated at α = 0.10. We used analysis of many proportions to determine differences among averaged annual causes of nest mortality.

Macrohabitats.-We used Chi-square goodness-of-fit corrected for continuity (Cochran 1963:57) to test that nest selection among macrohabitats by Merriam's turkeys was similar to random expected use. Bonferroni confidence intervals were used to determine macrohabitats selected for turkey nests that differed from availability (Neu et al. 1974, Byers et al. 1984).

Microhabitats.-We weighted random data by relative area of macrohabitats to accommodate deviations from proportional sampling. We used t-tests derived from individual group variances to test hypotheses that vegetative characteristics at nests did not differ from random sites and successful nests did not differ from unsuccessful nests. A multi-response permutation procedure (Mielke 1984) was used to test hypotheses that vegetation characteristics at nests did not differ among nest attempts. We used Box-and-Whisker plots to display habitat components occurring at ≥ 20 nests. The hypotheses that VOR surrounding nests (<5 m from nest) did not differ between successful and unsuccessful nests, or among nest attempts was analyzed by Brown-Forsythe 2-way analysis of variance with distance from nest as a factor. We evaluated the asymptotic relationship of VOR with distance from the nest using nonlinear regression. We used t-tests derived from individual group variances to test the hypothesis that average VOR <5 m from nests did not differ from random sites. With Chi-square tests for

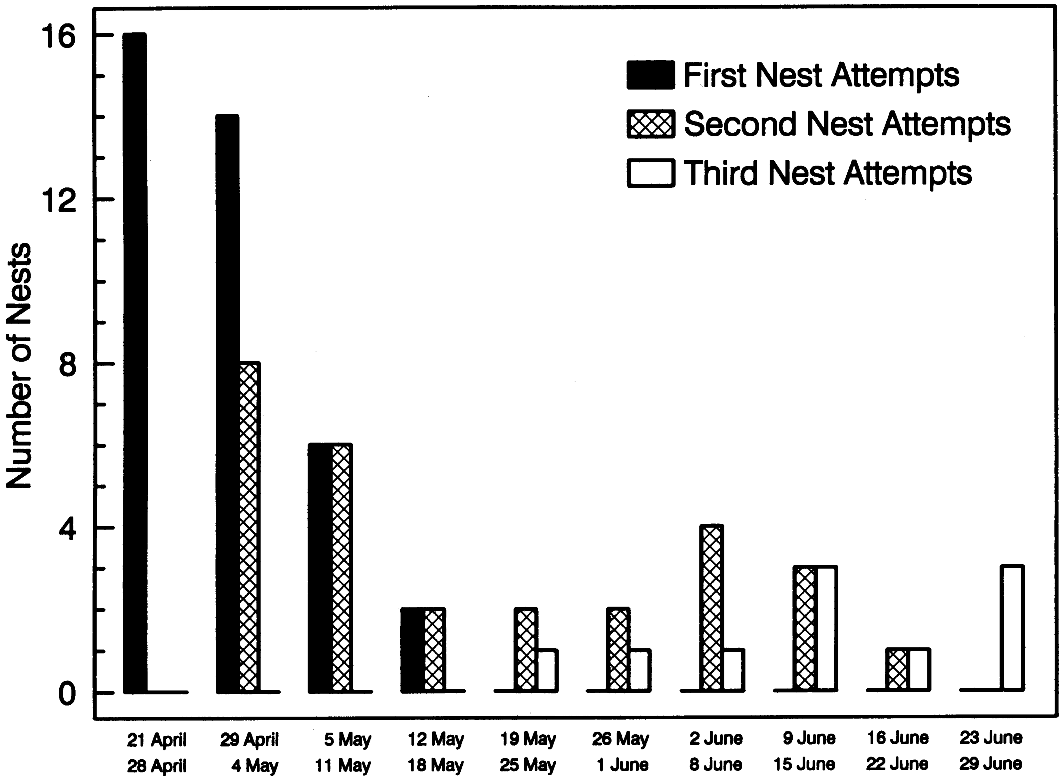

Fig. 1. Number of first, second and third nest attempts by Merriam's wild turkeys during weekly intervals beginning 21 April and ending 29 June in the Black Hills, South Dakota, 1986–91.

independence, we tested hypotheses that aspect, prescription, time since cut, and stand structure were similar between successful versus unsuccessful nests, and among nest attempts. Significant Chi-square tests were evaluated for differences among categories using analysis of many proportions. We evaluated hypotheses that categorical variables at nest sites were similar to random sites with Chi-square goodness-of-fit tests and Bonferroni confidence intervals.

Terminology in this paper regarding "habitat use," "habitat selection," and "habitat preference" follows Johnson (1980) and Thomas and Taylor (1990). Tests of hypotheses regarding nest locations for aspect, time since cut, and stand structure considered all possible responses and significant deviations from random inferred preference or avoidance.

We determined statistical significance at $\alpha \leq 0.10$. We selected this α level because it provides a high degree of confidence in our reported results; yet, it provides a high degree of protection against Type II error. When managing and/or protecting species and their habitats, Type II errors would result in no management when management could be applied.

RESULTS

Nesting and Success

The number of radio-marked adult and yearling (in parentheses) hens alive on 21 April each year of the study were 8 (3), 7 (7), 13 (8), 11 (1), 16 (5), and 12 (5) for 1986–91, respectively. The nesting season began 21 April and all first nest attempts occurred within a 3-week period ending 18 May (Fig. 1). Hens began second nest attempts approximately 1 week later. The latest nests (all third nest attempts) were initiated during the week of 23–29 June; the latest nest was initiated on 28 June. Nests began hatching 1 June and the last nest hatched on 14 August.

A high proportion of yearling hens (73%) in our study attempted nests; 97% of adult hens attempted nests. Nest survival for adults (0.36) and yearling hens (0.23) did not differ ($P = 0.18$) (Table 1). Hen success was higher ($P = 0.03$) for adults (0.48) than yearlings (0.24). Com-

Table 1. Nest survival, hen success, and egg hatching rates for Merriam's wild turkeys in the Black Hills, South Dakota, 1986–91.

Year	Age	No. of nests	Nest[a] survival	Hen[b] success	Hatching[c] rate (%)
1986	Yearling	4	0.25	0.33	
	Ad	14	0.36	0.63	
	Combined	18	0.34	0.55	88A[d]
1987	Yearling	8	0.51	0.57	
	Ad	10	0.30	0.43	
	Combined	18	0.39	0.50	93A
1988	Yearling	11	0.09	0.13	
	Ad	16	0.56	0.62	
	Combined	27	0.37	0.43	83A
1989	Yearling	1	0.0	0.0	
	Ad	11	0.64	0.64	
	Combined	12	0.59	0.58	80A
1990	Yearling	4	0.25	0.20	
	Ad	17	0.18	0.19	
	Combined	21	0.19	0.19	83A
1991	Yearling	3	0.0	0.0	
	Ad	22	0.23	0.33	
	Combined	25	0.20	0.24	89A
All yearling		31	0.23A	0.24A	
All ad		90	0.36A	0.48B	
All hens[e]		121	0.32	0.41	86

[a] Estimated SE = SQRT[$(p \cdot 1 - p)/n - 1$] + $1/2n$ (Cochran 1963).
[b] Hen success is the probability of a hen alive on 21 April hatching ≥1 egg.
[c] Hatch rates calculated only from nests in which ≥1 egg hatched.
[d] Averages followed by different letters vertically differ ($P \leq 0.10$) in analysis of many proportions (Fleiss 1981) for nest survival and hen success, and analysis of variance for hatching rate.
[e] All data pooled.

bined hen success for our study was 0.41. Nest survival varied among years for adults and yearlings and showed a nonsignificant ($P = 0.32$) decline in 1990 and 1991. Survival of third nest attempts (0.67, $n = 12$) was higher ($P = 0.02$) than first nest attempts (0.27, $n = 72$); survival of second nest attempts (0.35, $n = 29$) did not differ from first or third attempts. Adult hens renested more (1.18/bird) than yearling hens (0.57/bird). Average annual nest attempts per bird were positively related to April–June precipitation (adjusted $R^2 = 0.93$, $P < 0.01$) (Fig. 2).

Causes of nest mortality differed ($P < 0.01$) (Table 2). Avian nest predators (crows) accounted for the highest ($P \leq 0.10$) nest mortality. Nest predation by crows was higher ($P \leq 0.07$) in 1990–91 and lower ($P \leq 0.05$) in 1987–88 than 1986 or 1989. Average mammalian-caused nest mortality did not differ from avian-, abandonment-, and weather-caused nest mortality. Predation by mammals of nests was greater ($P = 0.05$) in 1987 than other years. Disturbance

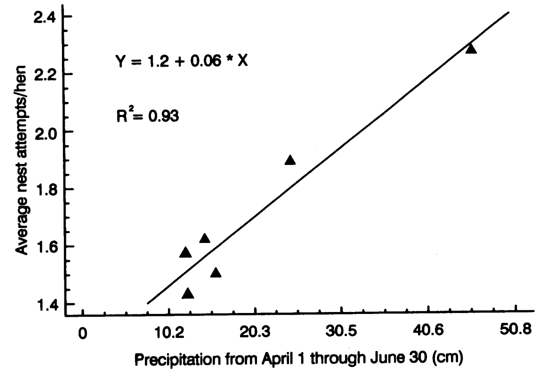

Fig. 2. Regression of precipitation during nesting season on average nest attempts per hen in the Black Hills, South Dakota, 1986–91.

was the lowest ($P \leq 0.10$) average annual cause of nest mortality and differed from avian and mammalian losses. Average weather related nest mortality differed only from avian causes. However, nest mortality from late spring snowstorms was greater ($P < 0.01$) in 1988 and lower ($P = 0.07$) in 1991 than other years.

Clutch size for turkey nests averaged 9.2 ± 0.3 ($\bar{x} \pm$ SE, $n = 38$) eggs. Clutch size did not differ ($P = 0.90$) between adults and yearlings nor among nest attempts ($P = 0.80$). The smallest clutch contained 7 eggs and the largest, 13. One nest contained 17 eggs, but appeared to be 2 separate attempts, 1 of which hatched. The mode of clutch size was 8 occurring in 45% of nests. Hatch rates (86 ± 2.6%) did not differ between adults and yearlings ($P = 0.84$), among nest attempts ($P = 0.66$), or years ($P = 0.77$).

Table 2. Causes of nest mortality for Merriam's wild turkeys in the Black Hills, South Dakota, 1986–91.[a]

Year	n	Cause of nest mortality (%) Abandoned	Mammals[b]	Disturbed	Avian	Weather
1986	12	33	42	8	17	0
1987	11	27	55+	18	0−	0
1988	17	18	6	0	6−	71+
1989	5	0	40	20	40	0
1990	17	12	18	0	65+	6
1991	20	5	20	10	65+	0−
Annual average[c]		16AB	26BC	7A	35C	16AB

[a] Signs following percentages indicate direction of difference for cells with standardized residuals that differ ($P \leq 0.10$); Chi-square test.
[b] Between 1986–91, 8, 9, 6, 20, 12, and 0%, respectively, of mammalian caused nest mortality was attributed to predation of the hen.
[c] Row averages followed by different letters differ ($P \leq 0.10$); analysis of many proportions (Fleiss 1981).

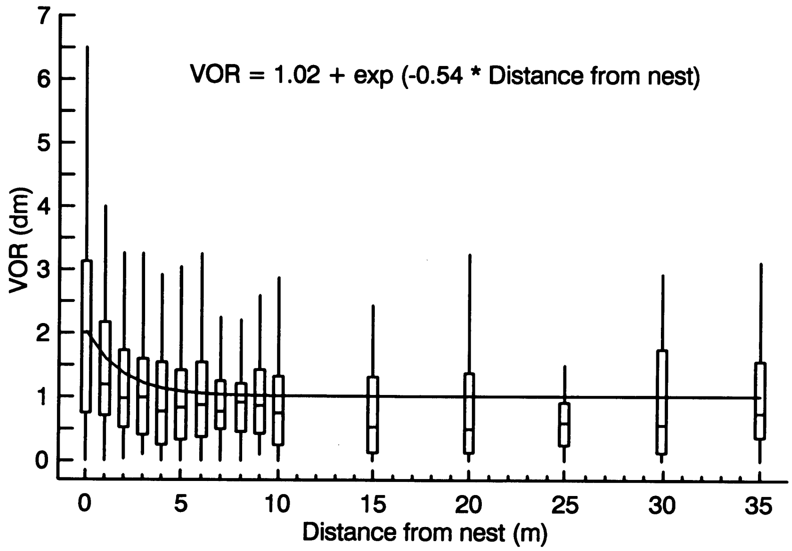

Fig. 3. Box-and-Whisker plots of horizontal cover (VOR) at Merriam's wild turkey nests in the Black Hills, South Dakota, 1986–91. The central line is the median, the box includes the 2 inner quartiles, the whiskers include the 2 outer quartiles. Nonlinear regression line on the means at each distance from the nest demonstrates the rapid decline in VOR within 5 m of nests.

Nest Habitat

Macrohabitats.—Our hypothesis that macrohabitats selected for nesting by Merriam's turkey hens were similar to random expected use was not rejected. The random use model adequately fit the data ($P = 0.45$).

Microhabitats.—VOR at nests was highly variable. Some nests were easily visible, but most had good horizontal cover with VOR's at most nests exceeding 2 dm (Fig. 3). Average VOR declined from about 2.3 dm at the nest to an asymptote of 1.0 dm, 5 m from the nest and could be described by VOR = 1.02 + EXP(0.54 • DIST); adjusted $R^2 = 0.93$.

Shrubs were the predominant vegetative component surrounding nests (Fig. 4). Rocks (>15 cm across) and/or logs (>2.5 cm diam) provided nest cover if displayed in the upper quartile or as outliers. Grasses and forbs provided little nest cover unless displayed as outliers. Kinnikinnick (*Arctostaphylos uva-ursi*) was common beneath the ponderosa pine canopy, but provided little protection for nests. Common juniper (*Juniperus communis*) provided suitable nest cover. Western snowberry (*Symphoricarpos occidentalis*), chokecherry (*Prunus* spp.), and Wood's rose (*Rosa woodsii*) rarely provided nest cover individually, but often cooccurred at nests and provided cover.

Successful Versus Unsuccessful Nests.—Few differences in microhabitat characteristics occurred between successful and unsuccessful nests. Overstory canopy cover was lower ($P = 0.05$) at successful nests (Table 3). Aspect differed ($P = 0.02$) between successful and unsuccessful nests; westerly aspects were selected more for successful nests.

Nest Attempts.—Slope differed among nest attempts ($P = 0.03$); first and second nest attempts occurred on steeper slopes ($P \leq 0.04$) than third nest attempts (Table 3). With effects of distance from nest removed (see above), VOR at third nest attempts was greater ($P < 0.01$) than first and second nest attempts. Common juniper tended to be selected most for first nests, but was not selected for third nest attempts; however these averages did not differ significantly. Canopy cover of snowberry was greater ($P < 0.01$) for third nest attempts than first and second nest attempts. Nest cover provided by logs was greater ($P < 0.01$) at second nest attempts than first attempts; log cover surrounding third nest attempts did not differ from first or second nest attempts. Percent cover of total vegetation ($P < 0.01$), total forbs ($P < 0.01$), total grasses ($P < 0.08$), and total shrubs ($P < 0.01$) was greater surrounding third nest attempts than first or second nest attempts. Canopy cover of these variables at first and second

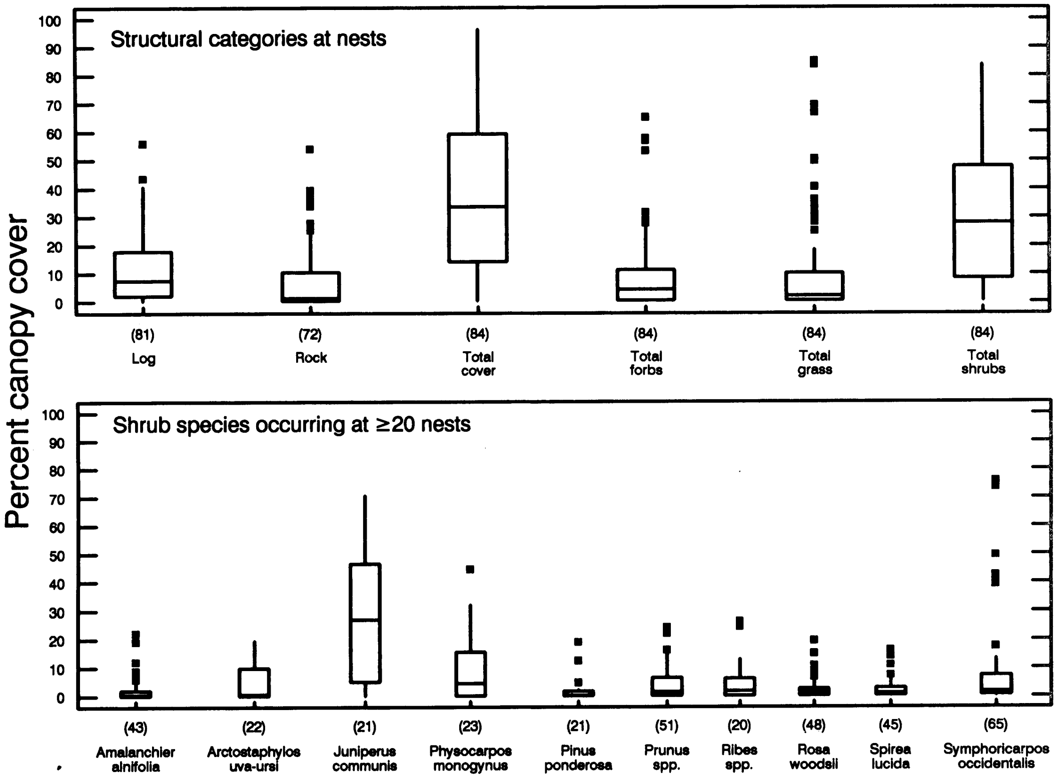

Fig. 4. Box-and-Whisker plots of microhabitat characteristics within 1.5 m of nests of Merriam's turkeys in the Black Hills, South Dakota, 1986–91. The central line is the median, the box includes the 2 inner quartiles, the whiskers include the 2 outer quartiles, and data more than 1.5 times the interquartile range are displayed as points. Number of nests at which each habitat component occurred is in parentheses.

nest attempts did not differ. Total BA at second and third nest attempts did not differ, but was lower ($P < 0.02$) than first nest attempts.

Nest sites versus random.—Habitat characteristics that differed between nest and random sites usually were more abundant at nests than random sites. Small diameter fuels ($P = 0.02$); large diameter fuels ($P < 0.01$); percent overstory canopy cover ($P = 0.04$); percent slope ($P < 0.01$); percent cover of juniper ($P < 0.01$), log ($P < 0.01$), western snowberry ($P = 0.05$), and shrubs ($P < 0.01$) were greater ($P \leq 0.10$) surrounding nests than random sites. Stands logged within 2 years were selected more than occurred at random ($P < 0.01$). Grass cover was greater ($P = 0.03$) at random sites than nest sites.

DISCUSSION

Nesting Chronology and Survival

Most populations of Merriam's turkeys initiate nests in late April (Lutz and Crawford 1987, Hoffman 1990, this study), but occasionally initiate nests 2–3 weeks earlier (Jonas 1968, Day et al. 1991*a*). Nesting chronology of Merriam's turkeys does not appear to be delayed at northern latitudes like it is in other subspecies of wild turkeys (Vangilder et al. 1987). Variability in altitude, spring migration distances, and interactions of regional weather patterns may obscure nesting chronology gradients related to latitude. Spring snowstorms caused some hens in our study to abandon nests, but did not influence nest initiation dates.

Nesting rates by yearling Merriam's turkeys are low (8–31%) (Schemnitz et al. 1985, Lockwood and Sutcliffe 1985, Lutz and Crawford 1987), and sometimes no yearlings attempt nests (Wertz and Flake 1988, Wakeling 1991). Yearling nesting rates in our study (73%) were higher than previously reported. Reduced propensity for yearling hens to nest (Lutz and Crawford 1987:784) is not confined to the Merriam's subspecies and also occurs in eastern wild turkeys

Table 3. Habitat characteristics at Merriam's wild turkey nests and random sites in the Black Hills, South Dakota, 1986–91.

Habitat variable (units of measure)[a,b]	Nest sites[c]												Random sites	
	Successful		Unsuccessful		First attempt		Second attempt		Third attempt		Total			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Nest overstory cover (%)	77.7	3.2	78.3	2.3	78.3	2.7	78.5	2.9	74.8	6.0	78.0	2.9		
Overstory canopy cover (%)	47.4	2.8A	55.3	2.8B	55.1	2.9	47.3	2.7	44.3	4.0	51.6	2.0A	46.9	0.9B
Fuels 2.5–7.6 cm (tons/ha)	4.9	1.3	6.3	0.9	6.4	1.2	5.7	1.0	4.3	1.5	5.8	0.7A	4.0	0.3B
Fuels >7.6 cm (tons/ha)	10.7	2.3	13.5	1.7	11.8	1.9	14.7	2.4	9.7	3.1	12.5	1.4A	7.6	0.3B
Slope (%)	37.5	3.5	38.7	3.0	40.4	2.9A	39.5	3.8A	21.2	7.3B	38.1	2.3A	26.3	0.7B
VOR (dm, ≤5 m from nest)	1.6	0.2	1.4	0.2	1.4	0.1A	1.4	0.1A	2.4	0.3B	1.5	0.1A	0.4	<0.1B
Multistory stand (% nests)[d]	56.3		55.9		50.0		57.9		71.4		56.0		50.6	
Guard object at nest (% nests)[d]	64.4		59.0		62.1		69.2		37.5		61.9			
Aspect (% nests)														
North (316–45°)	13.9		35.0		23.3		24.0		37.5		25.0		20.3	
East (46–135°)	33.3		45.0		39.5		40.0		37.5		39.5		36.0	
South (136–225°)	22.2		10.0		18.6		12.0		12.5		15.8		15.8	
West (226–315°)	30.6A		10.0B		18.6		24.0		12.5		19.7		19.7	
Silvicultural prescription (% nests)														
Commercial thin	18.8		23.5		45.5		45.5		14.3		22.0		17.7	
Seed tree cut	6.3		5.9		0.0		10.5		14.3		6.0		2.2	
Precommercial thin	31.3		35.3		41.7		31.6		14.3		34.0		34.8	
Clear cut	0.0		0.0		0.0		0.0		0.0		0.0		1.7	
Not cut	43.8		35.3		37.5		31.6		57.1		38.0		43.6	
Estimated time since harvested (% nests)[e]														
<2 years	37.5		14.7		16.7		31.6		14.3		22.0A		5.1B	
2–5 years	0.0		11.8		12.5		5.3		0.0		8.0		10.3	
>5 years	18.8		38.2		33.3		31.6		28.6		32.0		41.1	

Table 3. Continued.

Habitat variable (units of measure)[a,b]	Nest sites[c]												Random sites	
	Successful		Unsuccessful		First attempt		Second attempt		Third attempt		Total			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Canopy cover of understory (%)														
Common juniper	4.3	1.8	4.9	1.8	6.7	2.0	2.1	1.2	0.0		4.6	1.3A	0.4	0.1B
Western snowberry	8.6	2.9	3.8	1.2	3.7	1.3A	4.6	2.2A	25.8	9.2B	6.1	1.5A	3.1	0.2B
Logs	8.7	1.6	11.3	1.7	8.0	1.1A	14.7	2.8B	8.3	2.5A,B	10.1	1.2A	4.0	0.2B
Rock (≥10 cm)	7.1	1.8	6.1	1.5	6.5	1.7	7.1	2.0	4.8	2.3	6.5	1.2	5.5	0.3
Total live vegetation	35.8	4.5	39.8	4.1	35.4	3.4A	30.4	5.3A	78.2	7.5B	38.0	3.0	33.7	1.0
Total forbs	9.0	2.0	11.4	2.2	7.3	1.0A	8.8	2.7A	33.1	8.8B	10.3	1.5	9.3	0.4
Total grasses	10.9	3.0	12.1	2.7	7.7	1.5A	11.9	4.1A	34.1	11.2B	11.5	2.0A	16.5	0.9B
Total shrubs	26.8	3.5	27.4	3.1	25.0	2.5A	21.6	4.1A	58.4	5.5B	27.1	2.2A	13.0	0.5B
BA ponderosa pine (m^2/ha)	17.9	1.3	20.8	1.4	21.2	1.3A	17.4	1.7A,B	15.2	1.5B	19.4	1.0	20.7	0.5
Total BA (m^2/ha)	19.7	1.3	22.9	1.4	23.9	1.3A	18.4	1.6B	16.0	1.6B	21.4	1.0	21.9	0.4
Tree density (trees/ha)	1,116	160	1,418	194	1,447	188	1,163	179	575	140	1,277	128	1,293	62

[a] Means followed by different letters within analysis group differ ($P \leq 0.10$); t-test for nest success and nests versus random, and multi-response permutation procedure for nest attempt. Chi-square tests were used for multistory guard object, aspect, silvicultural prescription, and estimated time since harvest tests.

[b] Conversions from metric to English units are BA (m^2/ha) = 0.2291•ft^2/acre; and fuels (metric tons/ha) = 2.24•tons/acre.

[c] $n = 39$ for successful nests, $n = 45$ for unsuccessful nests; $n = 50$ for first attempts, $n = 26$ for second attempts, and $n = 8$ for third attempts; and $n = 570$ for random sites. Sample sizes for Fuels 2.5–7.6 cm, Fuels >7.6 cm, Multistory, Prescription, and Time since harvest were 34 and 16 for unsuccessful and successful nests; 24, 19, and 7 for first, second, and third nest attempts. See methods for explanation.

[d] Data for positive response to this variable reported.

[e] No evidence of cutting at the site is included in this category; values were the same as 'No cut' under silvicultural prescription.

(M. g. silvestris) (Hillestad 1973, Still and Baumann 1990).

Nesting rates for adults in our study also were higher than reported for Merriam's turkeys (Schemnitz et al. 1985, Lockwood and Sutcliffe 1985, Lutz and Crawford 1987, Wertz and Flake 1988, Wakeling 1991). Consequently, we found a positive correlation ($r = 0.75$, $n = 6$, $P \leq 0.05$) between adult and yearling nesting rates from our and those studies. We believe this relationship between adult and yearling nesting is related to habitat quality. Low adult and yearling nesting was postulated by Wertz and Flake (1988) to be a density-dependent interaction with habitat.

Fertility and hatching rates of eggs for all subspecies of wild turkeys eggs are generally high ($\pm 90\%$) and similar for yearling and adult hens (Everett et al. 1980, Ransom et al. 1987, Hengel 1990). Clutch sizes of wild turkeys are variable, but they average 9-11 eggs and are generally similar for adults and yearlings (Vangilder et al. 1987, Lutz and Crawford 1987, Schmutz and Braun 1989). Clutch size may decline (Vangilder et al. 1987, Schmutz and Braun 1989) or increase (Lockwood and Sutcliffe 1985) in renests. Clutch size in our study showed a slight, but nonsignificant, increase in renests. Average clutch size in our study was almost 2 eggs/nest less than reported by Petersen and Richardson (1975) for the Black Hills. We do not know the cause for these differences in clutch size.

Nest survival rates of 0.3-0.4 are typical for adult Merriam's turkeys (Lockwood and Sutcliffe 1985, Schemnitz et al. 1985) and comparable to our study. Renests in this study had higher survival than first nests. In contrast, renests had lower survival in Colorado (Schmutz and Braun 1989) and South Carolina (Still and Baumann 1990) than first nests. Although yearling hens in the Black Hills had high nesting rates, adults renested more frequently and had higher hen success than yearlings.

During drought periods (1988-90), renesting was uncommon after incubation began; 83% of third nest attempts occurred during years of above average April-June precipitation. Our results suggest that spring precipitation, or some correlate thereof, may act as a proximate cue for renesting by hens in the Black Hills. Schmutz and Braun (1989) thought that spring vegetative growth, or some correlate thereof, controlled nesting of turkeys in Colorado. Vangilder et al. (1987) and Hoffman (1990) thought that nesting in turkeys was regulated by photoperiod. The mechanisms controlling renesting by turkeys remain unknown.

Mammals are the primary predators of turkey nests (Schemnitz et al. 1985, Ransom et al. 1987, Wertz and Flake 1988), but crows accounted for the greatest nest mortality in our study. Years of high nest predation by crows also had the lowest nest survival rates. Predation by crows resulted in complete loss of all first nest attempts in 1991. Crow populations on our study area appeared to be more abundant during 1990-91, but data are lacking. Crows and magpies *(Pica pica)* were responsible for 30% of predation on Merriam's turkey nests in southeastern Montana during the same period (W. Thompson, Mont. State Univ., pers. commun.).

Nest Habitats

Macrohabitats.-Lutz and Crawford (1987), Still and Baumann (1990), and Sisson et al. (1990) reported significant patterns of macrohabitat selection for turkey nests. We did not find differences from random selection of macrohabitats, suggesting that potential nest sites occurred in all macrohabitats as described in this study.

Microhabitats.-Wild turkeys occur over most of the United States, and structural descriptions of microhabitats surrounding nests tend to be similar across subspecies and regions. Live vegetation, often shrubs, compose nest cover (Lazarus and Porter 1985, Schmutz et al. 1989, Day et al. 1991*a*). Logging slash provided better nest cover for some populations of Merriam's turkeys (Schemnitz et al. 1985, Lutz and Crawford 1987) and may reflect a lack of available shrubs. Logs occurred within I.5 m of most nests in our study, but provided significant nest cover (>20% canopy cover) at approximately 25% of nests. Logging slash selected as nest cover was usually scattered (not piled) with needles still attached. The preference for nesting in areas logged <2 years previously reflected nests for which logging slash composed the majority of the nest cover.

Merriam's turkeys frequently select nest sites on steep slopes (Petersen and Richardson 1975, Schemnitz et al. 1985, this study). Aspect appears to influence the location of nests (Petersen and Richardson 1975, Lockwood and Sutcliffe 1985). In our study, a greater proportion of cessful nests were located on westerly aspects, but we failed to find any preference relative to aspect for nest sites overall.

Potential brood rearing habitats occurred within 0.8 km of all nests in our study. However, hens often move broods up to 3.5 km to brood rearing areas within a few days after hatching (Day et al. 1991b, Rumble and Anderson 1993), suggesting that proximity to brood habitat is not important in nest site selection.

Because third nest attempts were more successful than earlier attempts, microhabitat relationships associated with successful nests were not independent of nest attempt. Higher western snowberry cover at successful nests also occurred at third nest attempts. Lower overstory canopy cover at successful nests reflected the shift to vegetation for nest cover on third attempts and the inverse relationship between shrubs and overstory cover (and BA) (Uresk and Severson 1989).

Wild turkeys typically take advantage of availability of more preferable habitats for renests (Williams et al. 1969, Lazarus and Porter 1985, Schmutz et al. 1989). Hens selected woodland sites for early nest attempts in central South Dakota, but selected grassland sites for later nest attempts because of increased cover (Day et al. 1991a). Deciduous shrubs were not leafed out during initiation of first nests in late April. By mid-May these shrubs provided good cover for renests. Cool season grasses had also reached peak standing crop before third nests were initiated after mid-June. The shift, on third nest attempts, toward nest sites with live shrub cover also resulted in increased VOR at third nests.

Deviations from random among the variables we examined also reflected the small area (<5 m across) with obstructed view. To assess the availability of nest sites on our study area, we conducted discriminant function analysis between nests and random sites for variables with numerical responses. Unbiased reclassification estimates (Jackknife approach [Lachenbruch and Mickey 1968]) classified 12% of random sites as potential nest sites. None of the random sites measured included a known nest site. To our knowledge, no nest site was used more than once, although hens sometimes nested within 50 m of an earlier nest. Despite sampling along a 60-m transect, several random sites had microhabitat characteristics similar to sites selected by hens for nests. Given the capability of turkeys to select small sites, we believe 12% represents a conservative estimate of nest site availability in this portion of the Black Hills.

MANAGEMENT AND RESEARCH IMPLICATIONS

Although Merriam's wild turkeys are generally not as productive as other subspecies of turkeys, those in the Black Hills are more productive than elsewhere within their current range. Nesting by yearling hens is a significant contribution to productivity and mechanisms for its variation need further investigation. Despite sharp declines in nesting success caused by crows, predation does not appear to limit turkey populations in this area because of renesting and yearling nesting. The probable interaction between nesting rates, habitat quality, and population density warrants further investigation.

Nest site availability does not appear to limit Merriam's turkey populations in this area and cannot be modelled at the macrohabitat scale of resolution. In the Black Hills, specific management to enhance nest site availability is not necessary. Similarly, nest site availability would not likely limit wild turkey populations in mesic habitats with abundant forested areas containing patchy rock and shrub components. However, in xeric habitats, with limited understory productivity, managers should monitor abundance, distribution, and dispersion of microhabitats structurally similar to the small areas described in this study.

LITERATURE CITED

AGRESTI, A., C. R. MEHRA, AND N. R. PATEL. 1990. Exact inference of contingency tables with ordered categories. J. Am. Stat. Assoc. 85:453-458.

AMERICAN ORNITHOLOGISTS' UNION. 1988. Report of committee on the use of wild birds in research. Auk 105 (Suppl.):1A-41A.

BUTTERY, R. F., AND B. C. GILLAM. 1983. Forest ecosystems. Pages 34-71 in R. L. Hoover and D. L. Wills, eds. Managing forested lands for wildlife. Colo. Div. Wildl. in cooperation with USDA For. Serv., Rocky Mt. Reg., Denver. 459pp.

BYERS, C. R., R. K. STEINHORST, AND P. R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48: 1050-1053.

COCHRAN, W. G. 1963. Sampling techniques. John Wiley and Sons, Inc., New York, N.Y. 413pp.

COWARDIN, L. M., D. S. GILMER, AND C. W. SCHAIFFER. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildl. Monogr. No. 92.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:44–64.

DAY, K. S., L. D. FLAKE, AND W. L. TUCKER. 1991*a*. 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.

———, ———, AND ———. 1991*b*. Movements and habitat use by wild turkey hens with broods in a grassland-woodland mosaic in the northern plains. Prairie Nat. 23:73–83.

EVERETT, D. D., D. W. SPEAKE, AND W. K. MADDOX. 1980. Natality and mortality of a North Alabama wild turkey population. Proc. Natl. Wild Turkey Symp. 4:117–126.

FLEISS, J. L. 1981. Statistical methods for rates and proportions. John Wiley and Sons, New York, N.Y. 223 pp.

GRIFFING, J. P. 1985. The spherical densiometer revisited. Southwest habitater. Vol. 6, No. 2. USDA For. Serv., Reg. 3. Albuquerque, N.M. 2pp.

HENGEL, D. A. 1990. Habitat use, diet, and reproduction of Merriam's turkeys near Laramie Peak, Wyoming. M.S. Thesis, Univ. Wyoming, Laramie. 220 pp.

HILLESTAD, H. O. 1973. Movements, behavior, and nesting ecology of the wild turkey in eastern Alabama. Pages 109–123 *in* G. C. Sanderson and H. C. Schultz, eds. Wild turkey management: current problems and programs. Missouri Chap. Wildl. Soc. and Univ. Missouri Press, Columbia. 355pp.

———, AND D. W. SPEAKE. 1970. Activities of wild turkey hens and poults as influenced by habitat. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 24:244–251.

HOFFMAN, R. W. 1990. Chronology of gobbling and nesting activities of Merriam's wild turkeys. Proc. Natl. Wild Turkey Symp. 6:25–31.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

JONAS, R. J. 1968. Adverse weather affects Merriam's turkey reproduction in Montana. J. Wildl. Manage. 32:987–989.

KENNAMER, M. C., R. BRENNEMAN, AND J. E. KENNAMER. 1992. Guide to the American wild turkey. Natl. Wild Turkey Fed. Edgefield, S.C. 158pp.

LACHENBRUCH, P. A., AND M. R. MICKEY. 1968. Estimation of error rates in discriminant analysis. Technometrics 10:1–11.

LAZARUS, J. E., AND W. F. PORTER. 1985. Nest habitat selection by wild turkeys in Minnesota. Proc. Natl. Wild Turkey Symp. 5:67–81.

LITTLE, T. W., AND K. L. VARLAND. 1981. Reproduction and dispersal of transplanted wild turkeys in Iowa. J. Wildl. Manage. 45:419–427.

LOCKWOOD, D. R., AND D. H. SUTCLIFFE. 1985. Distribution, mortality, and reproduction of Merriam's turkey in New Mexico. Proc. Natl. Wild Turkey Symp. 5:309–316.

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

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

MEHRA, C., AND N. PATEL. 1991. StatXact: statistical software for exact nonparametric inference. Cytel Corp. Cambridge, Mass. 423pp.

MIELKE, P. W., JR. 1984. Meteorological applications of permutation techniques based on distance functions. Handbook of Stat. 4:813–830.

MOSTELLER, F., AND A. PARUNAK. 1985. Identifying extreme cells in a sizeable contingency table: probabilistic and exploratory approaches. Pages 189–224 *in* D. C. Hoaglin, F. Mosteller, and J. W. Tukey, eds. Exploring data tables, trends, and shapes. John Wiley and Sons, Inc., New York, N.Y. 527pp.

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.

PETERSEN, L. E., AND A. H. RICHARDSON. 1975. The wild turkey in the Black Hills. Tech. Bull. No. 6. S.D. Game, Fish and Parks, Pierre. 51pp.

RANSOM, D., JR., O. J. RONGSTAD, AND D. H. RUSCH. 1987. Nesting ecology of Rio Grande turkeys. J. Wildl. Manage. 51:435–439.

ROBEL, R. J., J. N. BRIGGS, A. D. DAYTON, AND L. C. HULBERT. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. J. Range Manage. 23:295–297.

RUMBLE, M. A. 1992. Roosting habitat of Merriam's turkeys in the Black Hills, South Dakota. J. Wildl. Manage. 56:750–759.

——, AND S. H. ANDERSON. 1992. Stratification of habitats for identifying habitat selection by Merriam's turkeys. Great Basin Nat. 52:1–6.

———, AND ———. 1993. Third-order habitat selection by Merriam's turkey hens with poults. Great Basin Nat. In Press.

SCHEMNITZ, S. D., D. L. GOERNDT, AND K. H. JONES. 1985. Habitat needs and management of Merriam's turkey in southcentral New Mexico. Proc. Natl. Wild Turkey Symp. 5:199–232.

SCHMUTZ, J. A., AND C. E. BRAUN. 1989. Reproductive performance of Rio Grande wild turkeys. Condor 91:675–680.

———, ———, AND W. F. ANDELT. 1989. Nest habitat use of Rio Grande wild turkeys. Wilson Bull. 101:591–598.

SHARPE, G. W., C. W. HENDEE, AND S. W. ALLEN. 1976. Introduction to forestry. McGraw-Hill Book Co., New York, N.Y. 544pp.

SISSON, D. C., D. W. SPEAKE, J. L. LANDERS, AND J. L. BUCKNER. 1990. Effects of prescribed burning on wild turkey habitat preference and nest selection in south Georgia. Proc. Natl. Wild Turkey Symp. 6:44–50.

SPEAKE, D. W. 1980. Predation on wild turkeys in Alabama. Proc. Natl. Wild Turkey Symp. 4:86–101.

STILL, H. R., JR., AND D. P. BAUMANN, JR. 1990. Wild turkey nesting ecology on the Francis Marion National Forest. Proc. Natl. Wild Turkey Symp. 6:13–17.

THOMAS, D. L., AND E. J. TAYLOR. 1990. Study designs and tests for comparing resource use and availability. J. Wildl. Manage. 54:322–330.

URESK, D. W., AND K. E. SEVERSON. 1989. Understory-overstory relationships in ponderosa pine forests, Black Hills, South Dakota. J. Range. Manage. 42:203-208.

VANGILDER, L. D., E. W. KURZEJESKI, V. L. KIMMEL-TRUITT, AND J. B. LEWIS. 1987. Reproductive parameters of wild turkey hens in north Missouri. J. Wildl. Manage. 51:535-540.

WAKELING, B. F. 1991. Population and nesting characteristics of Merriam's turkeys along the Mogollon Rim, Arizona. Tech. Rep. No. 7. Ariz. Game Fish and Dep., Phoenix, Ariz. 110pp.

WERTZ, T. L., AND L. D. FLAKE. 1988. Wild turkey nesting ecology in south central South Dakota. Prairie Nat. 20:29-37.

WILLIAMS, L. E., D. H. AUSTIN, N. F. EICHHOLZ, T. E. PEOPLES, AND R. W. PHILLIPS. 1969. A study of nesting turkeys in southern Florida. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 22: 16-30.

——— ———, AND T. E. PEOPLES. 1974. Movement of wild turkey hens in relation to their nest. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm.

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