

Nest-site Selection and Survival of Wild Turkeys in Tennessee

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Abstract: Spring harvest of wild turkey (*Meleagris gallopavo silvestris*) has declined in many eastern states since 2010. In Tennessee, spring harvest declines of 30%–50% in south-central counties from 2005–2015 caused concern among hunters and managers. To determine how turkey productivity might be related to the perceived population decline, we radio-tagged and tracked 152 females with VHF transmitters throughout the 2017–2018 nesting seasons. We documented nest-site selection, nesting rate, clutch size, hatching rate, re-nesting rate, and daily nest survival. We used conditional logistic regression to determine which landscape-scale and nest-site vegetation characteristics were most related to nest-site selection by females. We used nest-survival models to determine which temporal, landscape-scale, and site-specific vegetation characteristics were most related to daily nest survival. On average, 75.7% of females incubated a nest, clutch size was 9.3 ± 0.4 SE (successful nests), and based on daily nest survival estimates, 33.9% of nests that were incubated hatched. Nest-site selection was positively associated with the amount of early succession and shrubland available in pre-nesting home ranges, and positively associated with visual obstruction (0–50 cm above-ground) and percent vegetation cover above the nest, but negatively associated with distance from trails or roads. The best-supported model for daily nest survival included a single covariate: percent vegetation cover above the nest. We documented that a gradient in the quality of cover available for nesting was directly linked to daily nest survival. Nesting cover, therefore, could be improved through targeted forest and field management prescriptions that specifically address vegetation structure.

Key words: *Meleagris gallopavo*, nest survival, resource selection, population decline

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Annual reproductive indices of eastern wild turkeys (*Meleagris gallopavo silvestris*; hereinafter “turkey”) have declined in the southeastern United States over the past decade, causing concern among turkey biologists, managers, and hunters that poor fecundity may be linked to population declines (Byrne et al. 2016). Reproductive parameters have been documented from many states within this region (Exum et al. 1987, Palmer et al. 1993, Thogmartin and Johnson 1999, Norman et al. 2001, Isabelle et al. 2016, Yeldell et al. 2017a). However, in Tennessee limited research completed during the turkey restoration phase in the state (1940–2005) provides the only opportunity for comparison with contemporary data in Tennessee (McGuinness and Smith 1990, Johnson 2019). Tennessee turkey hunters and managers have been concerned because spring turkey harvest declined 30%–50% in south-central Tennessee counties from 2005–2015 (Tennessee Wildlife Resources Agency, unpublished data), and 68% of turkey hunters within these counties reported observing significant population declines (Poudyal et al. 2016). Documenting contemporary nest-site selection

and reproductive rates in Tennessee will allow managers to understand how nesting cover and fecundity might have changed since the restoration phase of turkey management in the state and will put Tennessee turkey population demographics in context with other southeastern states. Replication of such studies over space and time serve as the cornerstone of wildlife science (Johnson 2002).

Predation typically accounts for 51%–93% of turkey nest failures (Vangilder et al. 1987, Palmer et al. 1993, Thogmartin and Johnson 1999, Kiss 2015). Vegetation structure that provides nest concealment is key to reducing predation risk (Badyaev 1995). Visual obstruction often is an influential factor in nest-site selection (Holbrook et al. 1987, Badyaev et al. 1996, Spears et al. 2007, Fuller et al. 2013, Wood et al. 2019), particularly visual obstruction in the 0–1 m range above ground (Badyaev 1995).

Female nest-site selection, and ultimately nest survival, may be related to habitat characteristics at multiple spatial scales. Shrubland, old-field, or young regenerating forest with relatively dense

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vegetation that limits visibility often are selected for nest sites compared to mature forest with little understory structure (Still and Baumann 1990, Streich et al. 2015). Understanding nest-site selection at the landscape scale and identifying characteristics linked to daily nest survival will inform management decisions aiming to improve nest success.

Our goal was to compare reproductive parameters in south-central Tennessee with studies in other areas in which turkey populations have been previously identified as increasing, stable, or decreasing to understand how nest-site selection and daily nest survival may be associated with turkey population declines. We hypothesized that both landscape-scale and nest-site selection were influenced by cover around the nest, and we predicted nests with greater cover would have greater survival.

Study Area

We conducted our study across the 2017–2018 nesting seasons in five counties of south-central Tennessee (Maury, Lawrence, Wayne, Bedford, and Giles). Our study was distributed across 26,000 ha of private land and 11,000 ha of public land on Yanahli (Bedford County) and Tie Camp (Wayne County) Wildlife Management Areas. Ten sites (two per county) were focal points for trapping and tracking females (Figure 1). These sites were on private ($n=9$) and public ($n=1$) lands with turkey densities sufficient to obtain the target sample size of 10 females per site per year for the nesting study. Based on U.S. Department of Agriculture (USDA) National Agricultural Statistics Service Cropland data (2017), the study area was mostly deciduous forest (46.5%), with early succession/pasture (28.1%) the next most frequent cover type, but sites varied in land cover composition. The pasture

cover type ranged from 14% to 50% of the total coverage in the five counties. Closed-canopy deciduous forests were dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), hackberry (*Celtis occidentalis*), maples (*Acer* spp.), and yellow-poplar (*Liriodendron tulipifera*). Eastern red cedar (*Juniperus virginiana*) was abundant in areas with low-nutrient and shallow soils, and working loblolly pine (*Pinus taeda*) forests were interspersed throughout the study area. The forest understory typically was sparse but often contained various tree seedlings, blackberry, and raspberry (*Rubus* spp.), coralberry (*Symphoricarpos orbiculatus*), Chinese privet (*Ligustrum vulgar*), sericea lespedeza (*Lespedeza cuneata*), white snakeroot (*Ageratina altissima*), and stiltgrass (*Microstegium vimineum*). Terrain throughout the study area varied from flat farmland to rolling hills and steep valleys. Multiple river systems flowed through the area juxtaposing floodplains with upland forest and row crops. Land use included forest management, cattle grazing, hay production, and poultry operations.

Methods

Field Methods

Trapping.—Turkey capture, handling, and radio-tagging methods were approved by University of Tennessee IACUC Protocol #561. Our goal was to trap and radio-tag 10 females (> 5 adults) per trap site, yielding ~ 100 females monitored per year. Prior to the nesting season each year, we baited each trap site with corn (cracked or whole kernel) to attract turkeys for trapping. We trapped turkeys with rocket nets (box set) based on Delahunt et al. (2011); see also Johnson (2019). We fitted each bird with an individually numbered metal leg band and we fitted the first 10 females at each site with a backpack-style VHF radio transmitter (Advanced Telemetry Systems [ATS] Isanti, Minnesota). The transmitters weighed 80 g, $\sim 2\%$ of the female's body weight. Each transmitter was equipped with an 8-h mortality switch and a motion-sensing switch to aid in detection of incubation. Battery life was sufficient to last the duration of the two-year study.

Monitoring.—We monitored each radio-tagged female 3 times per week prior to 1 April each year by triangulation using three intersecting compass bearings from fixed locations (Vangilder et al. 1987). We loaded each bearing and base station location into LOAS version 4.0.3.8 (Ecological Software Solutions, Urnäsch, Switzerland) to determine the estimated location and error polygon. Beginning on 1 April, we monitored females every other day to detect the initiation of incubation (Vangilder et al. 1987, Norman et al. 2001). We noted female activity (active/inactive) and used those data and localized movement data to determine if the female had begun incubation. We assumed a female was incubating if it was in the same approximate location on two consecutive

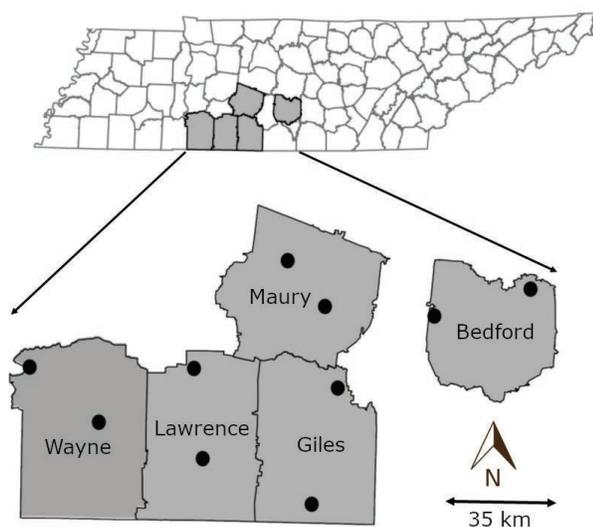


Figure 1. Study area and wild turkey trap site locations (dots) within each county of south-central Tennessee, 2017–2018.

days, if there were prolonged periods of inactivity (e.g., ≥ 1 hour) based on the motion sensor, or if there was a mortality signal. We estimated nest location by circling within 25–50 m of the female (Vangilder et al. 1987, Miller et al. 1998, Thogmartin and Johnson 1999). We calculated expected hatch date by adding 28 days to the first day incubation was detected. We back-dated nests that hatched by 28 days to determine actual onset of incubation. Most nesting attempts were documented within three days of the onset of incubation.

We checked incubating females for activity via telemetry every one-two days. We searched for the nest if a female was off the nest for >3 h or was >200 m from the estimated nest location. We recorded nest location with a GPS and determined nest fate as either active, hatched, abandoned, or depredated. If depredation was apparent, we looked for tracks, scat, and other field sign to determine which species possibly predated the nest. When a nest was depredated or abandoned, we monitored the female's subsequent activity every one-two days to document re-nesting. We considered successful nests as those with ≥ 1 egg hatched (Vangilder et al. 1987, Miller et al. 1998, Thogmartin and Johnson 1999). We considered an egg hatched if the eggshells still had a membrane attached and by the general appearance of the shells and nest (tops pecked off or eggshells still all within or on edge of the nest bowl). In cases where we could not definitively determine if a nest hatched or was depredated, we continued to monitor female activity and flushed the female to determine if poults were present. If we determined poults were present, we classified the nesting attempt as successful. If nest sites were on a property to which we did not have access, we assumed incubation if the female was triangulated at the same bearings each day and the motion sensor was inactive. Once the female became active, we calculated the incubation period based on days of inactivity at the apparent nest location to estimate apparent nest fate and flushed the female once she was on accessible property to confirm hatch by the presence of poults.

Nest-site evaluation.—We evaluated each nest site within 4 wk after a nest was abandoned, hatched, or depredated. We selected and evaluated one random site per nest to determine selection of various vegetation characteristics. Although recent research has suggested that female turkeys may not engage in habitat sampling prior to nesting (Conley et al. 2016), we defined available habitat based on the area the hen likely resided in during the pre-nesting period. We restricted random site selection and therefore available habitat to a circle centered on the nest site that equaled the size of the average female home range (190 ha) from the two months prior to the nesting season. We used the HRT 2.0 package (Rodgers et al. 2015) to calculate 95% convex polygon home ranges of females with ≥ 10 locations. We randomly assigned a distance (within the

average radius of the home-range circle, 779 m) and an azimuth from which to select random points. We checked the random locations in ArcGIS 10.4.1 (Environmental Systems Research Institute, Redlands, California) to confirm random locations fell in potential habitat (i.e., not areas of human-development or water bodies) and were accessible (i.e., we had permission of the landowner). Vegetative structure and composition at each nest and associated random site were measured within a 11.3-m radius plot (Badyaev 1995, McCord et al. 2014). We located perimeter points in each cardinal direction 11.3 m from plot center. The density of vegetation above the nest was measured using a spherical densiometer held at a height of 0.46 m (Seiss et al. 1990). Visual obstruction readings (VOR) were recorded by using a vegetation profile board (Nudds 1977) divided into three height classes of (0–50 cm = VORlow; 51–100 cm = VORmedium; 101–200 cm = VORhigh) to measure understory cover (Badyaev 1995). Percent coverage of each stratum was broken into six classes (Badyaev 1995, McCord et al. 2014): 1) $<2.5\%$, 2) 2.5% – 25% , 3) 26% – 50% , 4) 51% – 75% , 5) 76% – 95% , 6) $>95\%$. We counted stems of shrubs, saplings, and brambles within a 5-m radius plot for stems >1.37 m tall and ≤ 11.4 cm dbh (McCord et al. 2014). The basal area of overstory trees within three size classes (<25 cm, 25–45 cm, >45 cm dbh) was measured with a 2.5 m²/ha-factor prism (Bidwell et al. 1989) centered at the nest. Other general characteristics of the nest site were recorded as slope (measured with clinometer), aspect (measured with compass), elevation (via GPS), distance to paths or roads, and distance to nearest edge (distances determined in ArcGIS 10.4), which we defined as a change between two or more vegetation types or distinct forest age classes.

Landcover data.—We chose relevant metrics to quantify landscape scale nest-site selection based on the literature for wild turkeys (Fuller et al. 2013, Pollentier et al. 2017, Yeldell et al. 2017a). We acquired 30-m land cover data from the USDA National Agriculture Statistical Services (2017) to determine the cover types across the study sites. We grouped land cover into six types: deciduous forest, evergreen forest, shrubland, fallow field/pasture/old-field/grassland (ES/pasture), row crop, and water/human developed. We calculated distance to cover types from each nest and random point using ArcGIS 10.4. We measured distance to nearest edge and road (primary and secondary roads; USDA Natural Resources Conservation Service 2015) for the nest and associated random point using ArcGIS 10.4. We used FRAGSTATS 4.1 (McGarigal et al. 2012) to quantify five landscape metrics using the 30-m landcover data in a 779-m buffer around each nest and random point. Clumpiness (CLUMPY) was an index of the dispersion of individual cover types; as CLUMPY approaches 1 for a given vegetation type, the vegetation type patches were highly aggregat-

ed. We calculated the percent cover of each cover type (PLAND) as the number of pixels of a given cover type divided by the total number of pixels. We considered edge density as the total amount of edge between all the cover types (Edge) within the 779-m radius. Contagion (CONTAG) was a measure of dispersion; large values of contagion indicated a given cover type was highly aggregated. The Interspersion and Juxtaposition Index (IJI) measured the extent to which the landscape was intermixed with different cover types.

Data Analysis

We calculated the nesting rate as the proportion of females alive and available on 1 April each year that incubated at least one nest during that nesting season. (Miller et al. 1998, Norman et al. 2001, Lehman et al. 2008). Renesting rate was the number of females that incubated a second nest in a season divided by the number of females that were unsuccessful in their first attempt. Female success was the number of females that ultimately hatched ≥ 1 egg (initial nests and re-nests) divided by the total number of females alive and available on 1 April (Vangilder et al. 1987, Paisley et al. 1998, Lehman et al. 2008). We recorded minimum clutch size of each nest that was examined, but average clutch size was calculated from successful nests because depredated nests may not contain all eggs laid (Palmer et al. 1993). We calculated hatchability as the number of poults that hatched from each successful nest divided by the clutch size. For nesting rate, renest rate, nest success, and female success, we used chi-square contingency tests to measure the relationship of each variable with year and age (Isabelle et al. 2016). We used univariate analysis of variance (ANOVA; JMP Pro 2019) to compare clutch size and hatchability by year and female age. We evaluated statistical significance at $\alpha = 0.05$. We report the reproductive parameters by female age class (adult, juvenile) to allow comparison with other studies.

Resource selection.—We evaluated resource selection at two spatial scales (2nd and 3rd order; Johnson 1980). We used a case-control resource selection function (RSF) of use versus availability (Johnson et al. 2006, Pollentier et al. 2017) modeled with conditional logistic regression in package *survival* (Therneau 2015) in R version 3.5. (R Core Team 2018) to calculate odds ratios for selection. We assumed nest-site selection during renesting was independent of the initial nest-site selection (Yeldell et al. 2017b). We conducted model selection in an information-theoretic framework (Burnham and Anderson 2004). We used the habitat metrics at the paired random locations for each nest to determine available habitat at the nest-site level. To determine available habitat for landscape analysis, we generated five random points within the average female pre-nesting circular home range (779 m radius) cen-

tered on the nest to represent an area from where she could have chosen a nest site based on her movements (Yeldell et al. 2017a, Wood et al. 2019). We also placed a 779-m buffer around each random point to use as the area of availability for landscape metrics for random locations. We checked explanatory variables used in the analysis for correlation using Pearson's correlation (r ; Fuller et al. 2013). We eliminated edge density and the visual obstruction reading from 51–100 cm from the models because we found they were highly correlated ($r > 0.7$) with other covariates. Before modeling habitat selection, we scaled distance variables by dividing each value by 100 m to provide easier interpretation of the Beta parameter estimates. The null model was that nest-site selection was not related to any covariate. Row crop and water/development cover types had too few nest observations for selection function analysis, so we removed them from analysis.

Daily nest survival.—We used the nest-survival model (Dinsmore et al. 2002) in program MARK (White and Burnham 1999) through RMark (Laake 2013) to calculate daily survival rate (DSR) of each nest and to determine if DSR was related to specific covariates. We created model suites based on *a priori* hypotheses involving the potential relationships of temporal, landscape, and nest-site specific vegetation covariates. We followed a similar model protocol used by Fuller et al. (2013) that involved the creation of three model suites each formed with a manageable subset of covariates. We standardized 8 April each year as the first day of the nesting season (first nest incubated) and standardized distances by dividing each value by 100 m but left the rest of the data unstandardized. Adult and juvenile nests were pooled because juvenile female nest sample sizes were too sparse to warrant standalone analysis. The best-supported model was chosen by using Akaike's Information Criterion adjusted for small sample sizes (AIC_c), and we accepted all models that had an $\Delta AIC_c \leq 2$ for evaluation (Burnham and Anderson 2004). Beta estimates in the top models which had 95% confidence intervals overlapping 0 were disregarded. The null model contained constant daily survival.

The first model suite included temporal variables including time (linear change in DSR), quadratic time (curvilinear change in DSR), nest age (the number of days since the first nest was incubated), year, and an interaction term between time and year. We hypothesized that as the nesting season progressed, DSR may increase as vegetation continued to develop providing more concealment for the nests (Badyaev 1995). We included quadratic time to model potential non-linear fluctuations in DSR related to changes in predator populations or predator activity. Nest age was included because as a nest progressed, females may spend more time off the nest foraging which may increase nest vulnerability to depredation (Thogmartin and Johnson 1999, Yarnall et al. 2020).

The second suite of models included landscape covariates used in the resource selection analysis. We hypothesized that shrubland would provide more visual protection for nesting females and therefore increase their nest survival if they nested in shrub cover compared to other vegetation types. We hypothesized that DSR also could vary in relation to the distance to the edge of specific cover types. We included CONTAG, CLUMPY, PLAND, and IJI in the second suite of models because we wanted to assess whether DSR was related to broader landscape context and configuration. DSR has been reported to vary with distance to edge (Seiss et al. 1990) and other landscape metrics (Lehman et al. 2008).

The third model suite included all the covariates from the best-supported models from the first two suites and the nest-site-specific covariates. We included a selection model in this suite that included each variable that females selected for compared to available habitat. We also included a global concealment model that included overhead cover, stem density, VORlow, and VORhigh, which described the horizontal and vertical cover associated with the nest. We identified the best-supported model and then ran it with year as a group variable to allow estimation of DSR in each year.

Results

We captured 235 females (191 adult and 44 juvenile) and radio-tagged 152 of them (130 adult, 85.5%; and 22 juvenile, 14.5%). By 1 April each year we had 107 (95 adult and 12 juvenile) females radio-tagged in 2017 and 99 females (92 adult and 7 juvenile) radio-tagged in 2018 (Table 1). The median nest initiation dates were similar between both years ($Z=1.27$, $P=0.203$). The earliest nest that was incubated for both years was 8 April; the combined median date of incubation was 27 April (Table 1), and the latest nest was incubated beginning on 5 July. We monitored 204 nests (194 adult

and 10 juvenile) which corresponded to a total average nesting rate of 75.7% (78.1% adult and 47.4% juvenile); 29.4% (60/204) of the nests were successful. Adult females had 28.4% (55/194) successful nests and juveniles had 40.0% (4/10) successful nests. The seasonal female success rate was 29.1% (29.4% adult, 21.1% juvenile; Table 1). Successful females had an average clutch size of 9.3 (9.3 adult, 9.6 juvenile) in their first nest attempt. Average clutch size estimated for all nests (depredated, hatched, or abandoned) was 8.9, and average clutch size of nests that were abandoned was 11.5.

Nesting rate varied by age ($\chi^2=5.332$, $P=0.021$); nesting rate of adult females (78.1%) was almost twice as great as the nesting rate of juvenile females (47.4%; Table 1). Adult nesting rate was greater in 2018 (84.8%) than 2017 (71.6%; Table 1) ($\chi^2=4.831$, $P=0.028$). Nesting rate did not vary by year for juvenile females ($\chi^2=0.091$, $P=0.763$), although sample sizes were small ($n=19$). Renesting rate did not vary by age ($\chi^2=1.985$, $P=0.159$), though juvenile sample sizes were limited ($n=5$); adult renesting rate was 40.2% ($n=102$) and juvenile renesting rate was 20.0%. Pooled across years, the overall renesting rate was 39.3% (Table 1). Nest success of adult females (28.4%) was lesser than nest success of juvenile females (40.0%), but juvenile sample sizes were low ($\chi^2=1.458$, $P=0.227$). Nest success did not differ by year ($\chi^2=2.550$, $P=0.110$; Table 1).

Clutch size and number of poults hatched per nest did not differ by female age or year. Average clutch size in 2017 was 9.06 and the average eggs hatched was 8.26, whereas in 2018, clutch size and eggs hatched were 8.82 and 7.77, respectively. Clutch size of initial nests ($\bar{x}=9.31$ initial, $\bar{x}=7.64$ renest), was ~20% greater than re-nests, and the number of poults hatched per initial nest ($\bar{x}=8.48$) was ~30% greater than re-nests ($\bar{x}=6.45$ hatched; Table 2).

Table 1. Reproductive parameters of adult (Ad) and juvenile (Juv) female wild turkeys in south-central Tennessee, 2017–2018.

Year	Female age	Date first nest incubated	Median nest incubation date	n^a	% Initial nesting (n^b)	% Initial nest success (n^c)	% Renest (n^d)	% Renest success (n^e)	% Third nest (n^f)	% Third nest success (n^g)	% Successful nests (n^h)	% Female success (n^i)	Initial clutch size
2017	Ad	8 Apr	28 Apr	95	71.6 (68)	35.3 (24)	31.8 (14)	35.7 (5)	22.2 (2)	50.0 (1)	35.7 (30)	31.6 (30)	9.1
	Juv	19 Apr	23 Apr	12	50.0 (6)	50.0 (3)	33.3 (1)	0.0 (0)	0.0 (0)	0.0 (0)	42.9 (3)	25.0 (3)	9.7
2018	Ad	9 Apr	26 Apr	92	84.8 (78)	21.7 (20)	37.5 (27)	18.5 (5)	22.7 (5)	0.0 (0)	23.6 (26)	28.2 (26)	9.5
	Juv	26 Apr	28 Apr	7	42.9 (3)	33.3 (1)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	33.3 (1)	14.3 (1)	–
Both	Ad	8 Apr	27 Apr	187	78.1 (146)	30.1 (44)	40.2 (41)	24.4 (10)	22.6 (7)	14.3 (1)	28.4 (55)	29.4 (55)	9.3
	Juv	19 Apr	27 Apr	19	47.4 (9)	44.4 (4)	20.0 (1)	0.0 (0)	0.0 (0)	0.0 (0)	40.0 (4)	21.1 (4)	9.7
Both	Both	8 Apr	27 Apr	206	75.7 (155)	31.0 (48)	39.3 (42)	23.8 (10)	21.9 (7)	14.3 (1)	28.9 (59)	28.6 (59)	9.3

a. The number of females available as of 1 April.

b. The number of females that incubated ≥ 1 nest.

c. The number of females that hatched ≥ 1 egg in the first attempt.

d. The number of females with potential to renest after a first nest failure.

e. The number of females that hatched ≥ 1 egg in their second attempt.

f. The number of females with potential to renest after a second nest failure.

g. The number of females that hatched ≥ 1 egg in their third attempt.

h. The number of nests that were successful between all attempts.

i. The number of females that hatched ≥ 1 egg in any attempt.

Table 2. Mean clutch size and number of poults hatched per wild turkey nest by female age, year, and nesting attempt, south-central Tennessee, 2017–2018.

Model	Category	n ^a	\bar{x}	SE	Lower 95%	Upper 95%	P
Clutch × age	Adult	50	8.92	0.37	8.18	9.66	0.632
	Juvenile	3	9.67	1.51	6.65	12.69	
Clutch × year	2017	31	9.06	0.47	8.12	10.01	0.736
	2018	22	8.82	0.56	7.70	9.94	
Clutch × attempt	Initial	42	9.31	0.39	8.53	10.09	0.055
	Renest	11	7.64	0.76	6.11	9.16	
Hatched × age	Adult	50	7.96	0.04	7.19	8.73	0.293
	Juvenile	3	9.66	1.56	6.53	12.80	
Hatched × year	2017	31	8.26	0.49	7.28	9.24	0.525
	2018	22	7.77	0.58	6.61	8.94	
Hatched × attempt	Initial	42	8.48	0.40	7.67	9.28	0.026
	Renest	11	6.45	0.78	4.88	8.03	

a. The number of successful nests that hatched ≥ 1 egg.

Nest-site Selection

We analyzed nest-site selection for 189 nest locations in 2017 and 2018; 15 nests were censored because they were on properties we did not have permission to access. Based on landscape covariates, four models showed strong support (i.e., $\Delta AIC_c \leq 2$; Table 3). The best-supported model for relating landscape covariates to nest-site selection included three cover types: evergreen forest, shrubland, and ES/pasture. Model-averaged estimates indicate evergreen forest ($\beta = 0.91$; SE = 0.29; CI = 0.35 to 1.47), ES/pasture ($\beta = 1.01$; SE = 0.21; CI = 0.59 to 1.43), and shrubland ($\beta = 1.45$; SE = 0.24; CI = 0.98 to 1.93; Table 4) were all positively associated with selection. Based on odds ratios, a female was 2.44, 2.75, and 4.27 times more likely to choose evergreen forest, ES/pasture, and shrubland cover types, respectively, for a nest site compared to the availability of those cover types on the landscape. For further analysis, we split ES/pasture into two categories (pasture/hay and old/

fallow field) to determine if selection varied between these separate grass-dominated cover types. Once separated, 23.5% of nests were in old fields and 6.4% were in pasture/hay fields. Old field was positively associated with selection ($\beta = 0.61$; SE = 0.29; $P = 0.03$), and pasture/hay was not selected ($\beta = -0.92$; SE = 0.48; $P = 0.06$).

Two models with support related nest-site-specific covariates to nest-site selection (i.e., $\Delta AIC_c \leq 2$; Table 3). The best-supported model contained five covariates: visual obstruction (0–50 cm), cover above the nest, slope, distance to nearest path or road, and the quadratic function of distance to nearest path or road (Table 3). Distance to nearest path and slope were negatively associated with nest-site selection ($\beta = -0.01$; SE = 0.01; CI = -0.03 to 0.01; $\beta = -0.14$; SE = 0.09; CI = -0.32 to 0.04, Table 3, respectively). Cover above the

Table 4. Model-averaged parameter estimates of the models that were predicting landscape and nest-site-specific variables selected for nest sites by hen wild turkeys in south-central Tennessee, 2017–2018. Positive values for distance variables indicate negative association with the variable.

Covariate	Estimate	SE	95% Confidence interval	
Landscape variables				
CoverShrub	1.45	0.24	0.98	1.93
CoverGrass	1.01	0.21	0.59	1.43
CoverEver	0.91	0.29	0.35	1.47
Rowcrop	-0.04	0.09	-0.21	0.13
RowQuad	0	0.01	-0.01	0.02
Near_Dist_Rd	0.03	0.08	-0.12	0.19
RoadQuad	0	0.01	-0.02	0.01
GrasslandPasture	-0.06	0.14	-0.34	0.23
GrassQuad	0.01	0.03	-0.05	0.07
Nest-site-specific variables				
VORlow	0.8	0.16	0.49	1.12
PercentCover	0.02	0.01	0.01	0.03
Slope	-0.14	0.09	-0.32	0.04
NearestPath	-0.01	0.01	-0.03	0.01
PathQuad	0	0	0	0
SlopeQuad	0	0	0	0.01

Table 3. Model selection using conditional logistic regression with matched-pairs case-control sampling that used nests as the case and random sites as the controls for hen wild turkey nest-site selection based on landscape and nest-site-specific variables in south-central Tennessee, 2017–2018.

Models ^a	K	AICc	ΔAIC_c	AICc Weight	LL
Landscape variables					
CoverEver + CoverGrass + CoverShrub	3	644.53	0.00	0.25	-319.25
CoverEver + CoverGrass + CoverShrub + Rowcrop + RowQuad	5	645.17	0.64	0.18	-317.56
CoverEver + CoverGrass + CoverShrub + NEAR_DIST_Rd + RoadQuad	5	645.65	1.12	0.14	-317.80
CoverEver + CoverGrass + CoverShrub + GrasslandPasture + GrassQuad	5	645.93	1.40	0.13	-317.94
Null	1	1032.09	387.56	0.00	-515.04
Nest-site-specific variables					
VORlow + PercentCover + Slope + NearestPath + PathQuad	5	157.12	0	0.47	-73.48
VORlow + PercentCover + Slope + SlopeQuad	4	157.77	0.65	0.34	-74.83
Null	1	335.14	178.01	0.00	-166.56

a. Additional models that were >2 ΔAIC_c are referenced in Johnson (2019).

nest and visual obstruction ($\beta=0.02$; $SE=0.01$; $CI=0.01$ to 0.03 ; $\beta=0.80$; $SE=0.16$; $CI=0.49$ to 1.12 ; Table 3) were positively associated with nest-site selection. With every 10% increase in visual obstruction at 0–50 cm, the site was 2.21 times more likely to be selected for nesting, which was the most influential covariate related to selection (Table 4). Thirty percent of the random points had visual obstruction at 0–50 cm, and percent cover above the nest within one standard deviation of the mean for nest sites.

Daily Nest Survival

We modeled nest survival using 188 nests from 2017 and 2018; 16 nests were censored either because of potential observer-caused abandonment ($n=10$) or the nests were on properties that we could not gain access ($n=6$). The best-supported model in the first suite with temporal covariates was constant daily survival ($K=1$, $\Delta AIC_c=0$, $w_i=0.20$, deviance = 836.05).

When the landscape covariates were included in the model suite, two models were supported above the null model of constant daily survival ($\Delta AIC_c \leq 2$). The best-supported model contained distance to evergreen cover ($K=2$, $\Delta AIC_c=0$, $w_i=0.18$, deviance = 833.31), whereas the second best-supported model contained distance to nearest road or path ($K=2$, $\Delta AIC_c=0.70$, $w_i=0.13$, deviance = 834.01). Beta parameter estimates for both distance to evergreen cover ($\beta=0.003$, $CI=-5.000^{-4}$ to 0.006) and distance to nearest road or path ($\beta=0.010$, $CI=-0.004$ to 0.023) had confidence intervals that overlapped 0 so no landscape covariates were included in the final model suite.

Only the nest-cover model was supported in the final model suite ($K=2$, $\Delta AIC_c=0.35$, $w_i=0.14$, deviance = 831.08; for compar-

ison, in this suite the model with constant daily survival had $\Delta AIC_c=3.32$, $w_i=0.03$, deviance = 836.05). Beta estimate confidence intervals for the nest-cover effect did not overlap zero ($\beta=0.005$, $CI=7.112^{-4}$ to 0.009). Daily survival rate was positively associated with cover above the nest (Figure 2). The DSR estimate from the best-supported model, after model-averaging, was 0.962150 ($SE=0.003$; $CI=0.955$ to 0.968). Of the nests that were incubated, 33.9% ultimately hatched at least one egg.

Discussion

The overall goal of our research was to document reproductive rates for south-central Tennessee where recent harvest and hunter observational data suggest wild turkey populations may be declining. We hypothesized population declines were linked to poor reproduction compared to reproductive rates when the population was increasing during the initial restoration phase in the 1980s–1990s. The key nesting parameter estimates in our study all were less than the estimates from the only other VHF telemetry-based nesting study in Tennessee, conducted during the turkey restoration phase. Incubation rate of radio-tagged females in 1988 was 86.7% (initial) and 60.0% (re-nesting) (McGuinness and Smith 1990), compared to our rates of 75.7% and 39.3%. Nest success in 1988 was about twice as great as nest success in our study (61.5% in 1988; 33.9% over 2017–2018). Our initial nesting and re-nesting rates and nest success, in contrast, were similar to the rates in populations perceived as declining in other southeastern states (Table 5).

Our documented clutch size (9.3) was similar to clutch sizes reported from declining populations and 1–2 eggs less than clutch sizes reported from studies where populations were reported as stable or increasing (Table 5). Nests that were abandoned in our study ($n=13$) had an average clutch size of 11.5, which suggests lower clutch sizes may not reflect nutritional limitations but more likely indicate partial nest predation. The number of poults hatched ($n=427$) per successful female ($n=60$) for our study (7.12; hatch rate = 76%) also was less than poult-to-female ratios for studies of stable or increasing populations (Table 5).

Across all key reproductive parameters, we documented apparent decreases in each vital rate compared to stable or increasing turkey populations in Tennessee during the restoration phase and elsewhere from across the range (Table 5). For many of these vital rates, a ~10% decrease individually may not seem significant until these reductions accumulate across the entire nesting cycle. This reduced fecundity, consistent with poult per hen data reported by Byrne et al. (2016), is at least correlated with the apparent population declines. Alternative explanations, such as density-dependent processes (Byrne et al. 2016), may still be more influential in determining turkey population status.

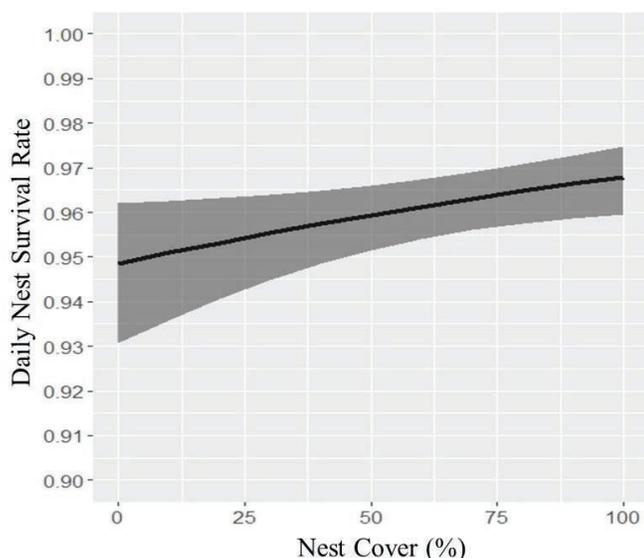


Figure 2. Best-supported model for wild turkey daily nest survival that shows how percent cover above the nest is related to daily nest survival in south-central Tennessee, 2017–2018.

Table 5. Nesting parameters for wild turkey populations rangewide, compared to nesting parameters in south-central Tennessee, 2017–2018. Transmitter technology differed between these studies with some using VHF and others using GPS.

Author	Years	State	Initial nesting rate (%)	Initial nest success (%)	Renesting rate (%)	Renesting success (%)	% Nest success (%)	Average clutch size
Vangilder and Kurzejeski 1995 ^{a, c}	1981–1988	MO	96.0	56.3	40.6	30.2	47.6	11.08
Miller et al. 1998 ^{a, e}	1984–1996	MS	72.3	27.9	34.8	24.6	29.7	9.40
Palmer et al. 1993 ^{a, e}	1984–1992	MS	74.0	30.8	34.8	26.1	31.0	9.10
Paisley et al. 1998 ^{a, d}	1989–1992	WI	92.7	13.6	55.1	21.0	38.2	11.20
Roberts et al. 1995 ^{a, d}	1990–1993	NY	98.5	37.4	67.2	45.8	37.9	12.04
Thogmartin and Johnson 1999 ^{a, e}	1993–1996	AR	62.2	16.5	35.0	36.0	13.6	8.43
Byrne and Chamberlain 2013 ^{a, f}	2002–2010	LA	60.0	39.3	26.7	25.0	37.5	–
Delahunt 2011 ^{a, d}	2008–2010	IL	98.5	23.0	75.6	16.0	35.4	13.10
Pittman and Krementz 2016 ^{a, e}	2012–2013	AR	92.0	26.5	37.5	7.0	26.8	10.00
Little et al. 2014 ^{b, f}	2011–2013	GA	70.0	42.1	36.8	42.0	–	–
Yeldell et al. 2017 ^{b, f}	2014–2015	LA	87.0	15.8	65.6	20.0	14.5	–
Wood et al. 2018 ^{b, f}	2015–2016	GA	96.2	34.0	61.8	65.0	41.4	–
Current study ^{a, e}	2017–2018	TN	75.7	31.0	39.3	26.2	29.4	9.30

a, b. a = VHF transmitters, b = GPS transmitters

c, d, e, f. Population status, c = increasing, d = stable, e = decreasing, and f = not stated in publication

We found female turkeys selected for vegetation types and site-specific conditions related to cover at the nest site, and this pattern of selection was linked to greater nest survival. Early succession and shrubland vegetation types occurred infrequently (<10% of potential nesting area) on our study sites but were strongly selected for nesting. When old-fields were separated from pasture/hay fields for analysis, females positively selected for old-fields, but showed no selection for pasture/hay fields. Selection of old-field and shrubland has been documented consistently for nesting regardless of population trend (Still and Baumann 1990, Thogmartin 1999, Streich et al. 2015). These vegetation types could be important determinants of nest success, but their limited availability on our study sites may have affected our ability to document a positive relationship with daily nest survival.

Avian species choose areas to nest with greater cover to minimize visual and olfactory cues of nest predators and increase predator search effort (Martin 1993). Ground nests that have increased nest concealment and vegetation heterogeneity generally have decreased risk of predation by mammals (Bowman and Harris 1980). Nest sites in our study were closer to paths/roads than expected by chance, consistent with previous studies (Kilburg et al. 2014, Yeldell et al. 2017b, Wood et al. 2019) in both stable (Still and Baumann 1990) and decreasing populations (Thogmartin 1999). Nests commonly are located near trails or roads, likely because these features provide easier access to and from the nest by the female in otherwise dense vegetation through which travel would be difficult. Proximity to paths/roads also may facilitate movement of broods post-hatching (Jones et al. 2008).

Despite the positive selection of nest sites based on landscape-scale and site-specific covariates outlined above, daily nest survival

was only related to one site-specific covariate (nest cover). Relatively dense vegetation around a nest may decrease the ability of nest predators to locate nests based on visual and olfactory cues (Bowman and Harris 1980, Martin 1993). Increasing the availability and distribution of nesting cover on a given property also may force nest predators to search larger areas to find turkey nests, thus leading to increased nest success. However, nest cover accounted for relatively little variation in survival (model weight = 0.14) which suggests that additional, unidentified factors may be influencing daily nest survival in south-central Tennessee.

Management Implications

In our study, wild turkey in Tennessee selected relatively dense vegetation for nesting when available, and we documented how relatively dense vegetation at the nest site may increase nest success. Increasing vegetation structure such that visibility is limited 0–50 cm aboveground with cover overhead and distributing such cover so that it is available across a management area should be an objective on properties managed for wild turkey. This type of structure can be provided in forests and woodlands by thinning to allow 30%–50% sunlight to the understory (McCord et al. 2014, Turner et al. 2020). Old-field and shrubland communities, which were highly selected by nesting females, can be maintained in this type of structure by burning on a three- to five-year fire-return interval (Gruchy and Harper 2014). Although use of such practices has been known among turkey managers for years, carefully designed field experiments are needed to measure how much potential increase in turkey productivity can be achieved through implementation of these management practices.

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