Research Article

Nest Site Selection and Nest Survival of Eastern Wild Turkeys in a Pyric Landscape

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ABSTRACT Pine (*Pinus* spp.)-dominated forests are commonly managed with prescribed fire in the southeastern United States to reduce fuel loads, maintain diverse plant communities, and increase habitat quality for wildlife. Prescribed fire alters understory vegetation, which is a key component of nesting habitat for ground-nesting birds. We assessed the influences of vegetation, prescribed fire, and landscape features (e.g., roads, edge) on nest site selection and nest survival of eastern wild turkeys *(Meleagris gallopavo silvestris)* in a pine-dominated ecosystem in west-central Louisiana. We radio-marked 55 female wild turkeys and evaluated vegetation and landscape characteristics associated with 69 nests during the 2014 and 2015 reproductive periods. We used conditional logistic regressions with matched-pairs case-control sampling and information-theoretic approaches to determine if vegetation characteristics within 15 m of a nest site, distances to surrounding vegetation communities and edges, and prescribed fire history of patches where a nest was located influenced nest site selection. We calculated hazard ratios for covariates in our top-performing models to determine if any of these characteristics affected nest site survival. Turkeys in our study had a longer reproductive season and higher nesting and renesting rates relative to other populations in the southeastern United States. At the local scale, turkeys nested in areas with higher percent ground cover vegetation. At the landscape scale, turkeys nested closer to roads and farther from edges of 2 plant communities. Turkeys selected to nest in forest stands burned 2 years prior. Nest survival was not affected by percent ground cover, distance to roads, or distance to edge but was negatively associated with time-since-fire; turkey nests in stands burned ≥3 years prior had lower survival than nests in stands burned the current year. We suggest that burning on a 3-year fire return interval is compatible with management for wild turkeys in southeastern pine-dominated forests. © 2017 The Wildlife Society.

KEY WORDS *Meleagris gallopavo*, nest site selection, nest survival, *Pinus* spp, prescribed fire, wild turkey.

Conifer forests, including the longleaf pine (*Pinus palustris*) ecosystem and commercially planted pines, comprise 34% of forestland in the southeastern United States (Wear and Greis 2012). Prescribed fire is a common management tool used to restore and maintain these forests. Historically, these pine-dominated forests were managed by frequent fire ignition, which promoted early successional grassland and prevented bottomland hardwood encroachment (Komarek 1964, Pyne 1982, Kennamer et al. 1992, Robbins and Myers 1992). Management of pine-dominated forests for threatened and endangered species that rely on frequent fire regimes (e.g., red-cockaded woodpecker [*Picoides borealis*]) and for wildlife species that prefer early successional vegetation (e.g., northern bobwhite quail [*Colinus virginianus*]) necessitates prescribed fire applied every 1–3 years to maintain open, park-like conditions (Alavalapati et al. 2002). Although eastern wild turkeys (*Meleagris gallopavo silvestris*; turkeys) occur throughout the pine-dominated forests of the southeastern United States, and seemingly prefer early successional vegetation communities provided in areas with frequently occurring prescribed fire (Miller et al. 2000, Miller and Conner 2007, Martin et al. 2012), a paucity of information is available concerning how prescribed fire may affect the reproductive ecology of female turkeys.

Predation is the primary cause of turkey nest failure (Miller and Leopold 1992, Lovell et al. 1997). Similar to other avian species, nest success of turkeys may depend on multi-scale processes including differences in vegetation structure around nest sites, and land cover composition at larger spatial scales (Thogmartin 1999, Batáry and Báldi 2004). Nest site selection at larger scales surrounding avian nest sites

may affect predation risk (Martin and Roper 1988). In addition, turkey nest site selection and success is affected by landscape features such as edge density (Thogmartin 1999, Byrne and Chamberlain 2013) and proximity of the nest to roads (Badyaev 1995, Thogmartin 1999, Moore et al. 2010). Collectively, this suggests a turkey's decision on where to nest and its chance of success is based on vegetation characteristics at the nest site, and the relative position of other variables across the landscape.

Prescribed fire has been recognized for its potential to increase habitat quality for turkeys and other upland game species (Stoddard 1935). Some uncertainty exists in regard to the preferred fire return interval in pine-dominated systems aimed at increasing turkey nest success while decreasing the likelihood of predation. For example, in pine-dominated systems, previous researchers have recommended longer burn intervals ranging from 3 years to 7 years to aid in development of concealment cover (e.g., increased hardwood communities; Glitzenstein et al. 2012) to reduce impacts of predation for wild turkeys and other ground-nesting birds (Miller et al. 2000, Miller and Conner 2007). However, longer fire return intervals may actually increase the risk of predation from predators such as raccoons (*Procyon lotor*; Chamberlain et al. 2002) that prefer hardwood patches created by infrequent fire return intervals. Biotic and abiotic processes operate and interact at multiple spatial scales on the landscape (Turner 1989). Although no single spatial scale likely exists for landscape metrics that may influence avian nest survival (Stephens et al. 2005, Richmond et al. 2012, Webb et al. 2012), application of prescribed fire can affect vegetation communities at multiple scales. Because fire immediately alters vegetation communities, it may have immediate effects on habitat quality for nesting turkeys and may affect nest survival.

The advent of global positioning system (GPS) transmitters for wild turkeys (Guthrie et al. 2011) has facilitated research possibilities (Collier and Chamberlain 2010) that were previously difficult, if not impossible, such as effects of hunting on behavior (Gross et al. 2015), influences of fire disturbances on movements (Oetgen et al. 2015), identification of precise nest initiation dates (Byrne et al. 2014), space use of incubating females (Conley et al. 2015), and movements of translocated individuals (Cohen et al. 2015). Therefore, the temporal and spatial resolution of data from GPS transmitters may enhance our detection of nest attempts and aid our understanding of the relationships between vegetation at the nest site, prescribed fire events, and turkey reproductive ecology. Our study was designed to address the following objectives: characterize reproductive parameters (e.g., nest timing, nesting rates, nest success, brood survival) from female turkeys equipped with GPS transmitters and evaluate the influences of vegetation, prescribed fire, and landscape features (e.g., roads, edge) on nest site selection and nest survival in a pine-dominated ecosystem.

STUDY AREA

We conducted research on Kisatchie National Forest (KNF) and Fort Polk Wildlife Management Area (WMA) in west-central Louisiana. Kisatchie National Forest and Fort Polk

WMA experienced subtropical climates, with mean daily temperatures ranging from a low of 9.4°C in January to 28.3°C in July, and mean annual rainfall of approximately 114 cm. Kistachie National Forest was owned and managed by the United States Forest Service (USFS) and is divided into 5 Ranger Districts. We conducted research on the Kisatchie Ranger District, Winn Ranger District, and the Vernon Unit of the Calcasieu Ranger District located in Natchitoches, Winn, and Vernon parishes, respectively. Fort Polk WMA was jointly owned by the USFS and the United States Army. The northern portion of Fort Polk WMA owned by the United States Army was within the Fort Polk Joint Readiness Training Center, whereas the southern portion was within the Vernon Unit of KNF. Environmental conditions and forest management practices were similar on the Vernon Unit and Fort Polk WMA; hence, we considered these areas as a single study site. The spatial extents of Kisatchie Ranger District, Winn Ranger District, and the Vernon-Fort Polk area were approximately 41,453 ha, 67,408 ha, and 61,202 ha, respectively. The area was composed of pine-dominated forests, hardwood riparian zones, and forested wetlands, with forest openings, utility right-of-ways, and forest roads distributed throughout. Overstory trees included loblolly pine (*P. taeda*), longleaf pine, shortleaf pine (*P. echinata*), slash pine (*P. elliottii*), sweetgum (*Liquidambar styraciflua*), oaks (*Quercus* spp.), hickories (*Carya* spp.) and red maple (*Acer rubrum*). Understory plants included yaupon (*Ilex vomitoria*), American beautyberry (*Callicarpa americana*), blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), wild grape (*Vitis* spp.), broomsedge (*Andropogon virginicus*), woodoats (*Chasmanthium* spp.), and panic grasses (*Panicum* spp. and *Dichanthelium* spp.). Privately owned land within and surrounding KNF was also available to turkeys. Much of this land was used for industrial timber production and comprised even-aged stands of loblolly pine and recent clearcuts ≤4 years old. Pine stands on private lands were typically not managed with frequent prescribed burns; hence, forest conditions on these lands generally differed from those on KNF. Forest stands on private lands typically had lower diversity of overstory tree species, greater canopy cover, and less dense understory growth than KNF. Other private lands in the area consisted of small rural settlements, agricultural fields, pastures, and hardwood-dominated forested wetlands. Common predators of turkeys and turkey nests at KNF and surrounding areas included coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), Virginia opossum (*Didelphis virginiana*), raccoon, Cooper's hawk (*Accipiter cooperii*), and barred owl (*Strix varia*).

Land managers on KNF used prescribed fire to promote the growth of longleaf pine, inhibit the growth of undesirable hardwood species, and reduce fuel loads (Haywood 2012). Prescribed fire was primarily applied to upland sites containing pine-dominated and mixed pine-hardwood stands. Prescribed fire was applied in both dormant seasons (Dec–Mar) and growing seasons (Apr–Jul), with most fires (71.3% of total area burned) applied in dormant seasons (Table S1, available online in Supporting Information). The

average size of burn patches on KNF was 484.9 ± 295.3 (SD) ha (Table S2, available online in Supporting Information) but ranged from 7.2 ha to 1,567.4 ha. The proportion of public land within the study area burned annually was 23.2% and 19.2% in 2014 and 2015, respectively (Table S2). Most upland pine stands were burned on a 3–5-year rotation, although some areas had no recent burn history at the time of this study. Prescribed burning was uncommon on private lands within the boundary of and surrounding KNF.

METHODS

Animal Capture and Monitoring

We captured female turkeys using rocket nets during January–March 2014 and 2015. We classified each turkey as adult or subadult based on presence of barring on the ninth and tenth primary feathers (Pelham and Dickson 1992). We also fitted each turkey with a backpack-style GPS transmitter equipped with a very high frequency (VHF) signal and mortality sensor weighing approximately 88 g (Lotek Minitrack Backpack L; Lotek Wireless, Newmarket, Ontario, Canada). We programmed GPS transmitters to record hourly locations from 0600 to 2000 each day and 1 nightly roost location at midnight, with the exception that in 2014, we collected only roost locations prior to 15 February. We released all birds on site immediately after processing. Turkey capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee at the University of Georgia (protocol no. A3437-01).

We used a hand-held, 3-element Yagi antenna and R2000 receiver (Advanced Telemetry Systems, Isanti, MN, USA) to locate and monitor status of radio-marked turkeys ≥1 time per week from mid-February to mid-August. We downloaded GPS locations from each turkey ≥1 time per week during the nesting period (Apr–Jul) to monitor nesting activity. We viewed GPS locations and considered a female to be incubating a nest when recorded locations did not significantly deviate from a central location for several days. Once we determined a female was laying or incubating a nest, we monitored its location using VHF telemetry and GPS locations until nest termination. After nest termination, we located nest sites using GPS locations to determine nest fate, clutch size (no. eggs incubated), brood size (no. eggs hatched), and to confirm the estimated nest location (via GPS locations) for future analysis. Wild turkey nests require approximately 27 days of continuous incubation before hatching (Williams et al. 1971), but incubation time in pen-raised turkeys has ranged from 25 to 29 days (Healy and Nenno 1985). Therefore, we considered a nest abandoned if the female left the nest before 30 days of incubation and only intact eggs were found at the nest bowl. We visually examined every nest after females had stopped incubating to inspect for egg shell remnants. We then located each female immediately post-incubation and conducted a brood survey in which we attempted to flush any potential poults that may have hatched. We assumed if we found a nest bowl with no eggs or egg shell remains nearby, and we were unable to identify any poults with the female post-incubation, that the nest had been predated. We recognize the possibility that a nest may have hatched and the poults were immediately predated on, but we conducted poult surveys as quickly as possible post-hatch to minimize this possible bias. We considered a nest successful if ≥1 live poult hatched, which we confirmed visually during our brood survey. We defined nesting rate as the proportion of females that initiated ≥1 nest. We defined second nesting rate as the proportion of females that initiated a second nest following the loss of the first nest or brood, and so on for all subsequent nest attempts. We defined nest success rate as the proportion of nests that were successful, and overall reproductive success as the proportion of females that attempted ≥1 nest and hatched ≥1 egg.

Explanatory Variables Influencing Nest Site Selection and Nest Survival

Local-scale characteristics at nest site.—After nest termination, we evaluated vegetation characteristics at nest sites by conducting vegetation surveys within a 15-m radius circular plot based on the methodologies of Streich et al. (2015) and Little et al. (2016) to facilitate comparisons. We recorded tree density, percent canopy cover, percent ground cover, average understory vegetation height (cm), and visual obstruction (cm). We measured tree density by counting all trees ≥10.16 cm diameter breast height (DBH) within 15 m of the nest bowl.

We measured percent canopy cover using a convex spherical densiometer (Lemmon 1956) held 1 m from the ground, such that vegetation within any strata above 1 m contributed to readings. We chose 1 m to best approximate the height of a wild turkey (Pelham and Dickson 1992). We measured canopy cover above the nest bowl and at a distance of 15 m in each of the cardinal directions using a densiometer, then calculated a mean of the 5 readings. We also measured percent understory canopy cover (i.e., ground cover) by placing a 1-m^2 quadrat frame on the ground and viewing the quadrat from directly overhead. We recorded percent ground cover as the percentage of ground within the quadrat that was visually obstructed by vegetation. We recorded percent ground cover at the center of the nest bowl and 15 m in each cardinal direction, and used the mean value from all 5 frames.

To evaluate height of understory vegetation and quantify visual obstruction, we used a 2-m Robel pole (Robel et al. 1970). We placed the Robel pole in the nest bowl and took readings from 15 m in each cardinal direction. We measured visual obstruction as the lowest point of the Robel pole we could see when viewing from a height of 1 m above the ground, and estimated average height of understory vegetation along our line of sight between the nest bowl and a point 15 m from the nest in each cardinal direction. We averaged Robel pole readings from all 4 readings to estimate mean vegetation height and visual obstruction. For each nest site, we randomly chose a location within 100–200 m of the actual nest site and conducted surveys identical to those at nest sites. This location was presumably a site that a female could have selected as an alternative nest site, and acted as a paired random location in our analyses.

Landscape-scale characteristics around nest site.—To delineate major plant communities within our study area, we obtained forest inventory data from the USFS, the United States Army Environmental and Natural Resources Division, and local timber companies. We then developed a 30-m resolution land cover map of major plant communities throughout our study area. We classified forest stands as pine if they consisted of ≥70% loblolly, longleaf, slash, or shortleaf pine in the overstory. We classified pine stands as mature if they were ≥20 years old and consisted primarily of trees in the pulpwood and sawtimber classes (≥20.4 cm DBH). We classified pine stands as immature if they were <20 years old and consisted of trees in the seedling, sapling, and pulpwood classes (range = 0–20.3 cm DBH). Mixed pine-hardwood stands consisted of a variety of tree species, including loblolly pine, longleaf pine, slash pine, sweetgum, white oak (*Quercus alba*), swamp chestnut oak (*Q. michauxii*), sassafras (*Sassafras albidum*), hickories, and Southern magnolia (*Magnolia grandiflora*). We classified stands as mixed pine-hardwood if they were 50–70% pine or hardwood. Within mixed-pine hardwood stands, trees ranged in size from seedling and sapling to mature sawtimber. Hardwood stands were confined to streamside management zones (SMZs), river bottoms, and forested wetlands. Hardwood stands comprised oaks, cypress (*Taxodium distichum*), and river birch (*Betula nigra*), with trees ranging in size from seedling and sapling to mature sawtimber. We classified wildlife food plots, pastures, agricultural fields, and clearcuts (≤4 yr) as open areas. Wetland areas were herbaceous or non-forested. Developed areas included human structures and settlements or barren land that was not considered to be turkey habitat.

Before calculating landscape-scale characteristics around known nest sites, we also generated random sites within each individual's available nesting area. We defined available nesting areas as the space used by each individual during the pre-nesting period. The pre-nesting period precedes the laying sequence during which females typically deposit 1 egg/day in the nest (Williams et al. 1971). Based on an average clutch size of approximately 12 eggs (Vangilder 1992), we estimated that the laying sequence would occur during the 12 days prior to onset of continuous nest incubation. We estimated pre-nesting range using a dynamic Brownian bridge movement model (dBBMM; Kranstauber et al. 2012) to calculate 95% utilization distributions (UDs) using each turkey's locations collected from time of capture until beginning of the laying sequence for the first nest of the season. We used a window size of 15 and a margin of 5 as input parameters for the dBBMM (Kranstauber et al. 2012, Byrne et al. 2014). To ensure we created enough random locations to capture the available landscape features for each turkey, we generated paired random locations for each individual by creating 5 random locations to 1 nest location within each individual turkey's pre-nesting range. For example, if a turkey attempted 2 nests during the reproductive season, we generated 10 random locations within its pre-nesting range.

Because features surrounding a nest site may affect resources available and predation risk, therefore influencing nest site selection (Martin and Roper 1988), we used Euclidean distance analysis (EDA; Conner et al. 2003) to calculate distances of nest and random sites to specific plant communities and landscape features. We calculated distances to the nearest plant community (e.g., mature pine, young pine, mixed pine-hardwood, hardwood, and open area) and landscape feature (e.g., road, and edge between 2 different plant communities [edge]; Little et al. 2016) by generating distance raster grids as described by Benson (2013). We then intersected all known nest locations and random locations with distance maps and extracted the distance to the nearest specified plant community and landscape feature. Before data analysis, we scaled all distance variables by dividing the linear distance by 100 m.

To evaluate influence of time-since-fire on nest site selection, we used spatial data of prescribed fire application history throughout our study area from public land management agencies and private timber companies, and classified each nest site based on history of prescribed fire at that location. Time-since-fire categories for each forest stand included not burned for ≥3 years (had experienced ≥3 growing seasons post-burn), burned 2 years prior (had experienced 2 growing seasons post-burn), burned the previous year (had experienced 1 growing season post-burn), or burned 0–5 months prior to the laying period (had experienced 0 growing seasons post-burn). As noted previously, we estimated that nest initiation occurred 12 days prior to onset of continuous incubation, and used the estimated nest initiation date as the reference date to calculate time-since-fire at each nest site. We then calculated time-since-fire at each random location generated within pre-nesting areas of use described above.

Analysis of Nest Site Selection

To examine if local- and landscape-scale characteristics affect nest site selection, we used conditional logistic regression with matched-pairs case-control sampling in package survival (Therneau and Lumley 2016) in program R version 3.1.1 (R Core Team 2013), where cases were nest sites and controls were random sites, to explain nest site selection of female turkeys (Keating and Cherry 2004). We assumed a lack of dependence of nests from the same turkey and treated each nest as an independent measurement even if it was a second or third nest from the same individual turkey. This approach allowed us to use model comparison and selection in an information-theoretic framework (Burnham and Anderson 2002). Similar to Little et al. (2016), we calculated Pearson's correlations (*r*) between explanatory variables at each scale prior to building our models. Because highly correlated variables ($|r| \geq 0.7$) included in the same model inflate estimates of variance and hinder biologically relevant interpretation of data, we only retained the variable that provided the simplest biological interpretation (Dormann et al. 2013). We then evaluated variance inflation factors of all variables to assess any remaining collinearity. All remaining variables contained variance inflation factor <4.0, suggesting collinearity would not affect the results of our analyses (Zuur et al. 2009).

We developed 7 models to understand what local vegetation variables best predicted nest site selection within 15 m of the nest (Table 1). We created our first 4 models

Table 1. Akaike's Information Criterion with small sample bias adjustment (AIC$_c$), number of parameters (K), ΔAIC$_c$, adjusted Akaike weight of evidence (w_i) in support of model, and log-likelihood (LL) for candidate models examining factors influencing nest site selection of female eastern wild turkeys at Kisatchie National Forest, west-central Louisiana, USA, 2014 and 2015. Models used a conditional logistic regression with matched-pairs case-control sampling, where cases were nest sites and controls were random sites, to explain nest site selection of female turkeys.

Model	K	AIC$_c$	ΔAIC$_c$	Adjusted w_i	LL
Local scale[a]					
Ground cover	1	109.65	0.00	0.68	−53.81
Ground cover + VO	2	111.61	1.96	0.25	−53.76
Global	4	114.67	5.02	0.05	−53.18
Null	0	119.57	9.92	0.00	−59.78
VO	1	119.78	10.13	0.00	−58.88
Trees per hectare	1	119.84	10.19	0.00	−58.90
Canopy cover	1	121.59	11.94	0.00	−59.78
Landscape scale[b]					
Road + edge + fire	5	256.79	0.00	0.58	−123.32
Road + edge	2	257.92	1.13	0.23	−126.95
Global	10	260.47	3.68	0.09	−119.95
Fire	3	273.03	16.24	0.00	−133.49
Landcover + fire	8	273.28	16.49	0.00	−128.46
Landcover	5	278.28	21.49	0.00	−134.10
Null	0	280.81	24.02	0.00	−140.40

[a] Models correspond to vegetation characteristics selected at the nest site and include variables percent canopy cover, percent total ground cover vegetation, trees per hectare, and lateral visual obstruction (VO).

[b] Landscape-scale variables within models include distances to the following land covers: hardwood, mature pine, mixed pine-hardwood, open areas, and young pine (landcover). Models also include distances to nearest road (road), edge between forested 2 different plant communities (edge), and the time-since-fire (fire; 0–5 months post-burn, 1 year post-burn, 2 yr post-burn, and ≥3 yr post-burn) in the forest stand where the nests and random locations were located.

based on predictions that nest site selection was influenced by tree density, canopy closure, percent ground cover, or visual obstruction provided by understory vegetation. Because nest site selection may be based on the ground cover available and the visual obstruction provided by vegetation (Little et al. 2016), our fifth model predicted that nest site selection was best explained by both percent ground cover and visual obstruction. Clearly, we measured all of these variables because we believed they may affect nest site selection. Therefore, we created a global model, which predicted nest site selection is best explained by all vegetation characteristics measured. We compared all of these models to a null model, which predicted nest site selection was not affected by any of the local vegetation metrics we measured at the nest site.

We developed 7 models to understand what landscape-scale variables best predicted nest site selection. Turkey nest site selection may be influenced by proximity to mature pine plant communities (Miller et al. 1999, Thogmartin 1999, Kilburg et al. 2014, Streich et al. 2015), young pine plant communities (Burk et al. 1990), mixed pine-hardwood plant communities (Burk et al. 1990, Streich et al. 2015), hardwood plant communities (Thogmartin 1999), and open areas (Byrne and Chamberlain 2013, Streich et al. 2015). Concurrently, turkeys are often reported to nest near linear landscape features such as roads or trails (Hon et al. 1978, Thogmartin 1999, Moore et al. 2010) and edges

between 2 vegetation types (Byrne and Chamberlain 2013, Kilburg et al. 2014). We created our landscape-scale models to incorporate previous findings and our prescribed fire data to better understand how time-since-fire affects turkey nest site selection. Our first model examined was based on vegetation communities and predicted that nest site selection was best predicted by proximity to mature pine, young pine, mixed pine-hardwood, and open areas. Our second model was based on turkey's affinity for linear landscape features and predicted nest site selection was affected by proximity to roads and forest edges. To determine if time-since-fire of the vegetation community was an informative parameter to our previous 2 candidate models, we added this covariate to each model to create our third and fourth candidate models. Our fifth candidate model examined if nest site selection was best predicted only by the time-since-fire covariate of the vegetation community. Our sixth model was a global model to determine if all landscape-scale variables we measured best predicted nest site selection. Our seventh model, a null model, predicted nest site selection was not affected by any landscape-scale variables we measured.

We used second-order Akaike's Information Criteria (AIC$_c$) to assess the amount of support for the different candidate models at each scale (Akaike 1973, Burnham and Anderson 2002). We calculated ΔAIC$_c$ values between the AIC$_c$ value for candidate model i and the lowest-ranked AIC value. We considered models with ΔAIC$_c$ values ≤2 to be good candidates for explaining patterns in the data. We also calculated adjusted Akaike's weights (w_i) for each model. We then calculated model-averaged parameter estimates, their standard errors, and associated P-values for all covariates in models within 2 ΔAIC$_c$ units of the lowest-ranked AIC value. We considered covariates to be statistically significant at $P \leq 0.05$ for all analyses. For statistically significant parameter estimates within each model, we calculated odds ratios to infer biological significance.

Modeling Nest Survival

To determine if nest site selection influenced the probability of nest success (e.g., ≥1 egg hatching), we evaluated patterns in nest survival in response to local- and landscape-scale covariates found to affect nest site selection using package survival (Therneau and Lumley 2016). The Cox proportional hazards model provides hazard ratios for each covariate term included in the model. Hazard ratios >1.0 indicate increasing probability of an event (e.g., nest failure) with increasing values for the covariate, whereas hazard ratios <1.0 indicate decreasing probability of an event with increasing values for the covariate. Prior to data analysis, we assessed the proportional hazards assumption for our models. We then calculated hazard ratios from Cox proportional hazards models using covariates included in the top-performing model (i.e., lowest-ranked AIC value) at both the local-scale and the landscape-scale. Because percent ground cover and visual obstruction were the covariates included in models ≤2 AIC$_c$ units of the lowest scoring model of nest site selection at the local scale, we developed a Cox proportional hazards model to examine the additive

influence of percent ground cover and visual obstruction on nest survival. At the landscape scale, time-since-fire, distance to edge, and distance to road were the covariates included in models ≤2 AIC_c units of the lowest scoring model. Therefore, we developed a Cox proportional hazard model examining the additive effects of time-since-fire, distance to edge, and distance to road to determine if these covariates affected nest survival.

RESULTS

We captured and radio-marked 55 female turkeys (45 adults and 10 subadults) during winters of 2014 and 2015. We monitored 69 nests from 40 individuals during the 2014 and 2015 nesting seasons. Two nests were discovered following the reproductive season via examination of turkey location data collected by GPS transmitters. Location data of the 2 females from these nests indicated that the turkeys were either stationary or moved very short distances for several days, which is characteristic of incubation behavior (Conley et al. 2015). Nesting rates were 87.0%, 65.6%, and 50% for first, second, and third nest attempts, respectively (Table 2) with 1 female attempting 4 nests, none of which were successful. Onset of initial nest incubation ranged from 5 April to 3 June ($\bar{x} = 28$ Apr; $n = 39$; Table S3, available online in Supporting Information). Onset of incubation of second nest attempts ranged from 26 April to 24 June ($\bar{x} = 23$ May; $n = 21$), third attempts ranged from 3 June to 12 July ($\bar{x} = 27$ Jun; $n = 7$) and 1 fourth nest attempt was incubated on 4 July (Fig. 1). We observed egg-laying behavior from approximately 25 March to 12 July, a span of 109 days (Fig. 2), and date of onset of continuous incubation ranged from 4 April to 19 July.

We censored 3 abandoned nests from analysis of nest success because abandonment was likely due to observer influence. Of the remaining 66 nests, 10 (15.2%) were successful, 36 (54.5%) were destroyed by predators, 3 (4.5%) failed because of predation of the female, 5 (7.6%) were abandoned, 1 (1.5%) was destroyed by a vehicle, and 11 (16.7%) failed because of unknown causes. One nest was exposed to fire after initiation, but the female returned to the nest the following day to continue egg deposition. No nests were exposed to prescribed fire during incubation. Nest success rates were 15.8%, 20.0%, and 0.0% for first, second, and third nest attempts, respectively (Table 2). Overall reproductive success (i.e., the proportion of females that attempt ≥1 nest and successfully hatched ≥1 nest) was 8.3% and 44.4% in 2014 and 2015, respectively.

In 2015, 1 female successfully hatched 2 broods within the same reproductive period. In 2014, of 24 females that nested, 2 hatched broods. In 2015, of 16 females that nested, 8 hatched broods. Six broods were lost within 14 days of hatching and 1 brood was lost between days 15–28 (Table S4, available online in Supporting Information). Of the 3 surviving broods, we estimated that in 2014 2 poults from 1 brood survived to 28 days, and in 2015 8 poults from 1 brood and 1 poult from another brood survived to 28 days.

Nest Site Selection

Females located nests in mature pine ($n = 55$; 79.7%), open area ($n = 5$; 7.2%), young pine ($n = 4$; 5.8%), hardwood ($n = 3$; 4.3%), and mixed pine-hardwood ($n = 2$; 2.9%). Of 51 nests located in pine stands with a prescribed fire history, nests were located in pine-stands burned ≤1 year prior ($n = 13$; 21.3%), 1 year prior ($n = 19$; 31.1%), 2 years prior ($n = 13$; 21.3%), and ≥3 years prior ($n = 16$; 26.2%; Table S5, available online in Supporting Information). At the local scale, average vegetation height was correlated with visual obstruction ($r = 0.854$), so we excluded average vegetation height from our models. Results from our AIC_c modeling exercise suggested percent ground cover ($w_i = 0.68$; Table 1) as the most informative covariate predicting nest site selection. The second best approximating model ($w_i = 0.25$; Table 1) indicated that visual obstruction and percent ground cover both affected nest site selection. Turkeys were more likely to nest in areas with increased percent ground cover ($\beta = 0.20$; $P \leq 0.01$; Table 3). Odds ratios indicated for every 5% increase in ground cover, female turkeys were 1.02 times more likely to select a site for nesting.

At the landscape scale, no covariates were significantly correlated in our candidate model set. The best approximating

Table 2. Nesting ecology of female eastern wild turkeys at Kisatchie Ranger District (KRD), Winn Ranger District (Winn), and Vernon Unit-Fort Polk Wildlife Management Area (V-FP) in west-central Louisiana, USA, 2014 and 2015.

Yr	Site	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]	% fourth nest (n)[h]	% fourth nest success
2014	KRD	21	85.7 (18)	5.9 (1)	60.0 (9)	0	33.3 (2)	0	0.0 (0)	
	Winn	7	85.7 (6)	16.7 (1)	80.0 (4)	0	100.0 (2)	0	50.0 (1)	0
2015	KRD	10	100.0 (10)	33.3 (3)	75.0 (6)	50.0 (3)	60.0 (3)	0	0.0 (0)	
	Vernon	6	66.7 (4)	25.0 (1)	33.3 (1)	0.0 (0)	0			
	Winn	2	100.0 (2)	0	100.0 (1)	100.0 (1)				
Pooled[i]		46	87.0 (40)	15.8 (6)	65.6 (21)	20.0 (4)	50.0 (7)	0.0 (0)	14.3 (1)	0

[a] Number of radio-marked females monitored from the earliest known nesting attempt (12 Apr 2014; 5 Apr 2015).
[b] Number of females initiating ≥1 nest.
[c] Number of first nest attempts hatching ≥ 1 live poult. Nests suspected of abandonment due to observer influence were censored from success estimates.
[d] Number of females initiating a second nest following the loss of a first nest or first brood within 30 days following hatch.
[e] Number of second nest attempts hatching ≥ 1 live poult. Nests suspected of abandonment due to observer influence were censored from success estimates.
[f] Number of females initiating a third nest following the loss of a second nest or brood within 30 days following hatch.
[g] Number of third nest attempts hatching ≥ 1 live poult.
[h] Number of females initiating a fourth nest following the loss of a third nest or brood within 30 days following hatch.
[i] Pooled across sites and years.
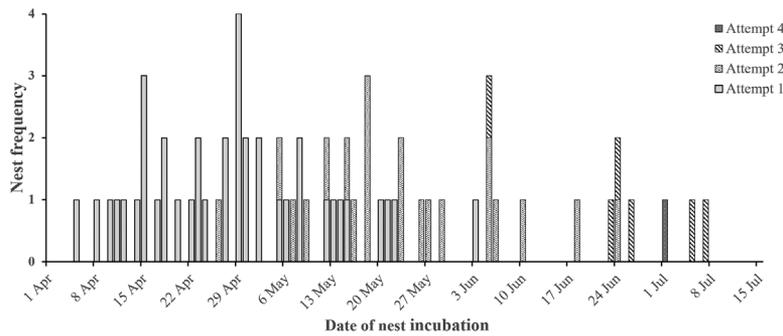
Figure 1. Chronology of onset of nest incubation for 40 female eastern wild turkeys at Kisatchie National Forest, west-central Louisiana, USA, 2014 and 2015. Nests are classified as first nest attempt (attempt 1), second nest attempt (attempt 2), third nest attempt (attempt 3), or fourth nest attempt (attempt 4).

AIC model ($w_i = 0.58$; Table 1) was the distance to edge, roads, and time-since fire model, indicating that nest site selection at the landscape scale was affected by proximity to these linear features (roads, edges), and years-since-fire. The second best approximating model ($w_i = 0.33$; Table 1), which was not statistically different from the best model, was the distance to edge and roads model, underscoring the strength roads and edges have in influencing nest site selection. Parameter estimates suggested turkeys preferred to nest closer to roads ($\beta = -0.31$; $P \le 0.01$; Table 3) and farther from edges ($\beta = 0.31$; $P \le 0.01$; Table 3). Odds ratios indicated nests were 1.36 times less likely to occur for every 100 m farther from roads and 1.36 times more likely to occur for every 100 m farther from edges. Also, turkeys tended to select to nest in areas 2 years post-fire when compared to areas burned 0–5 months before incubation, 1 year prior, and ≥ 3 years prior (Table 3). Odds ratios indicated turkeys were 3.81 times more likely to nest in an area burned 2 years prior.

Nest Survival

We excluded 3 nests that failed because of observer influence and 2 nests that were predated prior to the onset of continuous incubation from our nest survival analysis. Therefore, our final dataset for modeling which variables at the local- and landscape-scale most affected nest survival consisted of 64 nests. At the local scale, percent ground cover ($\beta = -0.16 \pm 0.09$; hazard ratio = 0.85; $P = 0.09$) and visual obstruction ($\beta = 0.03 \pm 0.04$; hazard ratio = 1.03; $P = 0.59$) did not influence nest survival (Table 4). At the landscape scale, time-since-fire influenced nest survival (Table 4). Nests located in stands burned ≥ 3 years prior to nest incubation were 3.84 times more likely to fail (Table 4). Distance to nearest edge ($P = 0.61$) and distance to road ($P = 0.13$) did not influence the likelihood of nest survival (Table 4).

DISCUSSION

Female turkeys on KNF had a longer reproductive season and higher nesting rates relative to other populations in the southeastern United States (Burk et al. 1990, Palmer et al. 1993, Miller et al. 1998, Thogmartin and Johnson 1999, Moore et al. 2010), and rates of second and third nest attempts were noticeably higher than in the aforementioned studies. We also observed 1 instance of a fourth nest attempt, which to our knowledge has only been reported once in the literature (Exum et al. 1987). In addition, we observed a female hatching a second brood following loss of the first brood; to our knowledge this has only been documented once in the
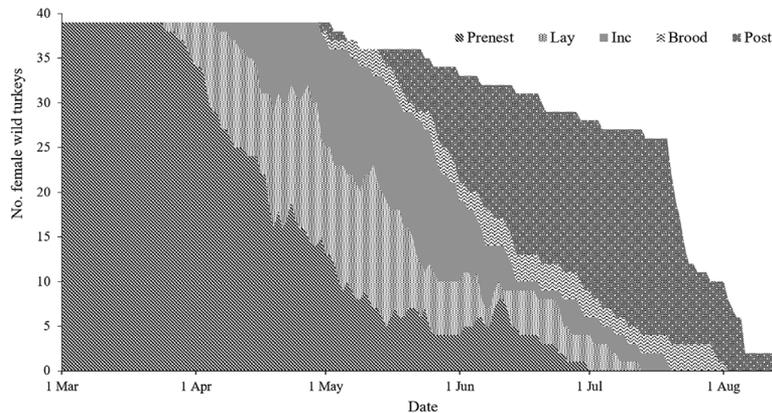
Figure 2. Chronology of female eastern wild turkey reproductive activity at Kisatchie National Forest, west-central Louisiana, USA, 2014 and 2015. Reproductively active females were grouped into the following categories based on reproductive phenology: prior to initiating first nest attempt (prenest), following nest failure or brood loss and prior to a subsequent nest attempt (prenest), laying a clutch associated with any nest attempt (lay), incubating a nest (inc), brood-rearing (brood), and following all nest attempts or after surviving poults reach 56 days old (post).

Table 3. Parameter estimates from the best approximating model predicting nest site selection of female eastern wild turkeys at Kisatchie National Forest, west-central Louisiana, USA, 2014 and 2015. Negative values associated with distance to nearest road and distance to edge are associated with nest sites being closer and are interpreted as selecting for these landscape features; positive values represent the opposite. Time-since-fire was a categorical covariate and values are in comparison to time-since-fire values of 0–5 months prior to incubation; positive values represent selection for the category compared to this baseline category.

Model	β[a]	SE	Z	P
Local-scale model				
Ground cover	0.20	0.06	3.09	≤0.01
Visual obstruction	0.00	0.03	0.31	0.87
Landscape-scale model				
Time since-fire				
1 yr	0.03	0.45	0.07	0.94
2 yr	1.34	0.57	2.36	0.02
≥3 yr	0.00	0.44	0.10	0.99
Distance to nearest road[b]	−0.31	0.11	2.91	≤0.01
Distance to edge[b]	0.31	0.10	3.24	≤0.01

[a] Parameter estimate on logit scale.
[b] Distances scaled by dividing by 100 m.

literature (Sisson et al. 1991). Predation was the primary cause of nest failure. Most brood loss occurred within 2 weeks of hatching when young poults were flightless and most vulnerable to predation (Glidden and Austin 1975, Everett et al. 1980, Speake et al. 1985). High reproductive effort, in the form of re-nesting after nest depredation, could result from good physiological condition attributable to habitat quality on site (Miller et al. 1998). Conversely, our findings could be an artifact of our increased ability to monitor movements and reproductive behaviors of females via the use of GPS transmitters (Collier and Chamberlain 2010).

Percent ground cover vegetation, which represents the direct overhead concealment provided by herbaceous and woody vegetation, best predicted nest site selection at the local scale. This is not surprising because most previous researchers evaluating vegetation conditions reported nest selection to be positively associated with percent ground cover or density of ground story vegetation (Chamberlain and Leopold 1998, Byrne and Chamberlain 2013, Fuller et al. 2013, Kilburg et al. 2014, Streich et al. 2015). Conversely, visual obstruction at the nest was not an

important predictor of nest site selection, contrary to several recent studies (Byrne and Chamberlain 2013, Streich et al. 2015, Little et al. 2016). In the closed canopy bottomland forests studied by Byrne and Chamberlain (2013), understory vegetation was reportedly sparse and limited availability of nesting cover. Likewise, the longleaf pine savanna studied by Streich et al. (2015) featured a more open canopy and was treated with prescribed fire on shorter return intervals (1–3 yr) than what occurred on KNF. Similar to Kilburg et al. (2014), although percent ground cover vegetation was an important predictor of nest site selection, it did not statistically affect nest survival. Nest concealment and vegetation structural heterogeneity have been reported to reduce predation risk (Bowman and Harris 1980), but predation risk might be more related to characteristics at larger scales (e.g., patch, stand) than vegetation characteristics at the nest site.

We found proximity to roads and proximity to edge of 2 different plant communities influenced nest site selection but not nest survival. Previous researchers have noted the propensity for turkeys to nest near roads and firebreaks (Hon et al. 1978, Badyaev 1995, Thogmartin 1999, Moore et al. 2010, Kilburg et al. 2014). Roads may represent one of several potential resources to reproductively active females. Badyaev (1995) suggested that females used roads to travel to and from nests during incubation, which may have reduced noise as compared to traveling through understory vegetation. Roadsides may also provide females quality foraging resources because they are typically dominated by herbaceous plant species capable of providing seeds and insects (Hurst and Stringer 1975). Conversely, higher predation pressure is associated with edges (Batáry and Báldi 2004, Sálek et al. 2010), and avoidance of these transitional areas may be a mechanism to decrease encounters with predators.

Female turkeys on KNF nested in forest stands of all burn history categories. However, females selected nest sites in forest stands burned 2 years prior compared to stands burned 0–5 months prior, 1 year prior, and ≥3 years prior. Similarly, both Sisson et al. (1990) and Still and Baumann (1990) reported most turkey nests were located in stands burned within 2 years. In an insular turkey population of coastal Georgia, USA, females nested in stands burned the current

Table 4. Results of Cox proportional hazards models of risk of eastern wild turkey nest failure at Kisatchie National Forest in west-central Louisiana, USA, 2014 and 2015.

Model	β[a]	SE	P	Hazard ratio	Hazard ratio CI Lower 95%	Upper 95%
Local-scale model						
Ground cover (%)	−0.16	0.09	0.09	0.85	0.70	1.03
Visual obstruction (%)	0.03	0.04	0.59	1.03	0.93	1.13
Landscape-scale model						
Time-since-fire						
1 yr	0.72	0.48	0.12	2.04	0.83	5.03
2 yr	0.85	0.54	0.13	2.34	0.78	7.03
≥3 yr	1.35	0.47	0.01	3.84	1.37	10.70
Distance to nearest road (m)[a]	0.14	0.09	0.13	1.15	0.96	1.36
Distance to edge (m)[a]	−0.05	0.10	0.61	0.95	0.77	1.17

[a] Distances scaled by dividing by 100 m.

or previous year and avoided nesting in an areas not burned for 15 years (Hon et al. 1978). In southern pine forests, shrubs and woody vines are prominent 2 years following prescribed fire applications (Hodgkins 1958). Conversely, fire exclusion results in a midstory of shade-tolerant trees and sparse understory vegetation (Lewis and Harshbarger 1976). The consensus among turkey managers remains that a forest with sparse understory vegetation and a dense midstory does not provide suitable nesting cover for turkeys (Kilburg et al. 2014). Concurrently, time-since-fire had greater influence on nest survival than any other landscape feature. In particular, nests in stands burned ≥3 years prior had the lowest probability of survival. Fire stimulates growth of non-woody plants and does not typically kill root systems of woody plants, providing dense understory vegetation, and higher percent ground cover, in the months and years following fire (Peterson and Reich 2001). In addition, prescribed fire may decrease predator efficiency by reducing structural complexity of an area. For example, raccoons forage for artificial nests more efficiently in areas with higher vegetation structural heterogeneity (Bowman and Harris 1980). Collectively, female turkeys select areas that providing concealment around the nest inside forested stands providing higher probability of reproductive success. These decisions affect reproductive success, suggesting there may be innate or learned cues associated with this behavior. Future research comparing the importance of learned and evolutionary responses in nest site selection would be another step in understanding selective pressures underlying turkey behavior (Ibáñez-Álamo et al. 2015) and may enhance future management efforts.

MANAGEMENT IMPLICATIONS

Our data demonstrate the relatively long duration of nesting behaviors in wild turkeys, and hence, the likelihood that females will attempt multiple nests well into summer. Concealment, particularly ground cover vegetation immediately surrounding the nest, is an important factor influencing nest site selection of wild turkeys. Given turkeys selected to nest in stands that had been burned 2 years prior and the decrease in nest survival in stands burned ≥3 years ago, turkeys may benefit from a 3-year fire return interval (i.e., applying prescribed fire after 3 growing seasons). At KNF, most fires were applied in the late dormant season, prior to the nesting period. Therefore, we suggest that burning on a 3-year fire return interval in southeastern pine-dominated forests such as KNF is compatible with management for turkeys.

ACKNOWLEDGMENTS

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