




Research Article

Wild Turkey Nest Success in Pine-Dominated Forests of the Southeastern United States

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ABSTRACT Nest success is a primary component of productivity for wild turkeys (*Meleagris gallopavo*; turkeys) and there is concern that turkey productivity is declining across the southeastern United States. We evaluated the influence of nest site and landscape characteristics on risk of nest failure for turkeys in pine (*Pinus* spp.)-dominated forests across the southeastern United States. We used Cox proportional hazard models to evaluate daily hazard of nest failure associated with nest site and landscape metrics within 500-m and 1-km buffers centered on nests. Of 451 nests monitored ($n = 320$ females) between 2014 and 2018, 76% failed, with predation as the primary cause. Daily hazard of nest failure increased by 1.2% for each day that females delayed nest incubation following the mean nesting date (29 Apr; $\beta_{\text{day}} = 0.010 \pm 0.002$ [SE]; hazard ratio [HR] = 1.01, 95% CI = 1.006–1.015). Environmental covariates associated with risk of nest failure included the maximum enhanced vegetation index (EVI) and distance to the nearest ecotone. Daily hazard increased with increasing distance away from an ecotone ($\beta_{\text{ecotone}} = 0.16 \pm 0.06$; HR = 1.17, CI = 1.03–1.32) and with lower EVI around the nest ($\beta_{\text{EVI}} = -0.30 \pm 0.06$; HR = 0.74, CI = 0.65–0.83). Additional nest site or landscape covariates were included in competitive models but did not influence risk of nest failure significantly. Our study highlights the importance of considering landscape context when designing and implementing land management actions intended to enhance wild turkey reproduction. Our findings suggest that landscape metrics thought to be important to turkeys in northern agro-forested landscapes may not be relevant to turkeys in pine ecosystems of the southeastern United States. © 2021 The Wildlife Society.

KEY WORDS habitat, landscape composition, *Meleagris gallopavo*, predation, prescribed fire, vegetation index.

Following successful restoration of wild turkeys (*Meleagris gallopavo*; turkey) during the twentieth century, biologists are expressing concern that turkey populations are declining across the eastern United States (Porter et al. 2011, Casalena et al. 2015, Eriksen et al. 2015). Brood surveys have indicated declines in productivity across the Southeast and in parts of the Northeast, but causes of population declines remain unclear (Byrne et al. 2015, Casalena et al. 2015). Productivity indices reflect the successful completion of several stages of reproduction, from nest initiation to poult survival, and each stage is accompanied by a set of intrinsic and extrinsic factors that influence the probability of surviving into the next stage (Healy and Powell 1999). Understanding factors that influence nest success is important because annual production is a key component of

population dynamics in turkeys (Roberts and Porter 1996, Pollentier et al. 2014a).

Turkeys benefit from landscapes with moderate amounts of interspersed forest and early successional land cover (Healy and Powell 1999). Within these landscapes, nest success is variable temporally and spatially, with predation being the primary cause of nest failure (Roberts et al. 1995, Miller et al. 1998, Hughes et al. 2007, Fuller et al. 2013, Little et al. 2014). Evaluations of factors influencing nest success for wild turkeys have focused on vegetative conditions immediately around the nest because ground cover and visual obstruction are thought to mitigate predation risk (Orians and Wittenberger 1991, Lehman et al. 2008, Fuller et al. 2013). Previous researchers noted that females selected nest sites in areas with sufficient ground cover to provide concealment from predators (Thogmartin 1999, Byrne and Chamberlain 2013, Fuller et al. 2013, Streich et al. 2015, Wood et al. 2019). But recent studies across the southeastern United States have reported little evidence that nest site vegetative conditions influence nest survival (Little et al. 2014, Streich et al. 2015, Yeldell et al. 2017a). Several authors have examined the influence of landscape composition at multiple scales on nesting ecology of turkeys

Received: 21 November 2019; Accepted: 28 December 2020

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(Thogmartin 1999, Byrne and Chamberlain 2013, Fuller et al. 2013, Pollentier et al. 2014b, Fleming and Porter 2015). To date, however, only researchers using artificial nests in their studies have reported relationships between nest survival and landscape configuration at larger spatial extents beyond the nest (e.g., 5–10 km around nests; Fleming and Porter 2015, Morris and Conner 2016).

The context in which landscape configuration and fragmentation occurs may influence the relative importance of predation on nest success in wild turkeys. Fragmentation in mixed agro-forested landscapes can promote high densities of nest predators (Prugh et al. 2009, Beasley et al. 2011). Likewise, the size of the forest stand and proximity of nests to edges influenced predation risk on artificial nests in agro-forested landscapes of the Northeast (Fleming and Porter 2015). But the degree to which landscape configuration influences predation risk in forested ecosystems of the southeastern United States is unclear. Pine (*Pinus* spp.) forests are the dominant cover type in the Southeast, and on public lands, may be maintained via prescribed fire every 3–5 years (Carter and Foster 2004). Fire plays an important role in creating suitable nesting conditions for wild turkeys (Cohen et al. 2019). Consequently, ground vegetation conditions on public lands in the Southeast may be considerably different from those in agro-forested regions of the Northeast and Midwest, and landscape metrics identified in northern studies may not be useful for turkey management in southern forests.

We evaluated factors that may influence nest success of 320 female wild turkeys inhabiting pine-dominated forests of the southeastern United States. We used a data set that spanned multiple study sites over a 5-year period to examine the degree to which landscape configuration at multiple scales influenced risk of nest failure. We hypothesized that

landscape variables would influence nest success of wild turkeys. We predicted that nests located closer to forest edges would have greater rates of nest failure because nest predators often travel and forage along edges. Likewise, we predicted that landscape fragmentation would increase risk of nest failure because nest predator densities often are positively associated with fragmented landscapes (Fleming and Porter 2015).

STUDY AREA

We conducted research on nest survival January–August 2014–2018 at 9 sites in Louisiana, Georgia, and South Carolina, USA (Fig. 1). All of our study sites were dominated by pine-hardwood forest communities managed with dormant and growing season prescribed fire to manage understory vegetation communities. Across study sites, mean temperature ranged from 17.9°C to 18.5°C (range = 3–34°C; <https://usclimatedata.com/>; accessed 15 Feb 2020), and average elevation ranged from 25 m to 520 m (<https://weatherspark.com/>; accessed 15 Feb 2020). Topography ranged from rolling hills to flat coastal plain, and climate was characterized by hot, dry summers (Jun–Aug) and cool, wet winters (Nov–Feb). Spring months (Mar–May) generally were warm and wet with last freeze dates occurring in March. Fall months (Sep–Oct) were warm and dry. We conducted research on the Kisatchie National Forest (KNF), Peason Ridge Wildlife Management Area (PRWMA), and Catahoula Ranger District (CRD) in west-central Louisiana. The spatial extents of KNF, PRWMA, and CRD were approximately 41,453 ha, 30,071 ha, and 49,169 ha, respectively. Kisatchie National Forest and CRD were owned and managed by the United States Forest Service (USFS), whereas PRWMA was owned by the United States

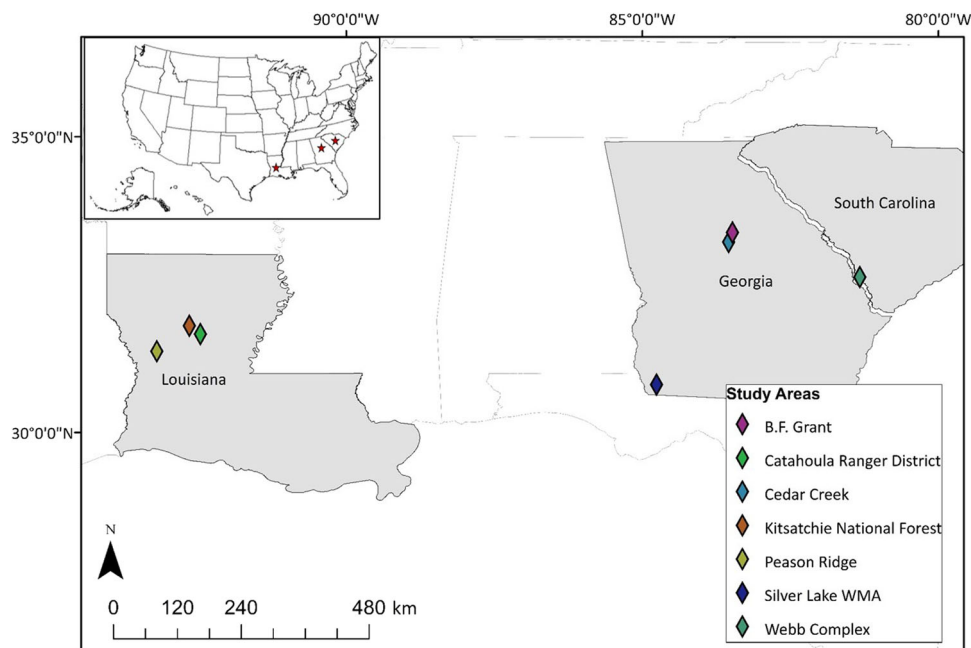


Figure 1. Locations of 9 field sites across the southeastern United States where we monitored wild turkey nests ($n = 451$) and assessed local habitat and landscape conditions, 2014–2018. The Webb Complex in South Carolina represented 3 contiguous wildlife management areas (WMAs).

Department of Defense (U.S. Army) but managed in collaboration with the Louisiana Department of Wildlife and Fisheries. Mammalian nest predators on these sites included bobcats (*Lynx rufus*), coyotes (*Canis latrans*), raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and striped skunks (*Mephitis mephitis*). Each site was composed of pine-dominated forests, hardwood riparian zones, and forested wetlands, with forest openings, utility right-of-ways, and forest roads distributed throughout. Primary overstory species included longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), oaks (*Quercus* spp.), hickories (*Carya* spp.), and red maple (*Acer rubrum*). Prescribed fire was applied on an approximately 3–5-year rotation. Yeldell et al. (2017a) provide a detailed description of site conditions on KNF.

We also conducted research on 3 wildlife management areas in Georgia: Cedar Creek, B. F. Grant, and Silver Lake Wildlife Management Areas (SLWMA), with spatial extents of approximately 15,873 ha, 4,613 ha, and 3,723 ha, respectively. The Georgia Department of Natural Resources-Wildlife Resources Division (GADNR) owned and managed SLWMA. Mature pine forests and forested wetlands were the dominant land cover types on the site. Overstory species were predominately longleaf pine, loblolly pine, slash pine (*P. elliotii*), oaks, and sweetgum (*Liquidambar styraciflua*). Prescribed fire was applied on an approximately 2–3-year return interval. Wood et al. (2019) provide a detailed description of site conditions on SLWMA. B. F. Grant Wildlife Management Area was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia, and was managed jointly by GADNR and the Warnell School. B. F. Grant was dominated by loblolly pine stands, agricultural lands, mixed hardwood and pine forests, and hardwood lowlands containing mostly oaks, sweetgum, and hickory. Agricultural lands were mostly grazed mixed fescue (*Festuca* spp.) fields and hay fields planted for rye grass. Cedar Creek Wildlife Management Area was owned by the USFS and managed in partnership with GADNR. Cedar Creek was composed primarily of loblolly pine uplands, mixed hardwood and pine forests, and hardwood lowlands of similar species composition as B. F. Grant. Prescribed fire was applied on an approximately 3–5-year rotation.

Lastly, we conducted research on 3 contiguous wildlife management areas (Webb, Hamilton Ridge, and Palachucola; Webb WMA Complex) in South Carolina, all managed by the South Carolina Department of Natural Resources (SCDNR). The 25,900-ha Webb WMA Complex was dominated by longleaf, loblolly, and slash pine forests with hardwood stands along riparian corridors, and expanses of bottomland hardwood wetlands. Prescribed fire was applied on an approximately 3–5-year return interval. Wightman et al. (2019) provide a detailed description of site conditions on the Webb WMA Complex.

METHODS

We captured female wild turkeys using rocket nets from January–March, 2014–2018. We determined age based on presence of barring on the ninth and tenth primary feathers (Pelham and Dickson 1992). We banded each bird with an

aluminum rivet leg band (National Band and Tag Company, Newport, KY, USA) and radio-tagged each individual with a backpack-style global positioning system (GPS)-very high frequency (VHF) transmitter (Guthrie et al. 2011) produced by Biotrack (Wareham, Dorset, United Kingdom). We programmed transmitters to take 1 location nightly (~2359) and hourly locations between 0500 and 2000 until the battery died or the unit was recovered (Cohen et al. 2018). We immediately released turkeys at the capture location after processing. All turkey capture, handling, and marking procedures adhered to guidelines for the use of wild animals in research and were approved by the Institutional Animal Care and Use Committee at the University of Georgia (protocol A2014 06-008-Y1-A0 and A3437-01) and the Louisiana State University Agricultural Center (protocol A2014-013 and A2015-07).

We located females ≥ 2 times per week via VHF to monitor survival and nesting activity. We downloaded GPS locations from each female ≥ 1 time per week, and viewed GPS locations to determine when female locations became concentrated around a single point (Yeldell et al. 2017a, b). Once we concluded females were laying or incubating, we monitored each individual daily using VHF telemetry and GPS locations to monitor activity on the nest. After nest termination, we visited the nest site to determine if hatching had occurred and to verify the precise location of the nest (Conley et al. 2016; Yeldell et al. 2017a, b; Bakner et al. 2019). When nests showed signs that eggs had hatched, we located each female and conducted a brood survey to determine if poults were present (Chamberlain et al. 2020). 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 considered a nest successful if ≥ 1 live poult hatched, which we confirmed visually during our brood survey (Chamberlain et al. 2020). Because our work focused on known nest attempts, we defined the 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 as the proportion of nests that were successful.

Nest- and Landscape-Scale Characteristics

Nest success may be influenced by where the nest is located relative to landscape features and by land cover composition and configuration at multiple scales around the nest. Incubating females, including females in our study, restrict their movements compared to pre- and post-nesting periods (Conley et al. 2016, Bakner et al. 2019). Females monitored at the KNF site during 2014 and 2015 had an average 95% incubation home range size of 5.33 ha (range = 2.57–20.0 ha; Conley et al. 2016). Females use considerably larger areas prior to incubation and rarely choose nest sites within their 50% pre-incubation core areas (Conley et al. 2016). The average 95% pre-incubation home range estimated for females at KNF was 1,139 ha (± 758 SD), with minimum and mean distances between daily GPS locations and nest sites of 235 m and 1,927 m, respectively (Conley

et al. 2016). Therefore, we calculated class and landscape metrics within 500 m (79 ha) around each nest to capture land cover potentially encountered by females during the reproductive period.

Predation is the primary cause of nest failure for turkeys (Healy and Powell 1999, Hughes et al. 2007). Predator densities and nest depredation may be higher in landscapes with greater landscape diversity and high edge density (Chalfoun et al. 2002); thus, greater fragmentation may increase predation risk (Thogmartin 1999, Fleming and Porter 2015). Therefore, we used a 1-km buffer (314 ha) around nests to capture landscape fragmentation at a spatial extent large enough to influence predators (Fuller et al. 2013, Fleming and Porter 2015).

We used land cover classes from 2016 National Land Cover Database land cover imagery (Dewitz 2019) with a 30-m² cell resolution to identify land cover and edges important to nesting turkeys in the Southeast. The evergreen forest class (pine) represented evergreen woody vegetation >5 m tall and was the most frequent forest cover at all study sites. The NLCD classified a raster cell as evergreen if coniferous forest made up ≥75% of the cell. The shrub-scrub class represented woody vegetation ≤5 m in height in ≥75% of the cell. Cells classified as shrub-scrub most likely represented regenerating forests following clearcuts. We reclassified grassland and shrub classes into a combined open class because grasslands were rare at all study sites. We reclassified the developed-open and developed low-intensity classes into a single developed class, which often corresponded to paved or gravel roads. We used the developed layer to aid in the identification of gravel roads not included in Census Bureau road data (see below). Mixed deciduous-evergreen, deciduous forest, and cultivated crop classes were rare in buffers around nests.

We measured variables at 3 spatial extents: the point location of the nest itself and within 500-m and 1-km circular buffers centered on the nest. We chose these buffer sizes to ensure that we captured the land cover patch in which the nest was located and land cover characteristics surrounding the patch that may influence predator movements or densities (as described above). At the nest site, we calculated distance-based metrics to evaluate the influence of proximity to roads and edges on nest survival using our reclassified land cover layer that contained only developed, pine (forest), and open land cover classes. Previous researchers reported that females nest close to roads (Thogmartin 1999, Yeldell et al. 2017a), which may increase predation risk (Thogmartin 1999). For each nest, we measured the straight-line distance to the nearest forest-open edge (ecotone) and the distance to the nearest paved or gravel road (road). We used the reclassified 2016 NLCD developed class, aerial photographs, and each state's TIGER road layer from the United States Census Bureau (2018) to delineate roads in each study area.

Within 500-m and 1-km buffers, we chose 4 class and landscape metrics *a priori* based on previous studies that identified landscape metrics believed to capture fragmentation in pine-hardwood ecosystems (Thogmartin 1999, Yeldell et al. 2017a, Wood et al. 2019). For each buffer, we used

FRAGSTATS (McGarigal et al. 2012) to calculate the percentage and edge density of each land cover class and the Shannon's diversity index (SHDI) of land cover using the original 2016 NLCD that included all land cover types. Values of SHDI at or near zero indicated that the landscape was typically composed of a limited number of class types (McGarigal et al. 2012). We processed land cover data, created buffers, and measured distances from nests to edges in ArcGIS 10.5 (Esri, Redlands, CA, USA).

We used a remotely sensed vegetation index within each buffer to describe vegetation conditions that NLCD land cover classification may not capture. For example, the pine class did not differentiate between younger age classes (e.g., 5–10 yr) and mature (>20 yr) stands. Vegetation indices, such as the normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI), directly correlate with vegetation biomass and have been used as a proxy for vegetative conditions in a wide variety of wildlife research (Pettorelli et al. 2005, 2011). The EVI adjusts NDVI imagery to minimize canopy-soil variations in reflectance, thereby improving sensitivity over dense vegetation conditions compared to the NDVI (Didan 2015). Therefore, we retrieved the EVI derived from the 16-day composite MOD13Q1 Terra Vegetation Indices (version 6) data product from the online data pool, courtesy of the National Aeronautics and Space Administration Land Processes Distributed Active Archive Center, United States Geological Survey Earth Resources Observation and Science Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov/data_access/data_pool; accessed 5 Apr 2018). We collected EVI data within a single Moderate Resolution Imaging Spectroradiometer (MODIS) tile (250 m²) that overlapped each nest location. For each female, we collected 16-day composite average EVI values beginning on the first day of nest incubation (or closest date for which we collected data) and ending 2 weeks after nesting ceased. Therefore, EVI values were specific to the location of the nest and dates of the nesting period for each female. We used the average maximum EVI score of maximum values recorded during the nesting period as a covariate in nest survival modeling.

Nest Survival Analysis

We used a time-invariant Cox proportional hazards model to evaluate the influence of demographic, nest site, and landscape characteristics on risk of nest failure. The model assumed that the baseline proportional hazard remained constant over time. We assessed the proportionality assumption of all models containing covariates by examining Schoenfeld residuals (Therneau and Grambsch 2000) and excluded models that failed to meet assumptions prior to evaluating model support. Renesting was common following nest failure or abandonment and occurred throughout the nesting season. We included all nesting attempts in the same model because the combined dataset did not violate the proportionality assumption ($\rho = -0.03$, $\chi^2 = 0.37$, $P = 0.54$).

We modeled nest hazards and tested proportionality assumptions using the survival package (Therneau 2015) in R

(R Core Team 2019). Hazard ratios >1 indicated an increased risk of nest failure with increasing values of the covariate, whereas ratios <1 indicated a decreased risk (Cox 1972). We used an information-theoretic model selection framework based on corrected Akaike's Information Criterion (AIC_c) to rank models and evaluate model support using functions in MuMIn (Barton 2017). We considered models competitive if they were ≤ 2 AIC_c units from the top model (Burnham and Anderson 2002). We did not consider covariates with large standard errors that resulted in hazard ratio confidence intervals that overlapped 1 to be biologically relevant.

For all models, we used the cluster function in the survival package to group observations by female to account for correlated observations of multiple nesting attempts per female. The cluster function estimates variance among correlated observations similar to a generalized estimating equation. Then, we ran an initial set of models to identify the appropriate stratification structure that would allow us to account for random effects of site, year, or latitude by estimating separate baseline hazards for each strata (Therneau 2015). Model selection of the initial set indicated strong support for differences in nest success among sites (AIC_c weight [w_i] = 1.0; ΔAIC_c = 28.87); however, only the Peason Ridge WMA had significantly lower risk of nest failure than other sites ($\beta = 0.64 \pm 0.21$ [SE]; hazard ratio [HR] = 1.90, 95% CI = 1.24–2.92). Nonetheless, we stratified observations by site using the strata function in all subsequent models to estimate a separate baseline hazard for each site.

We used a tiered modeling approach to evaluate hazards associated with nest failure at multiple spatial extents. In our first model set, we modeled hazards of intrinsic attributes associated with each nesting attempt, including the ordinal day that females initiated nest incubation (day), latitude, year, and age (adult, juvenile). We evaluated support for the 4 single-covariate models, a global model, and a null model, and included important covariates from competitive models in subsequent landscape models. Prior to evaluating landscape models, we reduced the set of landscape metrics to exclude correlated metrics ($|r| \geq 0.7$). All forest classes were correlated and we retained the pine class because it was the most frequent forest type within buffers. Edge density and percentage of each class were highly correlated and were not included in the same model. Likewise, landscape metrics within 500-m buffers were correlated to those same metrics in 1-km buffers; therefore, we did not combine covariates from different buffer extents into the same model.

We constructed 9 landscape models to evaluate covariates measured at the nest site and within buffers around each nest (Table 1). We built 3 models to evaluate the influence of EVI values around the nest and proximity to edges and roads. Females nest in areas with lower canopy cover that offer dense ground vegetation for nest concealment (Fuller et al. 2013, Streich et al. 2015). Accordingly, we predicted that EVI would be positively associated with nest survival because areas of higher EVI should correspond to areas of higher green biomass. We evaluated a habitat model that included the average maximum EVI value within the 250-m² cell around the nest. Predation risk may be

Table 1. Environmental conditions around turkey nests at the nest and within 500-m and 1-km circular buffers ($n=451$) for 320 wild turkey females monitored at 9 field sites across the southeastern United States, 2014–2018.

Variable	Unsuccessful		Successful	
	\bar{x}	SE	\bar{x}	SE
Nest site				
Road ^a (m)	342	18	395	43
Ecotone ^a (m)	309	17	253	24
Max. EVI ^b	0.48	0.004	0.51	0.001
500-m				
% pine	61	1.3	56	2.1
% open	11	0.87	10	1.1
% developed	3.5	0.16	3.6	0.28
Pine edge density (m/ha ²)	70	1.8	75	3.2
SHDI ^c	0.88	0.02	0.90	0.04
1-km				
% pine	63	1.5	58	58
% open	10	0.65	9.0	0.85
% developed	3.4	0.10	3.1	0.18
Pine edge density (m/ha ²)	70	1.0	75	2.8
SHDI	1.04	0.02	1.08	0.04

^a Straight-line distance to nearest road or forest-open ecotone.

^b Average maximum enhanced vegetation index collected from a 250-m² sampling tile surrounding the nest during the nesting period.

^c Shannon's diversity index.

associated with proximity to roads and edges that are used as travel corridors for predators (Oehler and Litvaitis 1996, Thogmartin 1999). Therefore, we built a predation model that evaluated the additive effects of distance to road and ecotone. We expected daily hazard of nest failure to decrease as the distance from road and ecotone increased. Lastly, we built a global model that included the additive effects of all nest-scale metrics.

We built 3 models at each buffer extent to evaluate hypotheses about the influence of land cover on nest survival. For both extents, we evaluated a habitat model that included the percentage of open land cover within the buffer, with the expectation that risk of nest failure would decrease with increasing amounts of open land cover. We also evaluated a predation model that included additive effects of percentage of developed, pine edge density, and SHDI. We hypothesized that daily hazard of nest failure would be positively associated with each metric because predator densities are higher in more fragmented landscapes. In addition, we constructed a global model for both buffer extents. We used AIC_c model selection to rank and evaluate support for models within each buffer extent such that we could identify important covariates at each scale. We did not perform cross validation or similar techniques to evaluate model success.

RESULTS

We monitored 320 nesting females ($n=285$ adults; 35 juveniles) between 2014 and 2018. The re-nesting rates for second and third nests were 35% and 7%, respectively. Of the 451 nests monitored, 341 (76%) failed, including 75% ($n=237$) of 316 first nests, 74% ($n=82$) of 111 second nests, and 87% of 23 third nests ($n=20$). One female attempted a fourth nest, which failed. Average annual nest

success was 24% among all sites; however, Peason Ridge had significantly lower nest success than the reference site, B. F. Grant (Table 2). The earliest incubation date was 12 March and mean date of nest incubation was 18 April, 20 May, and 10 June for first, second, and third nesting attempts, respectively. Average nest initiation dates for first nests for sites in Georgia, Louisiana, and South Carolina were 13 April (range = 18 Mar–13 May), 24 April (12 Mar–5 Jul), and 15 April (1 Apr–22 May), respectively. The mean date of nest incubation for all nesting attempts pooled was 29 April. On average, the active incubation period before nest failure was 12.0 (± 9.0 [SD]) days. We identified predation as the cause of nest failure in 85% of nests for which we could attribute cause (59% of nests that failed). Other causes of nest failure included abandonment (9%) and nest destruction from mowing (6%).

Our first set of hazard models indicated that risk of nest failure increased with date of nest initiation. The global and day only models were both competitive and together received all model support (global $w_i = 0.66$; day $w_i = 0.34$; Table 3). The day model indicated that risk of nest failure increased by 1.2% for each day that nest incubation was delayed beyond the mean nesting date of 29 April ($\beta_{\text{day}} = 0.010 \pm 0.002$ [SE hereafter]; HR = 1.01, 95% CI = 1.006–1.015; Fig. 2). Nests at higher latitudes had a slightly increased risk of nest failure; however, the coefficient and associated standard error produced a hazard ratio confidence interval that overlapped 1 ($\beta_{\text{latitude}} = 1.38 \pm 0.66$; HR = 4.01, 95% CI = 0.82–19.61). Similarly, other variables included in the global model (year, age) had high standard errors that resulted in hazard ratio confidence intervals that overlapped 1, suggesting little influence on risk of nest failure. We included the day covariate in all subsequent nest and landscape models.

At the nest scale, the global model received 75% of model weight and was the top-ranked model in the model set, followed by the habitat model (Table 3). Daily hazard increased with increasing distance away from an ecotone ($\beta_{\text{ecotone}} = 0.16 \pm 0.06$; HR = 1.17, CI = 1.03–1.32). The hazard ratio indicated that the daily hazard increased by 2.5% for every 50-m increase in distance from an ecotone (Fig. 2). The daily hazard of nest failure decreased by 75% for every standardized unit increase in average EVI value ($\beta_{\text{EVI}} = -0.30 \pm 0.06$; HR = 0.74, CI = 0.65–0.83; Fig. 2).

The habitat model was the second-ranked model ($w_i = 0.26$) and also indicated that risk of nest failure decreased with increasing maximum EVI in the MODIS tile immediately around the nest ($\beta_{\text{EVI}} = -0.20 \pm 0.07$; HR = 0.74, CI = 0.002–0.089). Distance to road was included in the global model but was associated with a high standard error ($\beta_{\text{road}} = -0.06 \pm 0.06$; HR = 0.94, CI = 0.84–1.06) and the predation model containing road and ecotone was not competitive.

Model support at the 500-m and 1-km buffer scales was more ambiguous; the null model was the top-ranked model in both sets and received approximately half of AIC_c model weight in each set. The habitat model that included proportion of open land cover within buffers received the remaining model weight in each set (Table 3). Increasing the proportion of open land cover decreased risk of nest failure only slightly at the 500-m scale ($\beta_{\text{open}} = -0.05 \pm 0.05$; HR = 0.96, 95% CI = 0.88–1.03) and the 1-km scale ($\beta_{\text{open}} = -0.05 \pm 0.04$; HR = 0.95, CI = 0.88–1.04), with hazard ratio confidence intervals that overlapped 1 at each scale. We did not find support for the predation model covariates within 500-m and 1-km buffers; predation models at these spatial extents were ≥ 4.37 AIC_c units from the null model in each set.

DISCUSSION

Recently, abundance, harvest, and metrics of productivity have declined throughout broad areas of the wild turkey's range (Porter et al. 2011, Tapley et al. 2011, Byrne et al. 2015, Eriksen et al. 2015, Parent et al. 2015). Specifically, declines in productivity have been attributed at least partially to reductions in nest success, as inferred from lower numbers of females observed with broods during summer (Byrne et al. 2015). Our observed nest success of 25% across all study areas is toward the lower range of success rates as reported for turkeys in southern populations (15–42%; Miller et al. 1998, Thogmartin and Johnson 1999, Byrne and Chamberlain 2013, Little et al. 2014). Our observation that most nest failures were the result of predation also is consistent with previous literature (Miller et al. 1998, Thogmartin 1999, Little et al. 2014, Yeldell et al. 2017a, Wood et al. 2019). Although we observed low nest success and high predation rates across our study sites,

Table 2. Mean apparent nest success (%) among years for 320 wild turkey females ($n = 451$ nests) monitored at 9 field sites across the southeastern United States, 2014–2018. The Webb Wildlife Management Area (WMA) Complex represented 3 contiguous WMAs in Georgia and was treated as 1 study site. We monitored turkeys at Catahoula Ranger District for 1 year (2018) only.

State	Site	$n_{(\text{nests})}$	Number of years monitored	Annual nest success %	
				\bar{x}	SE
GA	B. F. Grant WMA	48	2	22	15
	Cedar Creek WMA	61	2	16	3.3
	Silver Lake WMA	62	2	47	3.1
LA	Catahoula Ranger District	15	1	20	
	Kisatchie National Forest	127	3	15	6.3
	Peason Ridge WMA	61	2	7	2.6
SC	Webb WMA Complex	77	4	47	7.9

Table 3. Model selection table for proportional hazards models of nest failure for 320 wild turkey females ($n = 451$ nests) monitored at 9 field sites across the southeastern United States, 2014–2018. We evaluated support using Akaike's Information Criterion for small sample sizes (AIC_c) for environmental covariates measured at 3 spatial extents around nests. We used the 2016 National Land Cover Database to classify land cover into 3 common classes: developed, open (shrublands or grasslands), and pine. All models stratified data by study site and clustered observations by individual to account for multiple nests per bird. All models at the nest and buffer extents, including the null model, included day as a fixed effect. K indicates the number of fixed effects in each model and w_i represents relative model weight for models within each spatial extent.

Name	Model	K	AIC_c	ΔAIC_c	w_i
Intrinsic					
Global	Day + year + age + latitude	4	2,479.34	0.00	0.65
Day	Day	1	2,480.62	1.28	0.35
Latitude	Latitude	1	2,492.96	13.61	0.00
Year	Year	1	2,495.53	16.19	0.00
Null	Strata (site) + cluster (female)	0	2,499.82	20.47	0.00
Age	Age	1	2,501.79	22.44	0.00
Nest					
Global	EVI ^a + ecotone ^b + road ^b	4	2,457.98	0.00	0.75
Habitat	EVI	2	2,460.19	2.21	0.25
Predation	Road + ecotone	3	2,479.41	21.44	0.00
Null	Strata (site) + cluster (female)	1	2,480.62	22.65	0.00
500-m buffer					
Null	Strata (site) + cluster (female)	1	2,480.62	0.00	0.54
Habitat	Open	2	2,481.24	0.62	0.39
Predation	ED ^c _(pine) + developed + SHDI ^d	4	2,485.81	5.19	0.04
Global	Open + ED _(pine) + developed + SHDI	5	2,486.28	5.66	0.03
1-km buffer					
Null	Strata (site) + cluster (female)	1	2,480.62	0.00	0.55
Habitat	Open	2	2,481.50	0.88	0.35
Predation	ED _(pine) + developed + SHDI	4	2,484.99	4.37	0.06
Global	Open + ED _(pine) + developed + SHDI	5	2,486.01	5.39	0.04

^a Average maximum enhanced vegetation index collected from the 250-m² sampling tile around the nest during the nest incubation period.

^b Straight-line distance to nearest pine forest-open ecotone or road.

^c Edge density of pine forest patches.

^d Shannon's diversity index.

we found few landscape characteristics associated with risk of nest failure (Fuller et al. 2013, Fleming and Porter 2015).

Numerous researchers have identified potential components of nest site selection in turkeys at multiple scales; however, there is limited support that vegetative characteristics at nest sites influence nest success (Thogmartin 1999, Byrne and Chamberlain 2013, Fuller et al. 2013, Kilburg et al. 2014, Streich et al. 2015, Yeldell et al. 2017a). Even with our spatially replicated sample, the only relevant covariates in our models were the date that females began nesting, distance to ecotone, and average maximum EVI values around nests. Our results support the importance of local conditions around a nest on the risk of nest failure but are more ambiguous regarding the effects of habitat availability and configuration at larger spatial scales beyond the nest. The amount of open land cover within 500- and 1-km buffers around nests received moderate AIC_c support, but the effects were weak and the null model outranked the habitat model in each set.

Creation and maintenance of nesting habitat is regularly identified as a manageable action to sustain populations of wild turkeys (Dickson et al. 1978, Healy and Nenko 1983) because vegetation conducive to nest success is thought to be limited (Thogmartin 1999, Isabelle et al. 2016). Several researchers have reported that females select nest sites with greater understory vegetation density and woody ground cover (Byrne and Chamberlain 2013, Fuller et al. 2013, Kilburg et al. 2014, Streich et al. 2015) as presumably

vegetative concealment dissuades predation attempts (Lehman et al. 2008, Byrne and Chamberlain 2013, Fuller et al. 2013). Our results indicate that nests located closer to ecotones (forest-open edges) and in areas with relatively greater amounts of green biomass (as measured by EVI) had lower risk of nest failure. Our findings are in agreement with other studies in southern pine ecosystems, where turkeys often nest within mature pine stands but locate nests within canopy openings with adequate understory vegetation (Byrne and Chamberlain 2013, Little et al. 2016, Yeldell et al. 2017b). We found that nests located closer to a forest-open edge had lower risk of nest failure, possibly because of the greater ground vegetation associated with the more open canopy at edges. At our study sites, areas with relatively greater amounts of green biomass and closer to forest-open edges may have represented recently burned pine stands; turkeys use stands burned in the last 1–2 years (Little et al. 2014, Yeldell et al. 2017a).

The effect of nest incubation date on nest failure has not received strong support in previous studies (Byrne and Chamberlain 2013, Little et al. 2014, but see Collier et al. 2009). In northern wild turkeys, Porter et al. (1983) reported that females in better body condition, as defined by individual mass at capture, nested earlier and had higher survival and nesting rates. Similarly, Thogmartin and Johnson (1999) reported that the 10% ($n = 4$) of heaviest females initiated nests earlier in the season. Alternatively, social hierarchies prevalent in wild turkeys may influence

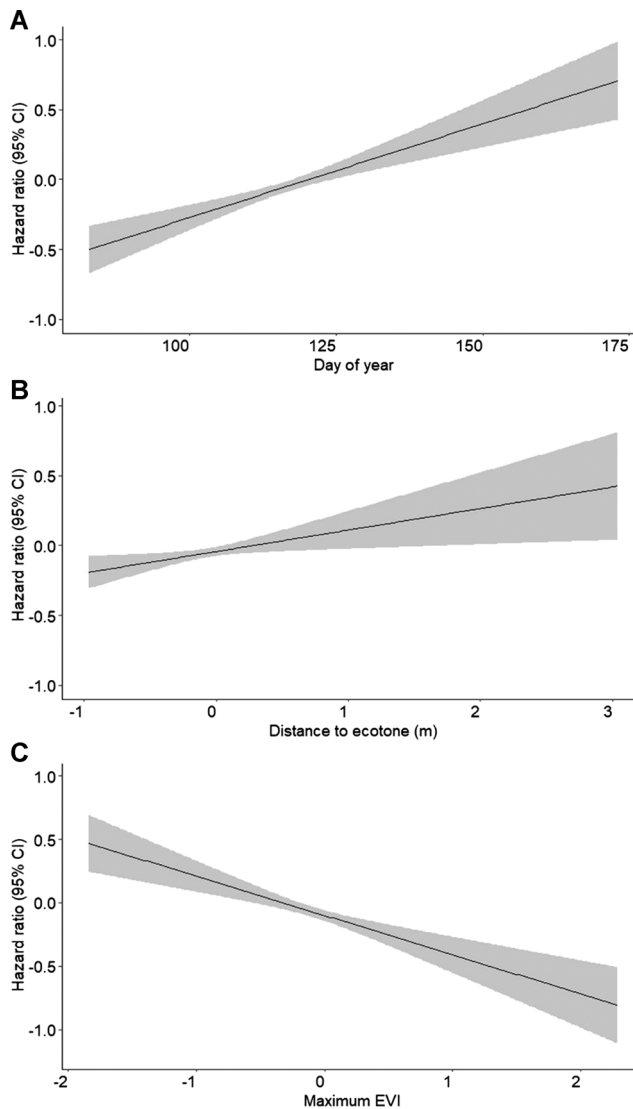


Figure 2. Effects plots of the influence of ordinal date (day of year) of initiation of nest incubation (A), distance to a forest-open ecotone (B), and average maximum enhanced vegetation index (EVI; C) around nests on daily hazard of nest failure for 451 wild turkey nests monitored at 9 field sites across the southeastern United States, 2014–2018. Hazard ratios <0 indicate decreased hazard relative to the reference value. The reference value (mean value) used to estimate hazard ratios for each covariate is indicated by the waist in each graph where $y=0$. Light gray shading around the line of predicted values represents the 95% confidence interval.

reproductive timing; these hierarchies mediate spacing and reproductive effort in various avian species (Ryder et al. 2009, Oh and Badyaev 2010). Socially dominant females copulate first and presumably nest earlier relative to conspecifics (Healy 1992), which could plausibly increase fitness benefits because of availability of quality foraging resources and reduced predation risk (Hogstad 1986, Suhonen 1993).

Several recent studies suggest landscape conditions beyond the nest do not influence nest success (Fuller et al. 2013, Little et al. 2014, Yeldell et al. 2017a). We found only weak support for our hypotheses about vegetation availability within buffered nest locations. We expected predation risk to be greater for nests located closer to roads or ecotones

because predators travel along linear features (Chalfoun et al. 2002), but neither proximity to roads nor percentage of land cover classified as developed (a proxy for density of roads) differed between successful and unsuccessful nests (Table 1). The lack of support for landscape metrics may be due to the resolution of land cover data that masked important, local-scale heterogeneity within land cover classes. For example, recent work in the southeastern United States has indicated that wild turkeys readily use mature pine forests wherein females select stands that have been recently burned (Kilburg et al. 2014, Streich et al. 2015, Yeldell et al. 2017a, Cohen et al. 2019, Wood et al. 2019), but site-specific spatial and temporal information on fire histories were necessary to evaluate and draw such conclusions. Our inability to capture potential differences in reproductive success relative to landscape metrics highlights the limitations of using coarse-grained remotely sensed data products in landscapes dominated by a single cover type. That our best-supported model included EVI may indicate this metric was capturing differences in green biomass between stand ages within pine forests, similar to other recent works that have identified relationships between NDVI, prey abundance, and breeding phenology in other avian species (Cole et al. 2015, Smith et al. 2017). Similarly, our finding of the association between EVI as a proxy for biomass and risk of nest failure reveals the potential utility of EVI metrics over large geographic extents in understanding variation in turkey productivity. In particular, EVI and other remotely sensed vegetation products represent temporal resolutions (e.g., weekly) not available with traditional categorical land cover data released every 5 years. We used average values of EVI that were tailored to the location and nesting dates of individual females, allowing us to examine differences in relative amounts of green biomass surrounding nests. But we were unable to ground truth all sites to calibrate EVI values to land cover types, limiting the utility of this variable without further testing and refinement.

In general, our findings suggest that different ecological processes are influencing nest success rates in the pine-dominated systems of the Southeast compared with those in agro-forested landscapes of the Northeast and Midwest. Forest edge density, proximity to roads, and landscape interspersed-juxtaposition and diversity have been related to nest success in landscapes characterized by relatively high landscape diversity compared to forested landscapes of the Southeast (Thogmartin 1999, Fleming and Porter 2015). Landscape metrics used in agro-forested landscapes (e.g., edge density, SHDI) likely fail to adequately quantify fine-scale attributes and cover type changes seen in fire maintained, pine-dominated systems. Consequently, results from studies in agro-forested landscapes may not be applicable to turkeys in pine-dominated systems of the southeastern United States.

MANAGEMENT IMPLICATIONS

Our study confirms the relative importance of forest management practices in the southeastern United States that focus on local-scale management activities that permit

growth and maintenance of understory vegetation. As such, we recommend that managers of pine forests focus on providing a mosaic of forest types, with a particular focus on ensuring widespread availability of land cover types capable of providing early successional vegetation communities. Application of prescribed fire and other management activities that stimulate early successional vegetation communities will ensure availability of vegetation required by female wild turkeys during nesting and brood-rearing periods, the periods that most influence turkey population trajectories.

ACKNOWLEDGMENTS

We are indebted to the suite of state and federal agency biologists and technicians across all our study sites who provided significant time and assistance with trapping and data collection. We appreciate the efforts of N. W. Bakner, A. P. Gerrits, A. K. Lohr, E. Ulrey, N. A. Yeldell, C. J. Wakefield, P. H. Wightman, and J. W. Wood who coordinated field data collection. This manuscript is based partially on work supported by the National Institute of Food and Agriculture, United States Department of Agriculture, McIntire Stennis project number 1005302. Funding and support were provided by the South Carolina Department of Natural Resources, Georgia Department of Natural Resources-Wildlife Resources Division, Louisiana Department of Wildlife and Fisheries, and the United States Department of Agriculture, Forest Service: Kisatchie and Catahoula Ranger District of Louisiana. Additional funding and support were provided by the Louisiana State University Agricultural Center, Warnell School of Forestry and Natural Resources at the University of Georgia, the Department of Fisheries and Wildlife and the Boone and Crockett Quantitative Wildlife Center at Michigan State University, and the Midwest Wild Turkey Consortium.

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Associate Editor: Christopher Williams.