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SPECIAL SECTION



Spatial distribution of potential wild turkey nest predators in west-central Louisiana

Erin E. Ulrey¹ | Cody A. Cedotal² | Michael J. Chamberlain³ Bret A. Collier¹

¹School of Renewable Natural Resources, Louisiana State University, Baton Rouge, LA 70803, USA

²Louisiana Department of Wildlife and Fisheries, Baton Rouge, LA 70808, USA

³Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA

Correspondence

Bret A. Collier, School of Renewable Natural Resources, Louisiana State University, Baton Rouge, LA 70803, USA. Email: bret@lsu.edu

Funding information

Louisiana Department of Wildlife and Fisheries; School of Renewable Natural Resources; Louisiana State University Agricultural Center; Warnell School of Forestry and Natural Resources at the University of Georgia

Abstract

Wild turkey nest success is variable spatially and temporally, with predation being the primary driver of nest loss. Historically, characteristics of nest site vegetation have been used to predict the probability of a nest being successful, a corollary to not being preyed upon. Implicit in nest success studies is that the density, distribution, and habitat preferences of predator species, relative to wild turkey nest distribution, drive the predation risk of nests on the landscape. We quantified diversity of wild turkey nest predator species within 11-ha incubation ranges centered on active nest sites, scent baited passive nest sites, and scent baited and unbaited random sites and developed a spatially explicit predictive model for potential nest predator distribution based on vegetation and landform characteristics that occurred within incubation ranges. We used 210 camera sites on passive (nesting area from previous year), active (nesting area same year), and random sites over 5,144 trap nights (TN) and recorded 2,925 photographs of potential nest predator species. Relative abundance indices (RAI) indicated greater abundance in passive (14.2/100 TN) and active (12.7/100 TN) nesting sites relative to random sites (3.13/100 TN). For active nesting sites, successful nests had lower RAI (1.8/100 TN) than unsuccessful nests (10.4/100 TN) and lower RAI than baited and unbaited random sites (2/100 TN and 4.3/100 TN, respectively). Our results indicate that potential wild turkey nest predator species regularly occurred within incubation ranges, but were more likely to occur in locations with nests than in random locations on the landscape. We did not document a strong

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relationship between potential nest predator occurrence and spatial vegetation metrics, which do not appear to affect the occurrence of generalist potential predator species. However, we did show evidence of avoidance by certain potential predators for certain vegetation types. Thus, our work indicated that the most important factor affecting a nest's outcome may be the placement of the nest on the landscape relative to use by potential predator species. We suggest future research evaluate how vegetation characteristics within wild turkey incubation ranges impact nest predator use.

KEYWORDS

distribution, habitat selection, Louisiana, nesting, nest predation, wild turkey

Identifying drivers of nest success is important because annual reproductive output influences population sustainability (Ghalambor and Martin 2002, Martin 2002). Across avian species, nest predation is the primary source of reproductive failure (Ricklefs 1969; Martin 1993, 1995; Thompson 2007), accounting for about 80% of avian nest loss (Martin 1993, Webb et al. 2012). As such, reproductive activities create periods of high predation risk for many ground nesting species (Martin 1993). Nest success is an important determinant of population trajectories, and intensity of predation largely drives patterns of reproductive success (Martin 1992). Life history theory suggests that in systems where nest predation rates are low, species with larger clutch sizes and extended incubation periods should be favored (Martin 1993).

Nest predation is commonly viewed as a process wherein nest sites are considered a resource to potential predatory species, and predator resource use is driven by density and accessibility of nests within the landscape. There exists a long history within the avian literature evaluating the location of nests sites, often tied to measurements of vegetation and how the selection of sites relates to habitat preference and hence reproductive success. For ground nesting birds, the corollary is that selected vegetation characteristics, as measured at the nesting location, mitigate predation via some undefined relationship between vegetation condition and nest concealment that reduces predator accessibility. However, predation risk for a nest also is influenced by the distribution and abundance of potential predators across the landscape (Dijak and Thompson 2000, Chalfoun et al. 2002, DeGregorio et al. 2014) as well as the concealment ability (limiting attack rate) of potential prey. Concomitantly, a standard assumption is that greater abundance of predator species should increase the probability of predation based on the likelihood of interactions occurring on the landscape (Martin 1993). Ultimately, however, predation risk has substantive influences on nest success, and understanding how specific predators interact with vegetative features thought to reduce accessibility is necessary.

The eastern wild turkey (*Meleagris gallopavo silvestris*; hereafter wild turkey) is a ground nesting uniparental galliform widely distributed across North America. Female wild turkeys lay between 10–12 eggs and continuously incubate their eggs from 25–29 days; thus, with >40 days required for each nesting attempt, life history theory would predict that predation risk for wild turkey nests should be low (Martin et al. 2006). However, nest predation is the primary cause of nest failure for wild turkeys (Vangilder et al. 1987, Vander Haegen et al. 1988, Vangilder and Kurzejeski 1995) and is commonly identified as the primary limiting factor to wild turkey sustainability. Across the United States, female wild turkeys locate nest sites in diverse vegetation conditions (Holbrook et al. 1987, Porter 1992, Badyaev 1995, Streich et al. 2015, Yeldell et al. 2017). Historically, researchers have focused on vegetation

characteristics at the nest site as a driver of predation risk (Badyaev et al. 1996, Miller et al. 1999) and have frequently linked these conditions at the nest site to nest success (Byrne and Chamberlain 2013, Conley et al. 2015, Streich et al. 2015, Little et al. 2016, Yeldell et al. 2017). Under the previously described assumption that vegetation mitigates predation of the adult female and the nest (Martin 1993), several studies have suggested that increasing visual obstruction and ground cover at nest sites increases reproductive success and decreases predation (Badyaev 1995, Nguyen et al. 2004, Conley et al. 2015, Streich et al. 2015, Yeldell et al. 2017). However, contemporary studies have suggested that wild turkey behavioral ecology may have greater effects on nest success than vegetation structure at the nest site (Borgo and Conover 2016, Dreibelbis et al. 2016, Bakner et al. 2019, Lohr et al. 2020, White et al. 2020) or at broader scales around the nest site (Crawford et al. 2021).

Decades of conservation efforts to mitigate nest loss in wild turkeys have primarily focused on vegetation management under the assumption that vegetation conditions exist that reduce the probability of nest-predator interactions and lead to increased nest success (Miller and Leopold 1992, Lehman et al. 2008, Fuller et al. 2013). Wild turkeys have a diverse array of nest predators that exhibit substantive plasticity in habitat selection (Miller and Leopold 1992), and female turkeys show similar plasticity in regards to nest placement relative to vegetation characteristics (Yeldell et al. 2017, Wood et al. 2019). Conversely, little work has been conducted to quantify the distribution and occurrence of potential nest predator species relative to vegetation conditions located within the incubation ranges used by wild turkeys (Conley et al. 2016, Bakner et al. 2019). Understanding how vegetation characteristics in areas used by incubating wild turkeys relate to specific predators of wild turkey nests is critical to identify and perhaps mitigate effects on wild turkey reproduction. Our objective was to quantify the occurrence, diversity, and distribution of potential wild turkey nest predator species across a broad spatial scale, to evaluate potential vegetation and landform characteristics that may influence predator occurrence, and to predict, spatially, based on local environmental metrics the likely occurrence of potential nest predators.

STUDY AREA

We conducted research on the Kisatchie National Forest (KNF) and Peason Ridge Wildlife Management Area (WMA) in west central Louisiana, USA. The KNF is owned and managed by the United States Forest Service (USFS), whereas Peason Ridge WMA is jointly owned by the USFS and the US Army. Both sites were pine (*Pinus* spp.)-dominated forests composed of rolling hills, high ridges, and sandy creek bottoms. Vegetation communities consisted of loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*), shortleaf pine (*Pinus echinata*), slash pine (*Pinus elliottii*), and mixed pine-hardwood forests, and hardwood riparian areas. Both sites contained forest openings, utility rights-of-way, and forest roads distributed throughout (Yeldell et al. 2017). Rural infrastructure, agricultural fields, pasture, and privately-owned lands used for industrial timber production bordered the study sites. Prescribed fire was applied on a 3–5 year return interval across both study sites on publicly-owned lands. The study sites 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 about 114 cm. Common predators of turkeys and turkey nests at KNF, Peason Ridge WMA, and surrounding areas included western rat snake (*Pantherophis obsoletus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), Virginia opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), Cooper's hawk (*Accipiter cooperii*), and barred owl (*Strix varia*).

METHODS

We captured female wild turkeys using rocket nets baited with cracked corn during January-March 2018-2019. We classified each individual as a subadult or adult based on presence of barring on the ninth and tenth primary feathers (Pelham and Dickson 1992). All individuals were fitted with a uniquely identifiable aluminum rivet tarsal band and backpack-style GPS/VHF transmitter (Biotrack Limited, Wareham, Dorset, UK; Guthrie et al. 2011).

We programmed GPS units to record one location/hour daily from 05:00 to 20:00 and one roost location at night (23:59:58) until the battery died or the unit was recovered (Cohen et al. 2018). We immediately released individuals at the capture location following processing.

We monitored live-dead status daily during the reproductive season using handheld Yagi antennas and Biotracker receivers (Biotrack Ltd., Wareham, Dorset, UK). We downloaded GPS locations once per week via a VHF/UHF handheld command unit receiver (Biotrack Ltd., Wareham, Dorset, UK). We derived dates of nest incubation from spatio-temporal GPS locational data and determined a female was incubating when an individual's locations became concentrated around a single point for several days (Guthrie et al. 2011, Conley et al. 2015, Yeldell et al. 2017, Wood et al. 2019). We defined the date of nest incubation initiation as the first day the nightly roost location was recorded at the nest site, indicating the female continued incubation during the night (Bakner et al. 2019). Nesting females were not disturbed or flushed from nest sites during monitoring, but were instead livedead checked daily via VHF from a distance >20 m. Wild turkey nests require about 27 days of continuous incubation before hatching (Williams et al. 1971), but incubation can vary from 25 to 29 days (Healy and Nenno 1985). After nest termination, we located nest sites using GPS locations to confirm the estimated nest location and to determine nest fate. We considered a nest to have been depredated or abandoned if the female left the nest ≤25 days into incubation, or if only intact eggs, no eggs, or egg fragments were found at the nest bowl. We considered a nest successful if ≥1 live poult hatched and was confirmed visually during subsequent brood surveys (Chamberlain et al. 2020).

Sample survey design

To quantify the distribution, occurrence, and richness of nest predator species within the landscape used by reproductively active GPS-tagged wild turkeys, we conducted camera surveys during the primary nesting period of wild turkeys on our study sites (1 April to 30 June). We conducted camera surveys using Bushnell trophy (Bushnell Outdoor Products, Overland Park, KS, USA) or Moultrie game cameras (PRADCO Outdoor Brands, Calera, AL, USA). We programmed all cameras to collect photographs using Passive Infra-Red (PIR) motion sensors over the daily cycle using a burst of 3 photos with a 1-minute delay between bursts. We placed cameras about 30–40 cm above the ground to allow the cameras to capture species such as squirrels (*Sciurus* spp.) or Virginia opossum (*Didelphis virginiana*) but also capture larger species such as white-tailed deer (*Odocoileus virginianus*) and black bear (*Ursus americanus*; Kelly and Holub 2008) that occur in the area but not considered regular nest predator species. We cleared understory from in front of each camera site when necessary to reduce the frequency of non-target images (Claridge et al. 2004, Meek and Pittet 2012).

We delineated 3 categories of camera sites—random, active, and passive. To generate random survey sites, we used GPS locations of females to create an approximate minimum convex polygon of wild turkey use that encompassed all GPS locations from all females during 2018. We then used the random point tool in ArcMap 10.6 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to randomly locate 36 sites (approximate number of nest locations each year, Yeldell et al. 2017, Bakner et al. 2019) with a minimum distance of 200 m between sites. We placed a single trail camera at each random site, and randomly selected 18 of the 36 random sites to be baited with disks impregnated with fatty acid scent (USDA Pocatello Supply Department, Pocatello, ID, USA). We used the bait disks as a strategy to evaluate whether the presence of scent, potentially similar to a wild turkey on a nest, had any effect on predator accessibility or attendance. Disks were roughly the size of a quarter and in dry weather, the scented disks were expected to be effective for 3 to 4 weeks, but in periods of greater precipitation the expected effectiveness range is reduced to about 5 days. Thus, we visited baited cameras every 14 days to rebait, as we assumed that time frame would not lead to potential nest predators following our trail (Dreibelbis et al. 2011). We operated the randomly distributed cameras continuously from 1 April to 30 June. We focused herein on data collected from 1 April to 1 May, which coincides with the peak period of wild turkey nest

incubation on our study sites (Yeldell et al. 2017, Bakner et al. 2019). Whereas temporal symmetry (e.g., all camera survey being initiated on the same day) would have been optimal, we were dealing with nest sites identified in 2018 and 2019 and logistical limitations restricted our ability to exactly time camera distribution to the start, or end, of nesting activities by individual birds.

We used known wild turkey nesting locations to generate active and passive sites. We classified nest site locations from the previous breeding season (2018) as passive sites. Passive sites were theoretically unoccupied during the 2019 reproductive season, but were known to be occupied by active turkey nests during the 2018 reproductive season. Following Conley et al. (2015), we defined the sampling area for passive sites by building incubation ranges for each unique nest using the nesting female's GPS locations during the incubation period to build 99% dynamic Brownian Bridge movement models in R (v.3.6.2 R Core Development Team 2020) and R package move (Kranstauber et al. 2013). We censored the first and last day of incubation to reduce spatial prediction bias caused by individuals that commenced incubation halfway through the day (Conley et al. 2015, Bakner et al. 2019). Within each of the estimated incubation ranges, we randomly generated 2 locations using the random point tool in ArcMap 10.6, and placed trail cameras at each sample location simultaneously during the period (adding one day to each end) that each nest was active during 2018. For example, the incubation range of a female that began incubating 9 April 2018 with an estimated hatch date of 6 May 2018 would have been sampled from 8 April to 7 May 2019. We baited all cameras at passive sites with attractants impregnated with fatty acid scent due to the absence of a potential incubating female that may have attracted potential predators to the area.

During 2019, we monitored female turkeys to determine nesting activity using aforementioned methods, and then generated camera sites associated with actively nesting female wild turkeys (active sites). We established 2 camera trap sites within about 5 days of a female beginning incubation. We used the mean incubation range size (11.4 ha) of female turkeys monitored during 2018 to generate 99% incubation ranges around nesting females during 2019, using a circular buffer with a radius of about 190 m. To ensure that incubating female turkeys were not disturbed during deployment of cameras, we did not locate any camera sites within the 100-m buffer around the nest. We then randomly generated locations in the area between the 100- and 190-m circular buffer, and operated cameras for a 28-day incubation period. We collected cameras after 28 days or once a female successfully hatched. We did not use scent tabs or monitor cameras during the 28-day period at active sites to reduce the possibility of disturbing the incubating female or attracting predator species to the camera site (Dreibelbis et al. 2011).

Analytical design

We visually evaluated all images collected at each camera location to quantify daily total occurrence of each predator species. We defined images as independent when consecutive images of a species were separated by ≥30 minutes (O'Brien et al. 2003, Kelly and Holub 2008). We treated both cameras as representative of an incubation range, we assumed that camera observations were independent, and we summarized the frequency of incubation ranges that had the same predator species photographed on both cameras during the sample period and on the same day within the sample period. We tallied the detections of nest predator species at each camera site for each day, classifying each image as a dependent or independent event, and calculated total captures for each camera site category (i.e., random, passive, active). We used the Shannon-Wiener diversity index to estimate the diversity of predator species for each camera site category, failed and successful nests, and baited and unbaited random sites. We used the relative abundance indices (RAI) as an index of species abundance by calculating the number of independent events of a species, divided by the number of trap nights (TN; nights the camera was deployed), multiplied by 100 (O'Brien et al. 2003), which scaled abundance relative to camera deployment time. We calculated RAI for each camera site category, failed and successful nest, and unbaited and baited random site. Relative abundance indice values were scaled to the total number of events and trap nights, and the summation of group level data (e.g., successful and unsuccessful passive nests) should equal the aggregate (e.g., total passive nests sites).

Next, we used occurrence data (presence or absence) of individual potential predator species within incubation ranges in conjunction with vegetation characteristics to develop a predictive model of the likely distribution of potential nest predators across study sites. We used 30-m resolution imagery from USGS Landsat-8 Operational Land Imager and delineated primary landcover types within the study area, excluding imagery with ≥10% cloud cover. We used supervised classification in ERDAS Imagine Software (v16.00.0000.00199, Hexagon Geospatial, Peachtree Corners Circle Norcross 2016) with 30 classes, and recoded and combined classes to create 6 unique landcover classes (water, coniferous, deciduous, mixed coniferous-deciduous, infrastructure, and open [e.g., pasture, cropland]). To quantify the density of plant growth, we calculated the Normalized Difference Vegetation Index (NDVI) with results for a given pixel ranging from −1 to 1, where no green leaves would provide values closer to 0, whereas values closer to 1 indicated high density of green vegetation. We used a 20-m resolution imagery from the European Space Agency (ESA) Sentinel 2 satellite, excluding imagery with ≥10% cloud cover. We used imagery from months of April, May, and June because these months encompass the primary period of nest incubation on the study site.

Prescribed fire can influence the occurrence and behavior of predators by altering the structural complexity of an area (Cherry et al. 2016a), so we calculated the delta Normalized Burn Ratio (ΔNBR) to estimate the burn severity in 2019. The ΔNBR formula is similar to NDVI except that it uses near-infrared (NIR) and shortwave-infrared (SWIR) wavelengths, where healthy vegetation has a high NIR reflectance and low SWIR reflectance pre-fire compared to burned areas that have relatively low NIR reflectance and high SWIR reflectance. We used a 20-m resolution imagery from ESA Sentinel 2 satellite, excluding imagery with ≥10% cloud cover. We calculated the ΔNBR using imagery from January (pre-burning) and June (post burning). To examine how the density of roads influenced predator occurrence, we acquired an ArcGIS shapefile depicting roads in Louisiana from OpenStreetMap.org and made available by MapCruzin. We buffered the line shapefile by 7.62 m because a standard lane is 3.65 m wide and therefore a typical rural road would be about 7.62 m wide (2, 3.65-m-wide travel lanes).

We used the mean incubation range size (11 ha) and created 11-ha hexagons centered on each random, passive, and active camera survey site from which we extracted camera survey landscape metrics from each hexagonal grid cell. Hexagons reduce sampling bias from edge effects related to high perimeter area ratios. Next, we regressed via a generalized linear model with a logit link function, the presence (1) or absence (0) of each predator species within an incubation range using a species-specific set of candidate models. For all candidate models, we used second-order Akaike's Information Criterion (AIC_c) to assess the amount of support for the different candidate models (Burnham and Anderson 2002). We provided the regression estimates for the best ranked species-specific model(s), and used them to project occurrence probabilities to 11-ha hexagons distributed across the study areas using the vegetative, fire, NDVI, and road density measurements best supported for predicting presence-absence of each predator species. We did not include type of camera site and presence or absence of bait as variables in spatial models because it was impossible to quantify the effect of the variables across the landscape where they did not exist.

RESULTS

We monitored 43 nests in 2018 (4 successful, 39 failed) and 44 nests in 2019 (6 successful, 38 failed). We used 210 camera trap sites (86 passive, 88 active, and 36 random) and after removing days due to malfunctioning cameras, we surveyed 5,144 trap nights. We recorded 2,925 photographs of known nest predator species, predominantly detecting nine-banded armadillo (*Dasypus novemcinctus*), coyote, bobcat, American crow (*Corvus brachyrhynchos*), white-tailed deer, feral pigs (*Sus scrofa*), gray fox, Virginia opossum, and raccoon. We limited analysis to the above mammalian and corvid species, but also recorded infrequent occurrences of striped skunk (*Mephitis mephitis*), red shouldered hawk (*Buteo lineatus*), barred owl, black bear, pileated woodpecker (*Dryocopus pileatus*), North American river otter (*Lontra Canadensis*), great blue heron (*Ardea herodias*), and greater roadrunner (*Geococcyx californianus*).

We recorded 668 independent capture events of the 9 focal predator species, and overall trap success for all predator species was 13/100 trap nights. We identified 42 incubation ranges where a picture of the same potential predator species was taken on both cameras; however, of those 42, only 4 incubation ranges had a picture of the same species on the same day, and none of them occurred during the sample window (1 April to 1 May).

Feral pigs were present at 58 camera sites, followed by coyote (n = 50), armadillo (n = 44), opossum (n = 25), raccoon (n = 23), crow and gray fox (n = 18), and bobcat (n = 15; Figure 1). Passive sites had a greater estimated potential predator species diversity (1.83) than active (1.70) and random (1.59) sites. Passive failed sites had a greater potential predator species diversity (1.53) than passive successful sites (1.19). Active sites had similar potential predator species diversity (failed = 1.70, successful = 1.75) as did baited and non-baited random sites (baited = 1.42, non-baited = 1.47).

Feral pigs were the most abundant species photographed (3.73/100 TN), followed by armadillo (2.74/100 TN), coyote (1.88/100 TN), opossums (1.4/100 TN), crow (0.93/100 TN), raccoon (0.85/100 TN), bobcat (0.46/100 TN), and fox (0.15/100 TN) across all sites combined (Figure 2). The RAI for all predator species combined varied among site categories ranging from 14.2/100 TN at passive sites, 12.7/100 TN at active sites, and 3.13/100 TN at random sites. At passive sites, the RAI at successful and unsuccessful nests was 0.66/100 TN and 13.78/100 TN, respectively. At active sites associated with successful nests and unsuccessful nests, the RAI was 1.8/100 TN and 10.4/100 TN, respectively (Figure 3). At baited and unbaited random sites, the RAI was 2/100 TN and 4.3/100 TN, respectively.

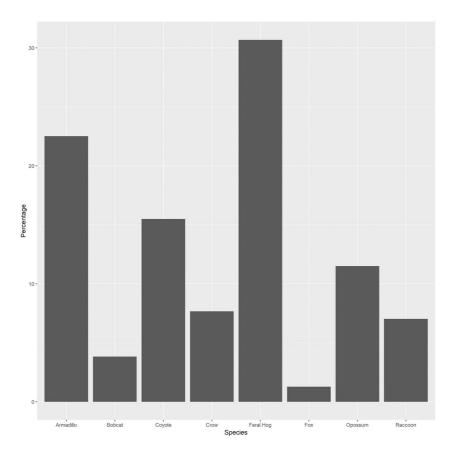


FIGURE 1 Relative percentage of all potential eastern wild turkey (*Meleagris gallopavo silvestris*) nest predators across Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA during 2019.

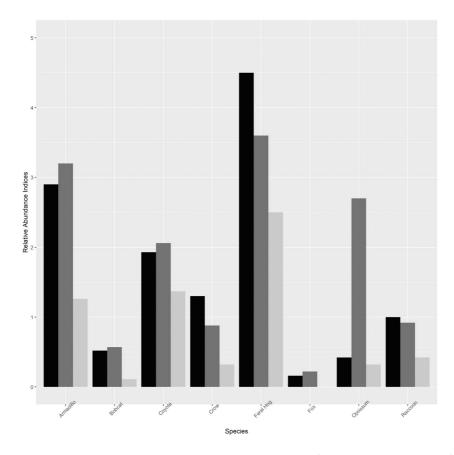


FIGURE 2 Relative abundance indices of potential eastern wild turkey (*Meleagris gallopavo silvestris*) nest predators at active (black), passive (dark gray), and random (light gray) camera sites across Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA during 2019.

The best approximating model for predicting coyote occurrence included main effects for the proportion of hardwood forest (β = 31.55, SE = 16.71) and NDVI (β = -0.22, SE = 5.66) and the interaction term (β = -46.09, SE = 24.39; Table 1), but we observed model selection uncertainty, and noted that 2019 Δ NBR (burn severity) (β = 4.31, SE = 2.07) also appeared to influence coyote occurrence. Using mean estimates of hardwood forest and NDVI, the naïve estimate of coyote occurrence was 0.376 (SE = 0.054) but showed considerable spatial variation (Figure 4A). Bobcat occurrence was best estimated based on road density (β = -22.61, SE = 12.30; Table 2), and although there was model selection uncertainty, road density was in the top 3 models supporting its relative importance. Using mean estimates of road density, the naïve estimate of bobcat occurrence was 0.119 (SE = 0.031) and showed little variation spatially (Figure 4B).

The best approximating model for raccoon occurrence included main effects for proportion of water (β = 61.93, SE = 29.10) and hardwood forest (β = -0.60, SE = 1.54) and their interaction (β = -169.1, SE = 83.95; Table 3). Using mean estimates of water and hardwood forest, the naïve estimate of raccoon occurrence was 0.238 (SE = 0.058) and showed negligible spatial variation (Figure 4C). Opossum occurrence was best estimated based on 2019 prescribed burning (β = 3.89, SE = 2.49; Table 4), but there was model selection uncertainty across the model set. Using mean burn severity, the naïve estimate of opossum occurrence was 0.150 (SE = 0.044) and showed only slight spatial variation (Figure 4D). Armadillos were ubiquitous on the landscape and occurrence was best predicted by infrastructure (β = -6.07, SE = 3.84; Table 5), and we estimated a naïve estimate of armadillo occurrence of 0.361

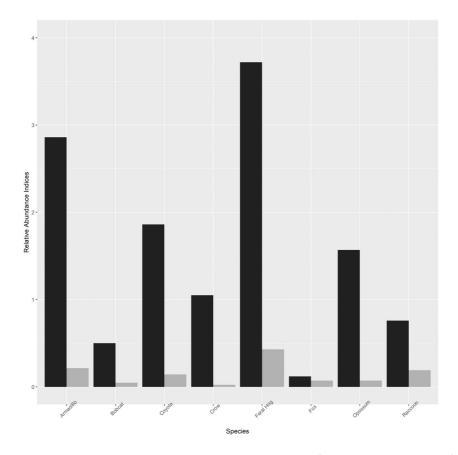


FIGURE 3 Relative abundance indices of potential eastern wild turkey (*Meleagris gallopavo silvestris*) nest predators at unsuccessful (black) and successful (gray) nests across Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA during 2019.

TABLE 1 Akaike Information Criterion (AIC $_c$), number of parameters (K), Δ AIC, Akaike weight (w_i), and log-likelihood (LL) for candidate models used to estimate coyote occurrence at Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA, 2019.

Occurrence model	К	AIC_c	ΔAIC_c	Wi	LL
Ψ (Hardwood Forest, May NDVI)	4	165.50	0.00	0.29	-78.58
Ψ (Burn 2019)	2	165.55	0.05	0.28	-80.73
Ψ (May NDVI)	2	165.64	0.14	0.27	-80.77
Ψ (Open)	2	169.39	3.88	0.04	-82.64
Ψ (Hardwood Forest)	2	169.83	4.32	0.03	-82.86
Ψ (Pine Forest)	2	170.00	4.49	0.03	-82.95
Ψ (Road Density)	2	170.09	4.59	0.03	-83.00
Ψ (Road Density, Open)	4	171.91	6.41	0.01	-81.79
Ψ (Road Density, Hardwood Forest)	4	173.84	8.34	0.00	-82.75

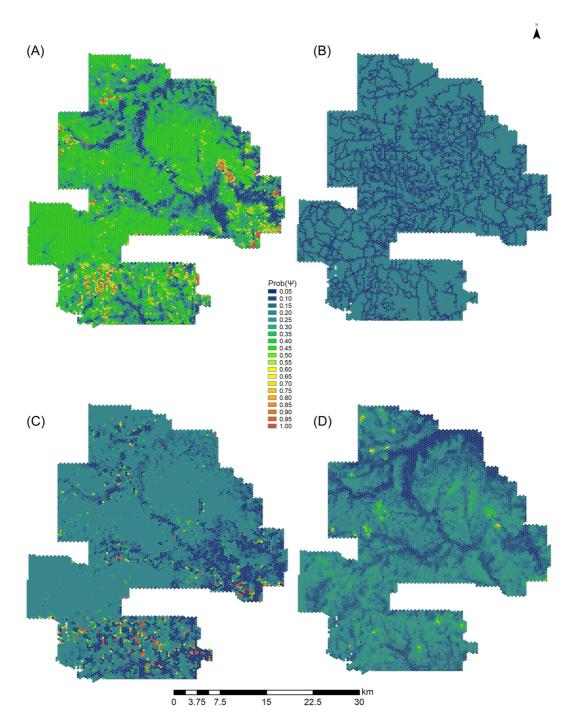


FIGURE 4 Predicted mean occurrence of nest predators across Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA during 2019. (A) coyote, (B) bobcat, (C) raccoon, and (D) Virginia opossum based on the best fitting candidate models.

TABLE 2 Akaike Information Criterion (AIC_c), number of parameters (K), Δ AIC, Akaike weight (W), log-likelihood (LL) for candidate models used to estimate bobcat occurrence at Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA 2019.

Occurrence model	К	AIC_c	ΔAIC_c	Wi	LL
Ψ (Road Density)	2	90.84	0.00	0.22	-43.37
$\Psi \text{ (Mix Pine Hardwood Forest, Road Density)}$	4	90.90	0.05	0.22	-41.28
Ψ (Burn 2019, Road Density)	4	91.05	0.21	0.20	-41.36
Ψ (Burn_2019)	2	91.31	0.47	0.18	-43.61
Ψ (May NDVI)	2	93.43	2.59	0.06	-44.66
Ψ (Open)	2	94.12	3.28	0.04	-45.01
Ψ (Hardwood Forest, Road Density)	4	94.73	3.89	0.03	-43.20
Ψ (Hardwood Forest)	2	95.00	4.16	0.03	-45.45
Ψ (Hardwood Forest, May NDVI)	4	96.46	5.61	0.01	-44.06

TABLE 3 Akaike Information Criterion (AIC $_c$), number of parameters (K), Δ AIC, Akaike weight (w_i), log-likelihood (LL) for candidate models used to estimate raccoon occurrence at Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA 2019.

Occurrence model	К	AIC_c	ΔAIC_c	Wi	LL
Ψ (Water, Hardwood Forest)	4	116.07	0.00	0.79	-53.87
Ψ (Hardwood Forest)	2	121.43	5.36	0.05	-58.67
Ψ (Road Density)	2	121.51	5.44	0.05	-58.71
Ψ (Infrastructure)	2	122.16	6.08	0.04	-59.03
Ψ (Water)	2	122.21	6.14	0.04	-59.06
Ψ (Road Density, Infrastructure)	4	123.48	7.41	0.02	-57.57
Ψ (Water, Road Density)	4	125.14	9.07	0.01	-58.40

TABLE 4 Akaike Information Criterion (AIC $_c$), number of parameters (K), Δ AIC, Akaike weight (w_i), log-likelihood (LL) for candidate models used to estimate Virginia opossum occurrence at Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA 2019.

Occurrence model	К	AIC_C	ΔAIC_c	Wi	LL
Ψ (Burn 2019)	2	125.70	0.00	0.41	-60.80
Ψ (Infrastructure)	2	126.58	0.88	0.26	-61.24
Ψ (Hardwood Forest, Infrastructure)	4	127.71	2.01	0.15	-59.68
Ψ (Road Density)	2	127.85	2.15	0.14	-61.88
Ψ (Road Density, Infrastructure)	4	130.06	4.36	0.05	-60.86

TABLE 5 Akaike Information Criterion (AIC_c), number of parameters (*K*), ΔAIC, Akaike weight (*wi*), log-likelihood (LL) for candidate models used to estimate nine-banded armadillo occurrence at Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA 2019.

Occurrence model	К	AIC_c	ΔAIC_c	Wi	LL
Ψ (Infrastructure)	2	161.24	0.00	0.58	-78.57
Ψ (Road Density)	2	163.81	2.57	0.16	-79.85
Ψ (Road Density, Infrastructure)	4	163.81	2.58	0.16	-77.74
Ψ (Hardwood Forest, Infrastructure)	4	164.93	3.70	0.09	-78.30

(SE = 0.044) and also documented limited spatial variation across the landscape (Figure 5A). Gray fox occurrence was best described using the proportion of hardwood forest (β = -12.98, SE = 8.66; Table 6), and the naïve estimate of gray fox occurrence was 0.005 (SE = 0.009), which varied little spatially (Figure 5B). Feral pig occurrence was best estimated by the proportion of hardwood forest (β = 1.49, SE = 0.97), open landcover (β = 0.81, SE = 2.60), and their interaction (β = 55.37, SE = 30.12; Table 7). Feral pigs were ubiquitous on the landscape, and the naïve estimate of occurrence was 0.661 (SE = 0.092) although feral pigs were predicted to occur primarily in riparian corridors (Figure 5C). Crow occurrence was best estimated based on road density (β = -36.49, SE = 23.34), proportion of pine forest (β = -3.24, SE = 1.39) and their interaction (β = 78.12, SE = 35.18; Table 8). The naïve estimate of crow occurrence was 0.126 (SE = 0.033), which varied considerably spatially (Figure 5D). For the 4 species that were present within the most incubation ranges (feral pigs, coyote, armadillo, opossum), successful nests were typically in areas wherein each species was predicted to have a <0.50 probability of occurrence (Figure 6).

DISCUSSION

Potential nest predator species were widely distributed and regularly occurred within the nesting areas (Conley et al. 2015, Bakner et al. 2019) used by reproductive wild turkeys. Nest success in our study (9% and 13% for 2018 and 2019, respectively) was slightly lower than recent estimates across the southeastern United States (21%, Chamberlain et al. 2020), indicative of a high rate of nest predation. In fact, successful nesting areas (both passive and active) had lower indices of predator abundance than unsuccessful nesting areas. However, the RAI was generally low with all predator species having a RAI < 5/100 TN. One possible explanation is that the cameras in our study were not located within known predator use areas, as along roads or trails (O'Brien 2011, O'Connell and Bailey 2011, Burton et al. 2015). However, our work evaluated the landscape where wild turkeys selected to nest, or at random locations within similar vegetative conditions. Thus, our camera design provided an unbiased estimate of potential predator occurrence, presumably resulting in the relatively low predator abundance indices compared to contemporary studies across North America (Gompper et al. 2006, Kelly and Holub 2008).

Passive sites (nesting areas from 2018 monitored in 2019) had greater diversity of nest predators than active sites (nesting areas from 2019 surveyed in 2019), possibly because the use of predator attractant at passive sites increased predator visitation (Linhart and Knowlton 1975, Linscombe et al. 1983). We assumed the predator attractant was no more noticeable to potential predators than the availability of a nesting wild turkey, but the assumption is tenuous as information on wild turkey accessibility due to scent is unknown. However, baited and unbaited random sites had similar estimates of predator diversity, which may indicate that presence of a predator attractant did not bias estimates of predator diversity. However, we were not able to quantify RAI for snakes, as we were focused on predator occurrence within a broader scale (Conley et al. 2015) beyond simply the nest site. Snakes represent an important predator of ground nesting birds (Patten and Bolger 2003), and snakes are known to depredate wild turkey nests (Dreibelbis et al. 2008, Dreibelbis et al. 2011).

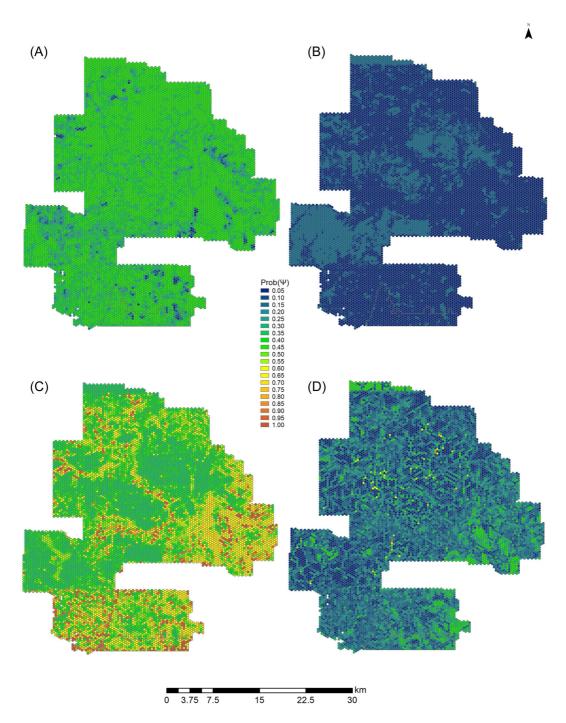


FIGURE 5 Predicted mean occurrence of nest predators across Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA during 2019. (A) nine-banded armadillo, (B) gray fox, (C) feral pig, and (D) American crow based on the best fitting candidate model.

TABLE 6 Akaike Information Criterion (AIC_c), number of parameters (K), ΔAIC, Akaike weight (w_i), log-likelihood (LL) for candidate models used to estimate gray fox occurrence at Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA 2019.

Occurrence model	Κ	AIC_c	ΔAIC_c	Wi	LL
Ψ (Hardwood Forest)	2	40.28	0.00	0.59	-18.09
Ψ (Open, Road Density)	4	42.66	2.38	0.18	-17.16
Ψ (Open, Hardwood Forest)	4	43.99	3.71	0.09	-17.83
Ψ (Mix Pine Hardwood Forest)	2	45.48	5.19	0.04	-20.69
Ψ (Open)	2	45.76	5.48	0.04	-20.83
Ψ (Burn 2019)	2	45.91	5.62	0.04	-20.90
Ψ (Infrastructure, Road Density)	8	46.84	6.56	0.02	-14.79

TABLE 7 Akaike Information Criterion (AIC_c), number of parameters (K), Δ AIC, Akaike weight (w_i), log-likelihood (LL) for candidate models used to estimate feral pig occurrence at Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA 2019.

Occurrence model	К	AIC_c	ΔAIC_c	Wi	LL
Ψ (Hardwood Forest, Open)	4	166.34	0.00	0.66	-79.00
Ψ (Pine Forest)	2	169.39	3.05	0.14	-82.64
Ψ (Pine Forest, Open)	4	170.90	4.56	0.07	-81.28
Ψ (Hardwood Forest)	2	171.61	5.27	0.05	-83.75
Ψ (Mix Pine Hardwood Forest)	2	172.73	6.39	0.03	-84.32
Ψ (Hardwood Forest, Water)	4	173.61	7.27	0.02	-82.63
Ψ (Road Density, Hardwood Forest)	4	173.88	7.54	0.02	-82.77
Ψ (Burn_2019)	2	174.15	7.81	0.01	-85.02
$\Psi \text{ (Mix Pine Hardwood Forest, Road Density)}$	4	174.24	7.90	0.01	-82.95

TABLE 8 Akaike Information Criterion (AIC_c), number of parameters (K), Δ AIC, Akaike weight (w_i), log-likelihood (LL) for candidate models used to estimate American crow occurrence at Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA 2019.

Occurrence model	К	AIC_c	ΔAIC_c	W_i	LL
Ψ (Road Density, Pine Forest)	4	101.86	0.00	0.40	-46.76
Ψ (May NDVI)	2	102.57	0.71	0.28	-49.24
Ψ (Open)	2	104.45	2.59	0.11	-50.18
Ψ (Mix Pine Hardwood Forest, Open)	4	105.15	3.29	0.08	-48.41
$\Psi \text{ (Road Density, Mix Pine Hardwood Forest)}$	4	105.29	3.43	0.07	-48.47
Ψ (Mix Pine Hardwood Forest)	2	105.87	4.01	0.05	-50.89

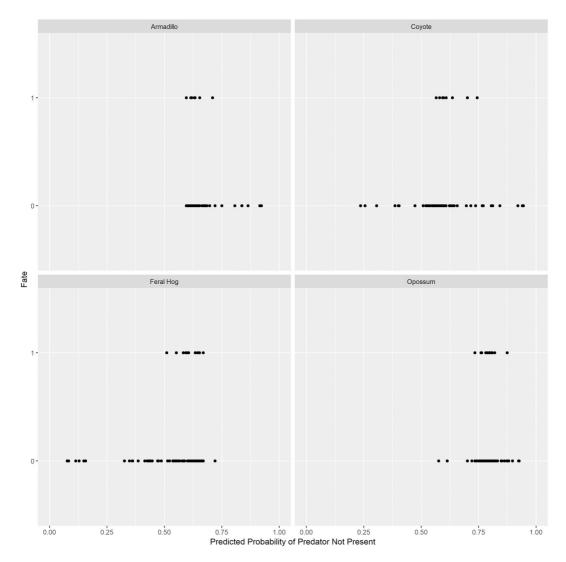


FIGURE 6 Nest success by predicted occurrence probability for the 4 most common potential nest predators across Kisatchie National Forest and Peason Ridge WMA, west-central Louisiana, USA during 2019.

Our results suggest the most important factor affecting a nest's outcome may be the spatial placement of the nest on the landscape relative to use by potential predator species. For several predator species, the modeled habitat-relationships indicated that there were areas of high occurrence of certain potential predator species. For example, coyotes and feral pigs had strong positive relationships with hardwood forest, and weaker association with vegetation density and open landcover. Hardwoods were primarily in riparian areas, and provide access to potential food sources and flooded areas used by feral pigs (Hayes et al. 2009). Coyotes tended to avoid areas of dense vegetation and were positively associated with burned stands, consistent with previous work (Hinton et al. 2015, Cherry et al. 2016b, Stevenson et al. 2018). Wild turkeys on our study sites are known to select upland areas and burned stands during nesting, which are often interspersed with riparian corridors (Yeldell et al. 2017, Bakner et al. 2019). Coyotes and feral pigs are ubiquitous within the landscape we studied, and although there is significant evidence of coyote predation on wild turkey nests, feral pig depredation of active wild turkey nests is rare and is typically tied to secondary predation events or studies using artificial nests (Dreibelbis et al. 2008, 2011; Melville

et al. 2014). In fact, our estimates of coyote occurrence could be biased low as coyotes are known to avoid cameras (Séquin et al. 2003, Gompper et al. 2006, O'Connell et al. 2006). Additionally, the high RAI for feral pig observations is likely related to group size and sociality present in feral pigs that are not present in the other potential predator species. Feral pigs are gregarious within matrilineal groups (sounders) but exhibit territoriality amongst groups (Sparklin et al. 2009). By default, numerous unique individuals could be detected simultaneously at camera sites, which would not occur for solitary species such as bobcats (Benson et al. 2006) or even for cooperative breeding species such coyotes (Ward et al. 2018).

Raccoons, foxes, and bobcats have regularly been identified as wild turkey nest predators (Schwertner et al. 2004; Dreibelbis et al. 2008, 2011; Fyffe et al. 2018). Raccoons prefer heterogeneous landscapes (Byrne and Chamberlain 2015) and typically select hardwood stands and areas adjacent to water because of foraging opportunities and available den sites (Chamberlain et al. 2002, 2003; Byrne and Chamberlain 2011), which was generally supported by our results. Conversely, gray fox and bobcat occurrence was low and was negatively associated with proportion of hardwood forests and density of roads within incubation ranges, respectively. Previous works have shown that foxes are known to avoid coyotes (Chamberlain and Leopold 2005), due both to competition for foraging resources and direct interference competition between the species (Fedriani et al. 2000, Chamberlain and Leopold 2002). Hence, the negative relationship between gray fox occurrence and proportion of hardwood forest may be related to spatial avoidance of coyotes. Bobcat avoidance of roads is consistent with previous studies reporting that bobcat occurrence increased in areas with fewer roads (Lovallo and Anderson 1996, Lesmeister et al. 2015). We note that our work only included secondary USFS roads, and did not include maintained but primitive roads used for private lands access, which can provide travel corridors and the forest edges that bobcats are known to select (Chamberlain et al. 2003).

The results of our study provide support that successful nests are located in areas with a lower probability of occurrence for potential predator species and had a much lower predator RAI on the landscape. As such, based on our work, we suggest that spatial placement of the nest on the landscape may be fairly informative to the likely probability of nest success, perhaps in conjunction with female behavioral activities (Bakner et al. 2019, Lohr et al. 2020). Additionally, as behavioral and movement ecology of most potential predatory species is unknown relative to actively nesting wild turkeys, there remains the need to better categorize space use by potential predator species during the reproductive season to quantify interactions between potential nest predators and nesting females.

MANAGEMENT IMPLICATIONS

Known nest predator species occurred frequently within the incubation ranges used by wild turkeys. Although the relative abundance of nest predators was similar for active and passive sites, relative abundance was much lower at random sites. One of the primary limitations managers face when addressing nest success is the lack of understanding of how wild turkeys and potential wild turkey nest predators use space during the reproductive period. Hence, we suggest future work on wild turkey nest success incorporate behavioral ecology of both wild turkeys and potential nest predators in conjunction with evaluations of vegetation structure such that further details on the mechanisms underlying drivers of interactions on the landscape can be identified.

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CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

Capture, handling, and marking procedures were approved by the Louisiana State University Agricultural Center Animal Care and Use Committee (Permit A2015-07 and Permit A2018-13).

ORCID

Bret A. Collier http://orcid.org/0000-0002-1867-0921

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