



# Nest site fidelity and nesting success of female wild turkeys

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## Abstract

Nest site fidelity is a common behavioral trait among birds that can positively influence reproductive success when there is spatial heterogeneity and temporal predictability in nest site quality. Nest site fidelity in wild turkeys (*Meleagris gallopavo*) has received little attention in the literature despite providing a potential link to nesting success. We used data from 32 female wild turkeys across 8 field sites ranging from South Carolina to Texas with 2 consecutive years of nest data to determine if females showed fidelity to nest sites, if distance between nest locations in consecutive years predicted nest success in the second year, and if females showed fidelity to specific areas within home ranges (patches) for nesting. Females tended to nest closer to previously successful nests (median distance = 920 m) than to unsuccessful nests (median distance = 1550 m) in the second year; however, we documented no evidence of fidelity to specific nest sites. There was widespread reuse of prelaying (89.5%) and laying (77.8%) ranges by females between years, indicating some evidence for patch fidelity. The lack of evidence for nest site fidelity may be a result of the temporally dynamic nature of turkey nesting cover and ubiquity of predation risk across the southeastern U.S, which ecological theory predicts would not provide the reproductive benefits of fidelity that hinge on predictability. Fidelity to patches within home ranges may represent an always-stay approach, which is expected when the cost of dispersing to new breeding areas outweighs potential benefits and may

allow females to draw on prior knowledge of areas within their home ranges. Although distance between nests was not a significant predictor of nest success, females that nested successfully in the first year had a probability of 0.63 of successfully nesting in the second year, whereas unsuccessful females had probability of success of 0.08 in the second year. The tracking of individual nesting success across years warrants further research, as our results imply that a disproportionate percentage of reproduction through time may be attributed to a subset of females that are consistently successful, which may have implications for our understanding of reproductive dynamics in low productivity populations.

#### KEYWORDS

*Meleagris gallopavo*, nest-site selection, reproduction, site fidelity, wild turkey

Memory and familiarity are important drivers of animal space use and habitat selection, and fidelity to specific locations or vegetation types are traits observed across a wide range of taxa (Piper 2011, Fagan et al. 2013). The accumulation of experience associated with site fidelity is believed to confer fitness advantages, including increased foraging success (Bradshaw et al. 2004, González-Gómez and Vásquez 2006), survival (Brown et al. 2008, Forrester et al. 2015), or reproductive success (Piper et al. 2008, Patrick and Weimerskirch 2017). In birds, fidelity to nest sites or breeding territories is a long-recognized behavioral trait (Greenwood 1980), and it is hypothesized that previous reproductive success likely influences breeding site fidelity. Birds can use previous experience when selecting breeding sites by using a win-stay, lose-switch (WSLS) strategy, where an individual returns to a site of previous success, but switches sites following failure (Switzer 1993). Widespread observational and experimental support for WSLS exists for a variety of birds, including passerines (Haas 1998, Hoover 2003), waterfowl (Gauthier 1990, Hepp and Kenamer 1992, Blums et al. 2002), and raptors (Jiménez-Franco et al. 2012). The expected benefits of the WSLS strategy are based on the assumption that prior success is a useful predictor of future success and is therefore dependent on temporal predictability of site quality (Switzer 1993, Schmidt 2004). Alternatively, in unpredictable environments where site quality is spatially homogenous, birds may adopt an always-stay strategy, because the cost of searching for a new site outweighs the potential reproductive benefits (Switzer 1993, Schmidt et al. 2010). For example, Gunnison sage-grouse (*Centrocercus minimus*) used an always-stay strategy in environments where nest predators were spatially ubiquitous and predation risk was temporally unpredictable (Gerber et al. 2019).

Fidelity can occur at multiple spatial scales, influenced by the spatial scale of heterogeneity in site quality. Given sufficient temporal predictability, the ecology of information theory predicts fidelity to occur at the site-level (i.e., at or near nest) when heterogeneity of site-level quality is greater than at the patch level, and fidelity to occur at the patch level when patch heterogeneity is greater (Schmidt et al. 2010). In this context, a patch refers to a larger area containing many potential nest sites. For example, cavity-nesting passerines and waterfowl exhibit fidelity to specific nest boxes or individual territories (Hepp and Kenamer 1992, Hoover 2003), whereas ground-nesting galliformes in grasslands show fidelity to habitat patches, but not to specific nest sites within those patches (Berry and Eng 1985, Fischer et al. 1993, Pitman et al. 2006, Gerber et al. 2019). Considering the important role of nest site selection in avian life history, understanding causes and consequences of nest-site fidelity is ecologically intriguing and can have implications to our understanding of demographic processes.

Given that wild turkeys (*Meleagris gallopavo*) are non-migratory birds that establish and maintain home ranges, it is logical they would develop familiarity of their range, and plausible that females would incorporate prior experience into nest site selection. However, wild turkeys are ground-nesting birds that often live in temporally-dynamic forest systems interspersed with dynamic early successional vegetation communities. For example, in the southeastern United States, wild turkeys often live and reproduce in ecosystems characterized by regular disturbances such as fire (Little et al. 2014, Yeldell et al. 2017, Wood et al. 2018, Cohen et al. 2019), flooding (Byrne and Chamberlain 2013), or unpredictable drought-precipitation cycles (Conley et al. 2015), in addition to temporal changes in ground cover resulting from succession and other natural processes. Furthermore, recent studies in the southeastern United States have failed to document consistent relationships between nest site vegetation characteristics and nesting success (Little et al. 2014, Conley et al. 2015, Yeldell et al. 2017, Wood et al. 2018), suggesting vegetation at nests may not be a reliable predictor of nest site quality in this region. In these cases, basing nest site selection decisions on previous success (WSLS strategy) may provide little benefit to subsequent reproductive success, given dynamic changes in understory vegetation, forage resources, and predation risk that can occur annually (Conley et al. 2016). However, if heterogeneity of nest quality is present at larger scales within a wild turkey's home range, it is plausible they may benefit from returning to familiar patches within individual home ranges for reproduction, using an always-stay strategy (Switzer 1993, Schmidt et al. 2010).

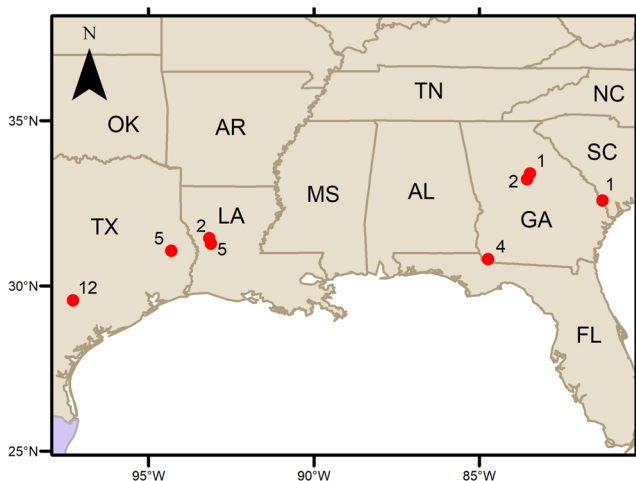
Despite the multitude of published studies of wild turkey reproductive ecology, few have reported nest site fidelity of individual females across consecutive years. Badyaev and Faust (1996) studied nest site fidelity of eastern wild turkeys (*M. g. silvestris*) in the Arkansas Ozarks and found mean distances between nests in consecutive years were >1.5 km. Distance was not correlated with nesting success in the first year, nor was distance between nests in consecutive years a significant predictor of nest success in the second year. Similarly, Locke et al. (2012) studied Rio Grande wild turkeys (*M. g. intermedia*) in central Texas and reported mean between year distances in initial nest sites of 1.4 km, with no relationship between distance and probability of a successful nesting attempt in the second year. The works of Badyaev and Faust (1996) and Locke et al. (2012) suggest fidelity to nest sites is not a common behavioral trait of wild turkeys. However, Badyaev and Faust (1996) also reported that ~70% of females used prenesting ranges (defined as the period from winter flock break-up to nest initiation) in consecutive years that overlapped  $\geq 10\%$ , which may represent evidence of fidelity to patches within home ranges, as observed in other galliformes (Berry and Eng 1985, Fischer et al. 1993, Pitman et al. 2006, Gerber et al. 2019). Given recent concerns regarding wild turkey populations in general, and reproductive success in particular (Byrne et al. 2015, Casalena et al. 2015), further work that explores potential connections between reproductive success and nest site selection and behavior, including site fidelity, could prove useful in understanding reproductive dynamics.

We explored relationships between fidelity and nest success using data from GPS-tagged eastern and Rio Grande female wild turkeys across multiple study sites in the southern U.S. We posed 2 questions regarding nest site fidelity: 1) does nesting success in year one influence nest site placement in year 2 (as quantified by distances between nest sites in consecutive years), and 2) does nesting closer to a previous year's nest site positively affect nest success in year 2? Further, we assessed patch fidelity based on proportional overlap of ranges encompassing 2 stages of wild turkey nesting phenology between consecutive years—the prelaying range, including the period from 15 March until nest initiation, and the laying range, including the time from nest initiation until onset of continuous incubation (Schofield 2019). Based on previous work (Badyaev and Faust 1996, Locke et al. 2012), and considering the unpredictability of site quality associated with the dynamic nature of ecosystems in the southern U.S., we predicted the WSLS decision strategy would not be used by female wild turkeys, and that distance between nests would not correlate to past or future nesting success. Conversely, we predicted that turkeys would show fidelity to patches within their home ranges, which would be manifested by overlap in prelaying and laying ranges in consecutive years.

## STUDY AREA

We conducted research across 8 study sites ranging from South Carolina to Texas (Figure 1), which included 4 Bird Conservation Regions (North American Bird Conservation Initiative 2000). We worked on 2 study sites in the Southeastern Coastal Plain region, characterized by extensive riverine swamps and marshes along the Atlantic coast, with interior vegetation dominated by fire-dependent longleaf pine (*Pinus palustris*), slash pine (*P. elliottii*) and loblolly pine (*P. taeda*) forests. The climate is characterized by hot humid summers and cool winters, with average rainfall of ~144 cm. The first site in this region included 3 contiguous wildlife management areas (Webb, Hamilton Ridge, and Palachucola; hereafter Webb Wildlife Management Area [WMA] Complex) managed by the South Carolina Department of Natural Resources in Hampton and Jasper Counties. The Webb WMA Complex landscape included expanses of bottomland hardwood wetlands (44.6%), and upland forests dominated by longleaf, loblolly, and slash pine (31.9%), with the remaining area consisting of a combination of openings and mixed hardwood-pine stands (23.5%). Primary management actions on the Webb Complex included timber management, agricultural management of wildlife food plots, and prescribed fire on a 3- to 5-year return cycle. For a detailed description, see Wightman et al. (2018). The second site was Silver Lake WMA located in southwest Georgia and managed by the Georgia Department of Natural Resources, Wildlife Resources Division (GADNR). Silver Lake WMA was dominated by upland pine forest and forested wetlands with openings scattered throughout. Silver Lake WMA was managed as a northern bobwhite (*Colinus virginianus*) focal area, with growing and dormant season prescribed fire serving as a primary habitat management tool (average burn size ~20 ha). For a detailed description, see Wood et al. (2018).

We worked at 2 sites in the Piedmont Region in Georgia, which serves as a transition zone between the Southeastern Coastal Plain and the Appalachian Mountains. The Piedmont sites were dominated by pine and mixed southern hardwood forests, along with diverse agricultural areas. Climate was characterized by hot, dry summers and cool, wet winters. B.F. Grant WMA was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia and jointly managed with GADNR. Cedar Creek WMA was owned by the U.S. Forest Service (USFS) and managed in cooperation with GADNR. Land cover composition on B.F. Grant and Cedar Creek was approximately 39.5% hardwood forest, 32.1% pine forest, 19.8% openings and 5.4% mixed forest. Surrounding areas consisted of pine forest and agricultural lands primarily used for grazing and hay production. Primary management actions include forest thinning and dormant-season prescribed fire applied on a 3- to 4-year interval. For a detailed site description of B.F. Grant and Cedar Creek WMAs, see Wakefield et al. (2020).



**FIGURE 1** Distribution of 8 study sites (red dots) across the southeastern U.S. where nest site fidelity of female wild turkeys was studied, 2015–2019. Numbers indicate the number of females included from each study site.

We conducted work within the West Gulf Coastal Plain region at 2 adjacent sites in Louisiana, Kisatchie National Forest (KNF) and Peason Ridge WMA, and Angelina National Forest (ANF) in Texas. Both ANF and KNF were owned and managed by the USFS, and Peason Ridge WMA was jointly owned by the USFS and the U.S. Army. Landscape composition at all 3 sites was similar and characteristic of the region, being dominated by loblolly, longleaf, and slash pine forests in uplands, bisected with hardwood riparian zones. Prescribed fire was used as a management tool of upland forests on KNF and Peason Ridge WMA. Prescribed fires occurred primarily during the dormant season (70% of area burned) on 3- to 5-year intervals, with an average burn patch size of 485 ha on KNF. See Yeldell et al. (2017) for more details. Large-scale prescribed fire is traditionally used as a management tool on ANF but was restricted during our study. For a detailed description of ANF, see Sullivan et al. (2020). Climate at study sites in this region were characterized by hot, humid summers, cool winters, and average annual rainfall ~114 cm.

We worked in the Oaks and Prairies region in southeastern Texas on private lands in Caldwell, Fayette, Lavaca, De Witt, and Gonzales counties within Texas Parks and Wildlife District 7 (hereafter TXD07). Climate was characterized by hot summers and cool winters, with average annual rainfall of ~37 cm. Average property size was 121 ha and properties were used for a variety of purposes, including livestock grazing, crop and hay production, oil and gas development, and wildlife-related recreation. Wildlife management cooperatives throughout the study area were primarily managed for white-tailed deer (*Odocoileus virginianus*) hunting. The landscape was comprised of a complex mosaic of forest patches and open areas. Forest communities primarily consisted of live oak (*Quercus virginiana*), post oak (*Q. stellata*) and sugarberry (*Celtis laevigata*), with live oak, elm (*Ulmus* spp.) and pecan (*Carya illinoensis*) characteristic along riparian areas. Common smaller trees and shrubs included yaupon (*Ilex vomitoria*), huisache (*Acacia farnesiana*), and mesquite (*Prosopis glandulosa*), whereas pastures were often monocultures of nonnative grasses. For more detail, see White et al. (2020). The Texas counties in District 7 were within the distribution of the Rio Grande subspecies, whereas all other sites contained turkeys of the eastern subspecies.

## METHODS

We captured wild turkeys using rocket nets, drop nets, or walk-in traps during December–March 2015–2019 as part of several ongoing studies investigating wild turkey reproductive ecology. We attached a VHF-GPS backpack transmitter (Guthrie et al. 2011) to each female wild turkey. We programmed transmitters to record hourly locations during daylight hours and a single roost location at midnight (Cohen et al. 2018). We only used females with known locations and success of nesting attempts that were known for 2 consecutive nesting seasons (hereafter referred to as Year 1 and Year 2 respectively) for this study. This included females who survived and had adequate transmitter battery power to persist into the following nesting season, or females recaptured between seasons and equipped with a new transmitter. Detailed tracking and nest site monitoring methods are reported in Yeldell et al. (2017), but in general, we monitored females regularly during the reproductive season, located active nests, and monitored them to determine nest fate. We considered a nest attempt successful if  $\geq 1$  poulthatched and considered any female that hatched a nest in a given year successful. We continued monitoring females if initial nest attempts failed to detect and determine fates of any renesting attempts within the same year.

We quantified nest site fidelity based on the distance between nest attempts in Year 1 and Year 2. Because females often renest within a season following nest failure, we calculated 2 distances: distance between the initial nest attempts in Year 1 and 2, and between the final nest attempt in Year 1 and initial nest attempt in Year 2. The first measure considered that initial nest locations in Year 2 were based on outcomes associated with a female's initial nest success during the previous year. The second measure considered the possibility that nest locations in Year 2 were based on outcomes associated with the last nesting attempt from the previous year, whether the last attempt was the initial or a renest attempt.

In addition to previous nest success, availability and configuration of nesting cover on the landscape may influence nest site fidelity through the degree to which they interact to constrain the availability and distribution of potential nest locations. To control for possible confounding effects of habitat availability and configuration, we extracted landcover data within a 5-km radius buffer around the initial nest attempt of each female in Year 1. We choose 5 km to provide a representation of the broader landscape available to a turkey within a year that was consistent across all study areas, and 96% of Year 2 nests were <5 km from Year 1 nest sites. We used the Cropland Data Layer (CDL) provided by the USDA National Agricultural Statistics Service (<https://nassgeodata.gmu.edu/CropScape/>). The CDL is a 30-m resolution landcover dataset updated annually based on a combination of satellite remote sensing and ground-truthing data (Boryan et al. 2011) and provided a consistent way to quantify landcover types across study areas. Within each 5-km buffer, we considered all forest and shrubland cover types (which included old and nonagricultural fields) as potential nesting cover. We calculated the amount of potential nesting cover (km<sup>2</sup>) and the division of potential landcover types using functions available in the landscapemetrics package (Hesselbarth et al. 2019) in R (v. 3.5.1; R Core Team 2019). Division is an aggregation metric that calculates the probability that 2 randomly-selected raster cells do not belong to the same landcover type (Jaeger 2000). A division value of zero would indicate a single contiguous patch of potential cover within a 5-km buffer, and a value of one would result from every 30-m cell of potential cover being separated from each other. Thus, increasing division values represent increasing fragmentation.

To test whether previous nest success influenced distance between nest sites in successive years while accounting for differences in fragmentation and habitat availability, we used a series of generalized linear models (glm) to estimate 1) the effects of Year 1 nest success, nest cover availability, and division on the distance between initial nest sites in Year 1 and Year 2; and 2) the effects of Year 1 nest success, nest cover availability, and division on distance between final nest sites in Year 1 and initial nest sites in Year 2. Because the distribution of distances between nests in Years 1 and 2 was >0 and right skewed, we used a glm approach to fit the data to a gamma distribution using a log-link function specified as follows: family = Gamma (link = log) within the glm function in R (R Core Team 2019). For each response variable (i.e., distance between initial nests, and distance between final and initial nests in years 1 and 2), we constructed 3 candidate models encompassing different combinations of predictor variables. Because nesting cover and division were strongly negatively correlated (-0.94), we did not include both together in any model to reduce issues of collinearity. We used Akaike's Information Criterion adjusted for small sample sizes (AIC<sub>c</sub>) to assess relative support of candidate models (Burnham and Anderson 2002), and identified informative parameters based on 85% confidence intervals of  $\beta$  estimates following the advice of Arnold (2010). If wild turkeys showed fidelity to nest sites based on prior success, we would expect to see a significant negative effect of Year 1 nest success on distance between nests in consecutive years.

To test if nest site fidelity affected nest success in Year 2, we performed a series of 3 logistic regression models. The first modeled the probability of nest success in Year 2 as a function of nest success in Year 1, and the distance between initial nest sites in Years 1 and 2. The second model considered the effect of nest success in Year 1 and the distance between final nest sites in Year 1 and initial nest sites in Year 2 (accounting for renesting attempts). Finally, we considered a model that estimated the probability of nest success in Year 2 only as a function of success in Year 1. We used AIC<sub>c</sub> to assess relative support of candidate models (Burnham and Anderson 2002), and identified informative parameters based on 85% confidence intervals of  $\beta$  estimates (Arnold 2010).

To identify and assess patch fidelity, we delineated 2 separate reproductive periods following Schofield (2019): a pre-laying period ranging from 15 March—nest initiation, and a laying period encompassing the time of nest initiation until the onset of continuous incubation. We chose 15 March as the start of the pre-laying period because recent research in the Southeast documented little evidence of reproductive behaviors prior to 15 March (Chamberlain et al. 2018, Wightman et al. 2019). Date of nest initiation was determined by examining GPS data for 20 days prior to incubation and identifying the first day in which the turkey was observed  $\leq 20$  m from the nest site (Schofield 2019). As wild turkeys rarely visit nests until immediately prior to egg laying (Conley et al. 2016, Collier

et al. 2019), this is a reasonable approximation of nest initiation date in the absence of direct egg-laying observations. Quantifying pre-laying and laying ranges provides 2 approximations of nest patches, areas within a turkey's annual home range encompassing multiple potential nest sites, which are directly informed by movement behavior of each animal. The pre-laying period range included dispersal from winter flocks, mating, and nest site selection. The laying period range represented the area used following nest site selection until incubation began, when movements are influenced by the need to access the nest site daily.

We used dynamic Brownian bridge movement models (dBBMM) to quantify space use for each reproductive period (Kranstauber et al. 2012). A dBBMM estimates an animal's utilization distribution (UD) for a given time period conditional on the animal's movements during that period, while accounting for heterogeneity in behavior (Kranstauber et al. 2012). We quantified pre-laying and laying ranges annually for each turkey as the area within the 99% UD isopleth. We fit dBBMMs using the move package (Kranstauber et al. 2019) in R (R Core Team 2019). We calculated separate laying ranges for individual nesting attempts, so turkeys that re-nested could have >1 laying range within a year. To quantify fidelity to pre-laying and laying ranges respectively, we calculated the proportion of the Year 1 range that was covered by the Year 2 range and considered a proportional overlap  $\geq 0.10$  to represent re-use (Badyaev and Faust 1996). For laying ranges, we calculated overlap between ranges associated with initial nests in Year 1 and Year 2, and between ranges associated with final nesting attempts in Year 1 and initial nests in Year 2 to account for re-nesting attempts.

## RESULTS

Thirty-two female wild turkeys met the criteria of having nest site location and success data available across 2 consecutive nesting seasons, 10 of which nested successfully in at least one year. Eight females nested successfully in Year 1 and 7 in Year 2 (Table 1). Of 24 females with unsuccessful initial nest attempts in Year 1, 9 re-nested at least once, 2 of which were successful. Median distance between initial nests of successful females in Year 1 and their initial nests in Year 2 was 840 m (range = 180–2,600 m) and median distance between initial nests of unsuccessful females was 1,390 m (range = 120–5,660 m; Figure 2). When considering distances between the final nest attempts of Year 1 and initial nests in Year 2, median distances between nests of females that were successful and unsuccessful in Year 1 was 920 m (range = 180–2,600 m) and 1,550 m (range = 380–5,490 m; Figure 2), respectively. Locations of Year 1 nest sites of females from study sites in SC and GA, and ANF in east TX ( $n = 13$ ) were not directly disturbed by management activities such as prescribed fire between Year 1 and Year 2. Year 1 nest sites used by females ( $n = 19$ ) at sites in LA (PRWMA and KNF) and TXD07 were either directly affected by or in close proximity to prescribed fire or grazing, respectively, between nesting seasons due to the ubiquity of these practices on those sites.

Model selection results indicated support for the model of distances between initial nests in consecutive years as a function of nesting success in Year 1 (Table 2). Parameter estimates indicated Year 1 success was an informative parameter ( $\beta = -0.63$ , 85% CI =  $-1.12$ – $-0.12$ ; Table S1, available online in Supporting Information), and that distances between initial nesting attempts in consecutive years were closer when a female was successful in Year 1. When considering models of the distance between final nesting attempts in Year 1 and initial nesting attempts in Year 2, models that considered the effects of Year 1 success and Year 1 success + fragmentation were well supported ( $\Delta AIC_c = 0.81$ ; Table 2). However, investigation of parameter estimates revealed that in each model, only Year 1 success was an informative parameter, and there was a negative relationship between distance and Year 1 nesting success ( $\beta = -0.59$ , 85% CI =  $-0.97$ – $-0.19$ ; Table S1). Although confidence intervals were wide, females with successful nests were predicted to nest on average 805 m closer to their final Year 1 nest site than unsuccessful females (Figure 3).

There was considerable model selection uncertainty in regard to Year 2 nesting success (Table 3); however, in all models the only informative parameter was nesting success in Year 1 (Table S1). Five of

8 successful females in Year 1 were also successful in Year 2 (Table 1), and model predictions indicated that a female that successfully hatched a brood had a 63% probability (95% CI = 28–87%) of successfully hatching a brood in the following year, whereas unsuccessful females had an 8% probability of success the following year (95% CI = 2–28%; Figure 3).

**TABLE 1** Year of first nesting season data, age (adult or juvenile), nesting success, first year reneating attempts and distance between the last nest attempt in Year 1 and initial nest in Year 2 for 32 female wild turkeys with 2 consecutive years of nesting data in the southeastern U.S., 2015–2019.

Site <sup>a</sup>	BCR <sup>b</sup>	First nesting season	Age	Year 1 success	Year 2 success	Year 1 reneating attempts	Distance (m)
SLWMA	SECP	2015	A	1	0	0	2603
SLWMA	SECP	2015	A	1	1	0	1251
SLWMA	SECP	2015	A	1	1	0	724
SLWMA	SECP	2015	A	1	0	1	991
Webb	SECP	2015	A	1	1	0	947
BFGWMA	P	2017	A	0	0	2	3089
CCWMA	P	2017	A	1	1	0	176
CCWMA	P	2017	A	0	0	1	1800
KNF	WGCP	2016	A	0	0	0	3147
KNF	WGCP	2017	A	0	0	0	1195
PRWMA	WGCP	2018	A	0	0	0	381
PRWMA	WGCP	2018	A	1	0	0	343
PRWMA	WGCP	2018	A	0	0	0	1803
PRWMA	WGCP	2018	A	0	1	2	1669
PRWMA	WGCP	2018	A	0	1	0	1370
ANF	WGCP	2016	A	0	0	0	1394
ANF	WGCP	2016	A	0	0	1	1294
ANF	WGCP	2016	A	0	0	0	3636
ANF	WGCP	2016	A	0	0	0	1560
ANF	WGCP	2016	A	0	0	0	604
TXD07	OP	2017	J	0	0	0	1220
TXD07	OP	2017	A	0	0	0	1542
TXD07	OP	2017	J	0	0	0	1388
TXD07	OP	2017	A	0	0	0	811
TXD07	OP	2017	J	1	1	1	892
TXD07	OP	2017	A	0	0	0	2643
TXD07	OP	2017	J	0	0	1	448
TXD07	OP	2017	J	0	0	0	1444

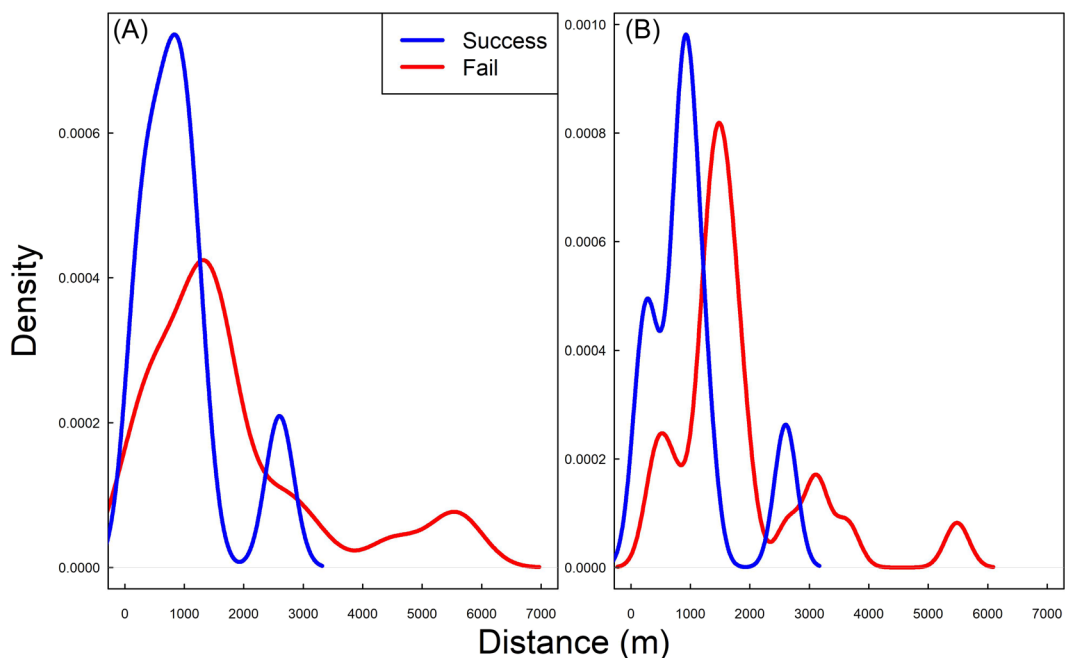


**TABLE 1** (Continued)

Site <sup>a</sup>	BCR <sup>b</sup>	First nesting season	Age	Year 1 success	Year 2 success	Year 1 renest attempts	Distance (m)
TXD07	OP	2017	A	0	0	0	5485
TXD07	OP	2017	A	0	0	0	1632
TXD07	OP	2017	A	0	0	1	1562
TXD07	OP	2016	A	0	0	1	1964

<sup>a</sup>Study sites; SLWMA = Silver Lake WMA, Webb = Webb WMA, BFGWMA = B.F. Grant WMA, CCWMA = Cedar Creek WMA, KNF = Kisatchie National Forest, PRWMA = Peason Ridge WMA, ANF = Angelina National Forest, TXD07 = Texas wildlife #7.

<sup>b</sup>Bird Conservation Regions: SECP = Southeastern Coastal Plain, P = Piedmont, WGCP = West Gulf Coastal Plains, OP = Oaks and Prairies.



**FIGURE 2** Kernel density plots illustrating the distributions of distance between initial nest sites (A) and final nest sites in year 1 and initial nest sites in year 2 (B) for 32 female wild turkeys with 2 consecutive years of nesting data in the southeastern U.S., 2015-2019.

We estimated 49 pre-laying ranges from 29 females, with a median range size of 4.09 km<sup>2</sup> (range = 1.59–16.4 km<sup>2</sup>). Sufficient GPS data were available to estimate pre-laying ranges in consecutive years from 19 females (15 adults, 4 juveniles). Proportional overlap ranged from 0–0.94, and 17 (89.5%) females re-used their Year 1 range (proportional overlap  $\geq 0.10$ ; Table 4). Only 3 of these females nested successfully in Year 1, making it impossible to quantitatively assess the effect of previous nesting success on pre-laying range fidelity, but the proportional overlap of the 3 successful females was not obviously different from unsuccessful females. The 2 females that did not revisit their Year 1 pre-laying ranges were from ANF and represented translocated birds in which Year 1 was their first nesting season on the study area.

**TABLE 2** Model selection results, including second order Akaike's information criterion ( $AIC_c$ ), difference from lowest  $AIC_c$  ( $\Delta AIC_c$ ), model weights ( $w$ ) and number of parameters ( $K$ ) for candidate models of the distance between initial nest sites in consecutive years, and distance between final nest sites of year 1 and initial nest sites of year 2 for 32 female wild turkeys across 8 study sites in the southeastern U.S., 2015–2019.

Model <sup>a</sup>	K	$AIC_c$	$\Delta AIC_c$	$w$
Distance between initial nests				
Success	3	536.32	0	0.64
Success + Nest cover	4	538.81	2.49	0.19
Success + Fragmentation	4	538.94	2.62	0.17
Distance between final and initial nests				
Success	3	527.00	0	0.50
Success + Fragmentation	4	527.77	0.81	0.33
Success + Nest cover	4	529.02	2.06	0.18

<sup>a</sup>Success = female nesting success in year 1, Habitat = nesting cover within a 5 km buffer surrounding initial nest sites, and Fragmentation = fragmentation of nesting cover within a 5 km buffer surrounding initial nest sites.

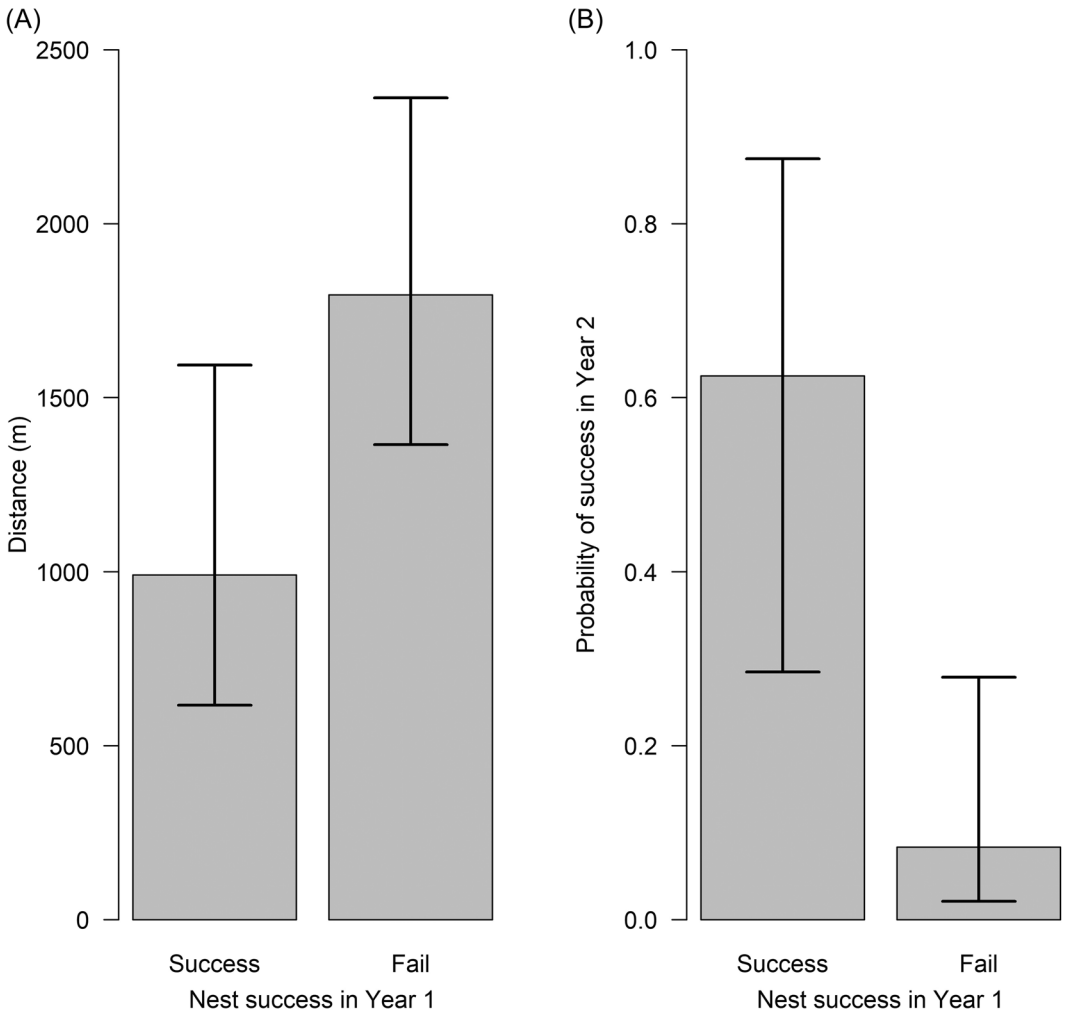
The Year 1 pre-laying ranges of females in ANF were among the largest in the study ( $n = 4$ ,  $\bar{x} = 13.2 \text{ km}^2$ , range =  $9.9\text{--}16.4 \text{ km}^2$ ), all of which reduced their range sizes by 62–89% in Year 2 ( $\bar{x} = 3.25 \text{ km}^2$ ).

We estimated 50 laying ranges from 26 females. Laying ranges were generally smaller than pre-laying ranges, with a median size of  $2.16 \text{ km}^2$  (range =  $0.22\text{--}9.73$ ). Sufficient GPS data were available to estimate laying ranges in consecutive years from 18 females (15 adults, 4 juveniles), 3 of which were successful in Year 1 (Table 4). When considering laying ranges associated with initial nesting attempts, 13 females (72.2%) re-used laying ranges in consecutive years. When considering laying ranges associated with final nesting attempts in Year 1 and initial nesting attempts in Year 2, 14 females (77.8%) re-used their Year 1 laying ranges in Year 2 (Table 4).

## DISCUSSION

Contrary to our initial prediction, successful females nested closer to their Year 1 nest sites in the following year than unsuccessful females. However, given that the median distance between successful nests in Year 1 and initial nest attempts in Year 2 was 920 m, it would be tenuous to conclude this represents fidelity to specific nest sites. Beyond the nest itself, it is reasonable to expand the definition of a nest site to encompass the surrounding area used by a female during incubation. Recent observations from GPS tagging studies of both eastern and Rio Grande subspecies reveal that on average, the distance travelled from the nest by females during incubation recesses is  $<100 \text{ m}$  (Conley et al. 2015, Bakner et al. 2019). All Year 2 initial nest attempts were  $>100 \text{ m}$  from successful Year 1 nests, which offers additional evidence that female turkeys were not exhibiting fidelity to nest sites. Additionally, distance between nests in consecutive years was not a meaningful predictor of nest success in Year 2.

Despite a lack of evidence of fidelity to nest sites, we observed widespread re-use of pre-laying and laying ranges in consecutive years, which we interpret as evidence that wild turkeys did show fidelity to patches within their home ranges. Badyaev and Faust (1996) similarly reported widespread overlap of prenesting ranges but were limited to VHF locations collected every 2 days and minimum convex polygon range estimates that are by default coarse metrics of space use. By using GPS data and a movement-based



**FIGURE 3** Generalized linear model predictions of distance between final nests in year 1 and initial nests in year 2 as a function of year 1 nesting success (A) and logistic regression model predictions of the probability of female wild turkey successfully nesting given nest success in the previous year (B) in the southeastern U.S., 2015-2019. Error bars represent 95% confidence intervals.

**TABLE 3** Model selection results, including second order Akaike's information criterion ( $AIC_c$ ), difference from lowest  $AIC_c$  ( $\Delta AIC_c$ ), model weights ( $w$ ) and number of parameters ( $K$ ) for candidate models of the probability of nesting success of 32 female wild turkeys across 8 study sites in the southeastern U.S., 2015-2019, as a function of nesting success in the previous year (Success), the distance between initial nesting attempts in year 1 and 2 (initial distance), and distance between final nests in year 1 and initial nests in year 2.

Model	K	$AIC_c$	$\Delta AIC_c$	$w$
Success	2	28.77	0	0.46
Success + Initial distance	3	29.50	0.73	0.32
Success + Final distance	3	30.32	1.56	0.21

**TABLE 4** Age (adult or juvenile), nesting success, and proportional overlap (proportion of Year 1 range covered by Year 2 range) of pre-laying and laying ranges for 21 female wild turkeys with 2 consecutive years of GPS movement data in the southeastern U.S., 2015–2019. Initial laying range overlap is the overlap between laying ranges associated with initial nesting attempts, and final laying range overlap is overlap between final laying range in Year 1 and initial laying range in Year 2 for females with >1 nesting attempts in Year 1.

Site <sup>a</sup>	Age	Year 1 success	Year 2 success	Pre-laying range overlap	Initial laying range overlap	Final laying range overlap
SLWMA	A	1	0	0.57	-	
Webb	A	1	1	0.71	0.23	
KNF	A	0	0	0.56	0.02	
KNF	A	0	0	0.75	-	
PRWMA	A	1	0	0.29	0.15	
PRWMA	A	0	0	0.26	0.46	
PRWMA	A	0	1	0.30	0.53	
PRWMA	A	0	1	-	0.27	
ANF	A	0	0	0.18	0.16	
ANF	A	0	0	0.01	0.00	0.21
ANF	A	0	0	0.00	0.00	
ANF	A	0	0	0.10	0.21	
TXD07	J	0	0	0.54	0.00	
TXD07	A	0	0	0.94	0.98	
TXD07	J	0	0	0.75	-	
TXD07	A	0	0	0.48	0.78	
TXD07	J	1	1	-	0.44	
TXD07	J	0	0	0.58	0.82	0.93
TXD07	J	0	0	0.73	0.73	
TXD07	A	0	0	0.38	0.00	
TXD07	A	0	0	0.52	0.77	

<sup>a</sup>Study sites; SLWMA = Silver Lake WMA, Webb = Webb WMA, KNF = Kisatchie National Forest, PRWMA = Peason Ridge WMA, ANF = Angelina National Forest, TXD07 = Texas wildlife #7.

range estimator (dBBMM), we were able to construct considerably more refined estimates of space use, and to calculate ranges for 2 biologically-distinct reproductive periods. Given the limited size (median = 2.16 km<sup>2</sup>) of laying ranges, that most females (77.8%) had overlapping laying ranges in consecutive years provides compelling evidence of patch fidelity, as has been observed in other galliformes, including sage grouse (*C. urophasianus* and *C. minimus*; Berry and Eng 1985, Fischer et al. 1993, Gerber et al. 2019), lesser prairie chickens (*Tympanuchus pallidicinctus*; Pitman et al. 2006), black grouse (*Tetrao tetrix*; Warren et al. 2012) and capercaillie (*T. urogallus*; Storaas and Wegge 1987). Badyaev and Faust (1996) reported greater overlap of breeding areas as a function of female age and Year 1 nesting success. Unfortunately, our sample sizes were insufficient to quantitatively test for such effects, but increased range overlap as a function of nesting success might provide a plausible explanation for why successful females nested closer in consecutive years

than unsuccessful females. Future studies using GPS telemetry across multiple years for individual birds would provide better insight.

Our results parallel extant wild turkey literature (Badyaev and Faust 1996, Locke et al. 2012) and support our initial predictions that wild turkeys do not apply the WSLs strategy to nest site selection. Fidelity to nest sites is expected to benefit individual and population-level reproductive success when there is sufficient predictable spatial heterogeneity at the nest-site scale, so that birds can reasonably predict nest sites that are of consistently greater quality than others, and when nest site quality is relatively predictable temporally (Switzer 1993, Schmidt 2004, Schmidt et al. 2010). Predation is the leading cause of nest failure across our study areas, and thus predation risk is a strong determinant of nest quality, where quality sites are defined as those that offer the greatest probability of hatching success. Predation risk should therefore be a primary factor in a female's assessment of potential nest site quality. However, recent studies have failed to identify a relationship between nest site vegetation and success (Little et al. 2014, Conley et al. 2015, Yeldell et al. 2017, Wood et al. 2018), which could indicate predation is a random event with respect to nest vegetation across our study sites. If wild turkeys cannot reasonably evaluate predation risk associated with a nest site, then nest site quality is relatively unpredictable, and consequently we would expect little benefit to be gained from females showing fidelity to specific nest sites. Additionally, as ground-nesting birds within disturbance prone and dynamic ecosystems, it reasonably follows that site quality is temporally dynamic, which would not support a strategy of fidelity to nest sites based on previous nesting success (Switzer 1993).

Wild turkeys may select nesting locations based on factors other than predation risk, particularly if predation threat at the scale of individual nest sites is difficult to predict. Evidence from our study and Badyaev and Faust (1996) of overlapping of ranges associated with time periods encompassing nest site selection and egg laying indicates wild turkeys may adopt an always-stay approach at the patch scale. Gerber et al. (2019) attributed high levels of nest patch fidelity in Gunnison sage-grouse to an always stay strategy (Switzer 1993) as a response to nest predation, arguing that the wide variety and mobile nature of nest predators creates a situation in which predation risk at nest sites is difficult to predict. Consequently, Gerber et al. (2019) suggested the always-stay strategy is an optimal response when predation risk is temporally unpredictable and spatially homogenous, and wild turkeys may encounter similar situations in many environments. Memory plays an important role in life history of many wildlife species (Piper 2011, Fagan et al. 2013), and the benefit of returning to familiar ranges may outweigh the costs of dispersing to unfamiliar nesting areas. In our study, the only 2 females that did not revisit their Year 1 pre-laying ranges were adults that were translocated to ANF in Year 1, which was their first nesting season at an unfamiliar site. Moreover, Badyaev and Faust (1996) reported that overlap of prenesting ranges was greater for adults relative to juveniles, and fidelity may strengthen as wild turkeys become more familiar with their ranges through time. More research is needed to understand the causes and prevalence of patch fidelity in wild turkeys and would be greatly benefited by longitudinal studies of individual females lasting  $\geq 3$  nesting seasons.

Although most studies of wild turkey reproductive ecology span multiple years, few report nest success of individual females through multiple nesting seasons, or test whether previous nest success predicted future success. Exceptions include Badyaev and Faust (1996) and Miller et al. (1998), both of which reported no evidence that prior reproductive success correlated to future success. Although our sample size was modest, we documented that females that were successful in Year 1 had a greater probability (63%) of being successful in Year 2 than unsuccessful females (8%), and that all successful nests were attributed to only 10 (31.3%) females. Similarly, Thogmartin and Johnson (1999) studied a declining population in the Ouachita Mountains of Arkansas and reported that 35% of all successful nests during a 4-year study could be attributed to 3 adult females. Females may use strategies or possess behavioral traits unrelated to nest site fidelity that allows them to be disproportionately more successful than others. For example, recess behavior of incubating females represents a behavioral tradeoff between maximizing female survival and nest success, and recent work suggests some females prioritize behaviors that maximize nest success (Lohr et al. 2020).

## CONCLUSIONS

With broad-scale declines in productivity apparent throughout portions of North America (Byrne et al. 2015, Casalena et al. 2015), and contemporary works noting low nest success across numerous wild turkey populations (Bakner et al. 2019, Chamberlain et al. 2020, Lohr et al. 2020), that reproduction within a population may be disproportionately attributed to a small subset of females is a topic that deserves more focused research attention. It would be illuminating to know to what extent reproduction is commonly attributable to a subset of consistently successful females, what specific behavioral traits are associated with nesting success, and the potential causes and demographic ramifications. We suggest research that collects longitudinal data on individual behavior and nesting success of individual females across years is warranted to fill these gaps in our understanding of wild turkey reproductive ecology.

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## CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

## ETHICS STATEMENT

All capture and handling procedures were approved by the Institutional Animal Care and Use Committee at the University of Georgia (UGA Permits A2014 06-008-Y1-A0, A3437-01, and A2015 07-009-Y1-A0) and the Institutional Animal Care and Use Committee at the Louisiana State University Agricultural Center (LSU Permits A2014-13, A2015-07, and A2018-13).

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## SUPPORTING INFORMATION

Additional supporting information, in the form of a table of parameter estimates and confidence intervals for all models may be found in the online version of this article at the publisher's website.

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