RECURSIVE MOVEMENTS OF FEMALE EASTERN WILD TURKEYS (*MELEAGRIS GALLOPAVO SILVESTRIS*) DURING THE REPRODUCTIVE PERIOD IN THE SOUTHEASTERN UNITED STATES

by

NICHOLAS WILSON BAKNER

(Under the Direction of Michael J. Chamberlain)

ABSTRACT

Understanding wildlife movement ecology is crucial for comprehending population dynamics, ecological processes, and behavioral patterns. The restoration of the wild turkey (*Meleagris gallopavo* spp.) across North America stands as one of the most successful conservation efforts following the species near extinction in the early 1900s. However, productivity and abundance have declined across various portions of their range. I investigated prospecting behaviors during laying and the landcover factors influencing them. I found that nest fate was positively affected by the number of patches a female visited during incubation recesses. Females selected for areas nearer to the nest site, secondary roads, hardwood and mixed pine-hardwood forests, water bodies, and shrub/scrub lands. Conversely, they avoided pine forests and open, treeless areas. Another aspect of my research delved into how state-dependent recursive movements influenced resource selection for wild turkey broods as they aged. Ground roosting broods in a restricted state spent less time in mixed pine-hardwoods and more time in areas with denser vegetation. Tree-roosting broods selected areas closer to shrub/scrub landcover types and those with higher vegetation density, less time in mixed pine-hardwoods, but these broods selected areas with greater vegetation density. Additionally, I calculated site fidelity, identified hub and satellite roost sites, and assessed landscape features selected at roosting areas during different reproductive phases. I found a scale-free network structure emerged in roosting behavior, with a small percentage of hub roost sites acting as connectors between satellite roost sites within the network. Female wild turkeys consistently selected roost areas at lower elevations with greater topographic ruggedness. The probability of being a hub roost was greater in areas nearer to secondary roads, water bodies, and open treeless areas. Furthermore, I observed that female survival throughout the breeding season varied. Daily survival probability was lower during incubation and brooding phases, but higher for non-nesting females, demonstrating a clear survival consequence to females who are reproductively active.

INDEX WORDS: behavior, *Meleagris gallopavo*, prospecting, recursive movements, reproduction, roosting, survival, wild turkey

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DEDICATION

I dedicate this dissertation to my parents and brother, Brian, Lisa, and Dylan Bakner. The love and support through the many years on the wildlife journey are what carried me through. The immense amount of passion and work effort you instilled in me helped me continue this path even in the hardest of times. I would have never been able to do any of this without each of you.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Study of wildlife movement is fundamental in understanding population dynamics, ecological processes, and behavioral patterns (Nathan et al. 2008, Chapman and Reyna-Hurtado 2019, Joo et al. 2020). Using movement data to develop survival and habitat selection models has become a standard in wildlife ecology (Chapman and Reyna-Hurtado 2019). Therefore, understanding the movement ecology of a species is crucial for managing wildlife populations.

Ecological processes operate at multiple spatio-temporal scales. For example, annual cycles such as reproductive, non-breeding, and migration/dispersal periods vary in duration and location (Marra et al. 2015). Annual cycles affect movement facilitated by internal and external stimulus (Doak et al. 1992, Fryxell et al. 2008, Nathan et al. 2008), where behavioral changes can occur (Martin et al. 2013, Kay et al. 2017). Hence, species develop behavioral strategies to ensure survival and reproductive success in dynamic landscapes (Orians and Wittenberger 1991, Lima and Zollner 1996, Morales and Ellner 2002, Gurarie et al. 2011).

Life-history theory predicts a trade-off between current reproduction and survival (McNamara and Houston 1996). Optimal resource allocation during reproduction is primarily dependent on an individual’s reproductive investment (Roff 2002). Specifically, females must balance their energetic needs as resources can only be directed toward one life-history trait (survival) and not another (reproduction; Audzijonyte and Richards 2018). To maintain a balance between survival and reproductive output, species develop diverse life-history strategies, such as bet hedging to reduce temporal variance in individual fitness (Simovich and Hathaway 1997, Fontaine and Martin 2006). By bet hedging, when an individual is faced with uncertainty, they intend to eliminate or reduce risk in a situation (Boyce et al. 2002). In the case of reproductive strategy, individuals may prioritize their survival over producing offspring to ensure future reproductive opportunities (Danforth 1999, Simovich and Hathaway 1997). Hence, individuals develop behavioral strategies during reproduction that could influence overall survival (Afton 1980).

The reproductive period is the most costly life-history period that impacts population dynamics of avian species (Martin 1995, Ghalambor and Martin 2002). Reproductive effort is known to result in periods of high predation risk, reduced energy acquisition, and impacts to embryonic development (Skutch 1962, Deeming and Reynolds 2015). Ground-nesting upland birds are constrained to nest locations during laying and incubation, which reduces foraging opportunity and increases predation risk (Deeming and Reynolds 2015). During incubation, individuals develop strategies making movements away from their nest locations (recesses) to obtain resources necessary for survival (Conway and Martin 2000, Coates and Delehanty 2008, Bakner et al. 2019, Lohr et al. 2020). Once individuals hatch clutches, they are faced with trade-off between increasing survival of the offspring and decreasing their own (Kear 1970, Afton and Paulus 1992, Boos et al. 2007). Hence, complex behavioral strategies occur during reproductive periods that can have substantive impacts on survival.

Recursive movement behaviors, defined as returns to previously visited areas, allow us to understand underlying mechanisms driving spatio-temporal patterns (Ohashi and Thomson 2005, Riotte-Lambert et al. 2013, Berger-Tal and Bar-David 2015, Bracis and Mueller 2017). As noted by Berger-Tal and Bar-David (2015), recursive movements are nearly universal in animals, but the phenomenon is given limited appreciation by researchers. Because literature has failed to use consistent terminology or cross reference the topic, recursive movement behaviors have often been overlooked and ignored (Berger-Tal and Bar-David 2015). There are three areas of research investigating recursive movement which differ in perspective but are all focused on identifying repeated visits to the same location (Berger-Tal and Bar-David 2015). Trapline foraging focuses on foraging from renewable resources such as insects and herbaceous vegetation (Ohashi and Thomson 2005). Path recursion focuses on movement between high quality foraging patches and returning in a regular manner (Bar-David et al. 2009). Lastly, ecology of fear studies seek to reveal underlying patterns of how risk shapes the movement of prey and vice versa (Mitchell et al. 2009). Although recursive movements are often conducted through other parallel lines of research, it provides a powerful tool to understand the connection between behavioral and ecological processes (Bracis et al. 2018).

Understanding how animals use space is an important component to wildlife management, conservation, and population health (Morris et al. 2016). One of the primary techniques used to model resources preferred or avoided by a species is resource selection function (RSF) modeling of wildlife movement data (Boyce et al. 2002, Manly et al. 2002, Morris et al. 2016). Traditional resource selection analyses associate animal movements to available resources within their home ranges (Boyce and McDonald 1999, Boyce et al. 2002, Manly et al. 2002). However, recursive movement analyses narrow the focus to areas of repeated use by animals, allowing for a more fine-scaled approach (Bracis et al. 2018). Therefore, recursive analysis has a direct link to behaviors driving animal decision-making and resource availability within home ranges (English et al. 2014, Berger-Tal and Bar-David 2015, Giotto et al. 2015).

WILD TURKEYS

Restoration of the wild turkey (*Meleagris gallopavo*) has been one of the greatest conservation successes in North America (Kennamer et al. 1992). During the 20th century, populations were restored or established throughout the species range due to restocking efforts, regulatory actions, and habitat restoration (Kennamer et al. 1992). However, in the southeastern United States, there has been a long-term decline in productivity, as noted by an increasing proportion of females observed without broods (Byrne et al. 2015).

The wild turkey is a ground-nesting uniparental Galliform widely distributed across the United States and southern Canada. The reproductive cycle is from March-July and consists of egg laying, incubation, and brood rearing periods (Healy 1992, Bakner et al. 2019, Lohr et al. 2019, Schofield 2019, Wakefield et al. 2020, Chamberlain et al. 2020). The egg laying period ranges from 1 to 14 days where an individual lays one egg a day (Williams et al. 1971, Healy 1992, Schofield 2019), and upon completion of laying the clutch, wild turkeys incubate eggs for 25 to 29 days (Healy 1992, Conley et al. 2015, Bakner et al. 2019, Lohr et al. 2019). Egg laying and incubation periods restrict females to a range surrounding the nest site (Conley et al. 2015, Bakner et al. 2019, Schofield 2019). Furthermore, once an individual successfully hatches a clutch they must find vegetative communities suitable for poult maneuvering and foraging, as poults lack the ability to fly until day 14 post hatch (Barwick et al. 1970, Healy 1992, Spears et al. 2007). Gaining an understanding of spatio-temporal processes underlying the reproductive period are critical in identifying drivers of reproductive success (Collier and Chamberlain 2011).

Understanding female wild turkey behavioral activities during the reproductive period provides insight into drivers of reproductive success and survival (Bakner et al. 2019, Lohr et al. 2020). Such information is important as it allows estimation of population growth rates, so that managers can assess population status. Previous studies focusing on female wild turkeys provided information on how behavior and movement influenced nesting success, but no studies have investigated how behaviors and movements influence breeding season survival. Survival of females is lowest during spring (Vander Haegen et al. 1988, Roberts et al. 1995, Pollentier et al. 2014), as they are faced with balancing risks associated with reproduction (egg laying, nest incubation, brooding) and individual survival (Conley et al. 2015, Bakner et al. 2019, Lohr et al. 2020). However, females may prioritize individual survival over reproductive success (Collier et al. 2009, Bakner et al. 2019).

Herein, I present this dissertation consisting of this introductory chapter, 4 chapters in manuscript format, and a concluding chapter. Chapter 2 evaluates if prospecting behaviors were occurring during laying and what landcover factors influenced prospecting. Chapter 3 examined how behavioral state-dependent recursive movements influenced resource selection of eastern wild turkey (*Meleagris gallopavo silvestris*) broods as they aged from day 1 to 28. Chapter 4 estimated site fidelity, identified hub and satellite roost sites, and evaluated landscape features selected at roost sites during different reproductive phases. Chapter 5 evaluated female wild turkey breeding season survival. Chapter 6 provides conclusions, management implications, and prospective topics for future research.

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CHAPTER 2

PROSPECTING DURING EGG LAYING INFORMS INCUBATION RECESS MOVEMENTS OF EASTERN WILD TURKEYS[1]

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[1] Bakner, N. W., E. E. Ulrey, B. A. Collier, and M. J. Chamberlain. In review at Movement Ecology.

ABSTRACT

Central place foragers must acquire resources and return to a central location after foraging bouts. During the egg laying (hereafter laying) period, females are constrained to a nest location, thus they must familiarize themselves with resources available within their incubation ranges after nest site selection. Use of prospecting behaviors by individuals to obtain knowledge and identify profitable (e.g., resource rich) locations on the landscape can impact demographic outcomes. As such, prospecting has been used to evaluate site quality both before and during the reproductive period for a variety of species. Using GPS data collected from female eastern wild turkeys (*Meleagris gallopavo silvestris*) across the southeastern United States, we evaluated if prospecting behaviors were occurring during laying and what landcover factors influenced prospecting. Specifically, we quantified areas prospected during the laying period using a cluster analysis and the return frequency (e.g., recess movements) to clustered laying patches (150-m diameter buffer around a clustered laying period location) during the incubation period. The average proportion of recess movements to prospected locations was 56.9%. Nest fate was positively influenced (μ of posterior distribution with 95% credible 0.19, 0.06-0.37, pd = 99.8%) by the number of patches (90-m diameter buffer around a clustered laying period location) a female visited during incubation recesses. Females selected for areas closer to the nest site, secondary roads, hardwood forest, mixed pine-hardwood forest, water, and shrub/scrub, whereas they avoided pine forest and open-treeless areas. Our findings suggest that having a diverse suite of clustered laying patches available to support incubation recesses is impactful to nest fate. As such, local conditions within prospected locations during incubation may be key to successful reproductive output by wild turkeys. We suggest that prospecting could be important to other

phenological periods. Furthermore, future research should evaluate how prospecting for brood-rearing locations may occur before or during the incubation period.

INTRODUCTION

Central place foragers travel from a central location on foraging excursions and return to that location between foraging bouts (Orians and Pearson 1979, Schoener 1979). Foraging bouts from centralized locations are known to incur a cost of time, energy, and mortality risk (Ydenberg et al. 1994). Avian species are constrained to nest sites during incubation and may have space use restrictions if low risk loafing and foraging areas are not adequately distributed within their available range (Kacelnik 1984, van Gils and Tijsen 2007, Lalla et al. 2022). Therefore, individuals should familiarize themselves with profitable areas within their incubation ranges that provide reduced risk or energetic benefit (Olsson et al. 2008).

Site prospecting is an exploratory behavior common across taxa which allows them to determine quality of areas within their ranges that would increase fitness (Zicus and Hennes 1989, Reed et al. 1999, Ponchon et al. 2013). Prospecting occurs at various time periods during the reproductive season (Schjørring et al. 1999, Dudko et al. 2019, Casazza et al. 2020). Among avian species, prospecting behavior has been related to identifying migratory stopover points (Moore and Aborn 2000) and pre- and post-breeding sites (Schjørring et al. 1999, Ottosson et al. 2001). Gathering information using prospecting behaviors allows individuals to reduce predation risk, while gaining resources supporting individual fitness and reproductive success (Reed et al. 1999, Ponchon et al. 2013).

Recursive movements are patterns of returns to previously visited areas which occur when individuals identify resources within a heterogeneous landscape (Ohashi and Thomson 2005, Riotte-Lambert et al. 2013, Berger-Tal and Bar-David 2015, Bracis and Mueller 2017).

Recursive movement behaviors benefit fitness by improving forage efficiency (Van Moorter et al. 2009, Ranc et al. 2021), increasing predator avoidance (Wittmer et al. 2006, van Beest et al. 2013), or in maintaining territories (Kokko et al. 2006, Hughes and Hyman 2011). For central place foragers, prospecting could be used as the mechanism to identify high-quality foraging areas (Pärt and Doligez 2003), preceding recursive movement to those profitable areas that were identified on the landscape (Berger-Tal and Bar-David 2015).

The onset of egg laying (hereafter laying) and incubation in avian species represents a time period during which individuals are spatially constrained on the landscape and yet is energetically costly (Deeming and Reynolds 2015). Uniparental incubators are faced with the tradeoff of remaining at the nest site or making recess movements (i.e. directional movements made away from nesting location) to gain resources (Skutch 1962, Williams 1996). Prior to incubation, prospecting by females to familiarize themselves with resource distribution could facilitate efficient travel to and from resources while reducing mortality risk (Reed et al. 1999, Piper 2011, Wakefield et al. 2015). Therefore, prospecting during the laying period could be important in supporting behavioral strategies used during incubation (Reed et al. 1999, Piper 2011).

Female eastern wild turkeys (*Meleagris gallopavo silvestris*; hereafter wild turkey) are uniparental ground nesters that maintain ranges, but do not maintain and defend territories (Healy 1992). During nesting, females are central-place foragers that make foraging bouts from the nest location during incubation (Conley et al. 2015, Bakner et al. 2019, Lohr et al. 2020). To survive the incubation period, females identify resources that provide foraging opportunities and concealment from predators (Green 1982, Williams et al. 1971, Bakner et al. 2019, Lohr et al. 2020). Contemporary research has shown that prior to laying, female wild turkeys do not prospect for potential nest sites (Conley et al. 2016), but it is plausible that individuals may prospect for resources during the laying period (Collier et al. 2019). Furthermore, pre-nesting and laying ranges show little overlap (Schofield 2019), and during laying, females increase daily movements but decrease space use, indicative of a lack of site familiarity (Schofield 2019, Moscicki et al. 2023, Heathcote et al. 2023). It is plausible that the movement behaviors may maximize foraging success and reduce predation risk during the incubation period (Byrne et al. 2014, Bakner et al. 2022). However, it is unclear if areas identified by females during laying are ultimately selected and visited during incubation when females take incubation recesses (Bakner et al. 2019, Lohr et al. 2020).

Our objectives were to determine if female wild turkeys returned to locations prospected during the laying period when making recess movements during incubation, and to assess the relationship between environmental and movement covariates during incubation recesses relative to areas they prospected during the laying period. We hypothesized that incubating females would return to sites previously visited during the laying period when taking incubation recesses, and such behaviors would positively affect nest fate. Specifically, we predicted that females who did not revisit sites previously visited during laying would have lower nest success.

STUDY AREA

We conducted research on 11 sites across the southeastern United States. In Louisiana, we conducted research on the Kisatchie National Forest (KNF), Fort Polk Wildlife Management Area (WMA), and Peason Ridge WMA from January 2014-August 2021. The KNF was owned and managed by the United States Forest Service (USFS), whereas Fort Polk and Peason Ridge WMA was jointly owned by the USFS and the United States Army. Louisiana sites were composed of pine (*Pinus* spp.)-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*). For a detailed description of site conditions on KNF and Fort Polk WMA see Yeldell et al. (2017*a,b*).

We conducted research on Lake Seminole and Silver Lake WMAs located in southwest Georgia from January 2015-August 2016. The Silver Lake WMA was owned and managed by the Georgia Department of Natural Resources-Wildlife Resources Division (GADNR), and the adjacent Lake Seminole WMA was owned by the U.S. Army Corps of Engineers and managed by GADNR. Both sites were predominantly mature pine forests and forested wetlands. Overstory species were predominately longleaf pine, loblolly pine, slash pine (*P. elliottii*), oaks, and sweetgum (*Liquidambar styraciflua*). For a detailed description of site conditions on Silver Lake WMA see Wood et al. (2019).

We conducted research on B.F. Grant and Cedar Creek WMAs located in the Piedmont region of Georgia from January 2017-August 2021. B.F. Grant WMA was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia, and was managed jointly by the GADNR and the Warnell School. B.F. Grant WMA landcover was primarily loblolly pine forest, agricultural lands, mixed hardwood and pine forests, and hardwood lowlands containing mostly oaks, sweet gum, and hickory. Agricultural lands were mostly grazed mixed fescue (*Festuca* sp.) fields and hay fields planted for ryegrass (*Lolium* sp.). Cedar Creek WMA was owned by the USFS and managed in partnership with GADNR. Cedar Creek WMA was composed primarily of loblolly pine uplands, mixed hardwood and pine forests, and hardwood lowlands of similar species composition as B.F. Grant WMA. For a detailed description of site conditions see Wakefield et al. (2020).

We conducted research on 3 contiguous WMAs (Webb, Hamilton Ridge, and Palachucola; hereafter, Webb WMA Complex; January 2014-August 2018) and the Savanah River Site (hereafter, SRS; January 2021-March 2021) in South Carolina. The Webb WMA Complex was owned and managed by the South Carolina Department of Natural Resources (SCDNR). The Webb WMA Complex was dominated by longleaf, loblolly, and slash pine forests with hardwood stands along riparian corridors, and expanses of bottomland hardwood wetlands. The SRS was owned by the United States Department of Energy and managed by USFS. The SRS was primarily forested and consisted of bottomland hardwoods, mixed-pine hardwoods, and planted stands of longleaf pine, loblolly pine and slash pine. For a detailed description of site conditions see Wightman et al. (2019).

METHODS

We used rocket nets to capture wild turkeys from January-March of 2014-2021. We aged captured individuals based on presence of barring on the ninth and tenth primary feathers and sexed them by the coloration of the breast feathers (Pelham & Dickson 1992). We banded each bird with an aluminum rivet leg band (National Band and Tag Company, Newport, Kentucky; female size = 8, male size = 9) and radio-tagged each individual with a backpack-style GPS-VHF transmitter (Guthrie et al. 2011) produced by Biotrack Ltd. (Wareham, Dorset, UK). We programmed transmitters to record 1 GPS location nightly (23:58:58) and hourly GPS locations from 0500 to 2000 (Standard Time and according to the appropriate time zones) for the duration of the study (Cohen et al. 2018). Each transmitter had a mortality switch that was programmed to activate after >23 hours of no movement. We released turkeys immediately at the capture location after processing. All turkey capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee at the University of Georgia (Protocol

#A2019 01-025-R2 and #A2020 06-018-R1) and the Louisiana State University Agricultural Center (Protocol #A2014-013, A2015-07, and A2018-13).

We located wild turkeys ≥2 times per week using a 3-element handheld Yagi antenna and receiver to monitor survival based on the presence of a mortality signal, general movements of individuals within their ranges, and onset of nesting activity. We remotely downloaded GPS locations from each turkey ≥1 time per week. In ArcGIS 10.8 (Environment Systems Research Institute, Redlands, California, USA), we spatially projected GPS locations to identify nest locations by determining when a female's locations became concentrated, which represented the onset of incubation (Conley et al. 2015, Bakner et al. 2019). When VHF tracking and GPS locations indicated nest termination, we located the nest site to determine if hatching had occurred (Conley et al. 2016, Yeldell 2017*a*, *b*).

We performed data processing and analysis in program R (v.4.1.0; R Core Team 2022). We processed and cleaned the raw GPS data by removing fix locations that had dilution of precision values (DOP) > 7. To determine dates of nest initiation (i.e. initiation of laying) and onset of incubation initiation, we mapped our spatial-temporal data using ArcGIS 10.8 (Environment Systems Research Institute, Redlands, California, USA). We identified the onset of incubation as the first time an individual remained on the nest overnight (Bakner et al. 2019, Lohr et al. 2020), and then evaluated hourly locations for the previous 20 days to determine when a female initially visited the nest site (defined as location being < 20 m from the known nest site, Conley et al. 2015, Conley et al. 2016, Schofield 2019). We considered the date of first visit as the date of nest initiation and used it as the beginning of the laying period as wild turkeys rarely visit nest sites before laying the first egg (Conley et al. 2016, Collier et al. 2019). Following Bakner et al. (2019), we classified recess movements during incubation as any location > 27.5 m (27.5 m is associated with the 90th percentile error of the transmitter) away from the known nest location and all other locations (< 27.5 m) as incubation and not recessing. We calculated the distance each recess location was from the nest location (distance to nest) to incorporate into our model to evaluate habitat selection.

MOVEMENT COVARIATES

We assigned a unique identification to each female GPS location for the duration of the laying period. To quantify location-specific revisitation for individual females, we combined laying locations that were to the same areas using a cluster analysis in program R (v.4.1.0; R Core Team 2022). Using estimates from Schofield (2019) who reported that female wild turkeys moved 300 m/hr during the laying period, we used a 150-m radius buffer of each unique GPS location to perform the cluster analysis (Figure 2.1). We then used the clustered laying period locations to quantify how many incubation recesses were made to that area.

Following Bracis et al. (2018), we calculated the revisit rate to assess whether female incubation recess movements were directed towards locations that had been previously visited during the laying period. This analysis was performed using the recurse package in program R (version 4.1.0; R Core Team 2022). We first assigned a unique identification to each of the clustered laying period locations (hereafter, clustered laying patch). We used estimates of daily distance traveled while on an incubation recess from Bakner et al. (2019; 90 m) to set an appropriate circular buffer size around each clustered laying patch. We then used the function getRecursionsAtLocation in package recurse in R (Bracis et al. 2018; v.4.1.0; R Core Team 2022) to calculate how many incubation recess locations fell within a 90 m diameter circular buffer of a clustered laying patch. Specifically, the function getRecursionsAtLocation allowed us to evaluate how many times an incubation recess movement was to a clustered laying patch.

We evaluated incubation recess movements in relation to nest fate (success or failure). We quantified the proportion of recess movements that went to a clustered laying patch, and the total number of clustered laying patches used during the incubation period. Therefore, we calculated the proportion of recess movements made to clustered laying patches by using the number of recesses to any clustered laying patch and dividing by the total number of recesses during the incubation period. To calculate the number of clustered laying patches used during incubation, we counted the number of clustered laying patches that were visited at least once during incubation recess.

Female wild turkeys are constrained to the nest location during incubation (Bakner et al. 2019, Lohr et al. 2020). Thus, we calculated the distance from the nest location to the recess movement locations to see if this distance influenced habitat selection. Understanding patterns of resource selection relative to the presence of recursive movements offers a mechanism to link resource availability and female behavioral decisions (Bakner et al. 2022). So, we evaluated resource selection using a set of landcover covariates relevant to female wild turkey reproductive ecology (Bakner et al. 2019, Chamberlain et al. 2020, Lohr et al. 2020). We obtained year-specific, 30-m resolution spatial data on landcover from the Cropland Data Layer (Cropscape) provided by the National Agricultural Statistics Service (National Agricultural Statistics Service 2015). We recoded and combined landcover in program R (v.4.1.0; R Core Team 2022) to create 6 unique landcover types (water, pine forest, hardwood forest, mixed pine-hardwood forest, open treeless areas, and shrub/scrub; Yeldell et al. 2017*ab*, Chamberlain et al. 2020).

NEST FATE MODEL

We constructed a Bayesian regression model to test our hypothesis regarding the relative importance of incubating females revisiting sites previously visited during laying on nest fate.

Specifically, we included the covariates proportion of recess movements to clustered laying patches and number of clustered laying patches visited to predict nest fate. We treated the probability of nest fate (success or failure) as a Bernoulli distribution. Our model included a unique identification number for each female turkey as a random effect. To improve model fit and allow for direct comparison of effect sizes of each predictor variable, we normalized all fixed effects included in the models using the scale function in R. We fitted models using package brms in program R (Bürkner 2017). We computed 4 MCMC chains for 8,000 iterations, discarding the first 1,000 iterations as a burn-in. We calculated 95% credible intervals that provided indices of uncertainty. We then computed the probability of direction (pd) which provided the probability each covariate either positively or negatively influenced nest fate. All estimated parameters had R-hat values <1, indicating that all chains converged (Gelman et al 2004).

RESOURCE SELECTION MODEL

We calculated 95% home ranges during the incubation period by fitting dynamic Brownian bridge movement models (dBBMMs) to the time-specific location data (Cohen et al. 2018) using package move (Kranstauber et al. 2012) in program R. We used an error estimate of 20 m, a moving window size of 7 locations, and a margin setting of 3 locations (Byrne et al. 2014, Cohen et al. 2018).

We used resource selection functions (RSFs) to examine relationships between 6 landcover types and distances traveled from nests to wild turkey incubation recess movements to clustered laying patches within individual incubation ranges (3rd-order selection) following design III approach suggested by Manly et al. (2002). We compared use (incubation recess movements to clustered laying patches) points within individual incubation ranges to 500 available points sampled within each range (Benson 2013). We tested for collinearity between each of our covariates and excluded covariates using Pearson's correlation with a $r > 0.60$ (Dormann et al. 2013). We created 5 models which included a global model (i.e., including all covariates), interactions between distance traveled and landcover covariates, distance traveled, landcover covariates, and a null model (Table 2.1). We used a generalized linear mixed model to include a random intercept for each individual turkey, with a binomial response distribution (logistic regression) and logit link to the used-available data for turkeys (Manly et al. 2002, Johnson et al. 2006). We used the lme4 R package (Bates et al. 2014) with a binary (0 = available, 1 = used) response variable to model resource selection. To improve fit, we rescaled all fixed effects by subtracting their mean and dividing by 2 standard deviations prior to modeling (Gelman 2008).

We used second-order Akaike's Information Criteria (AIC*c*) to assess the amount of support for the different candidate models (Akaike 1973, Burnham & Anderson 2002). We calculated ΔAIC*c* values between the AIC*c* value for candidate model *i* and the lowest-ranked AIC value. We also calculated Akaike's weights (w_i) for each model. We then calculated parameter estimates and their standard errors for all covariates in models within 2 ΔAIC*c* units of the lowest-ranked AIC value.

RESULTS

We monitored 692 nesting attempts by 485 (427 adults and 55 juveniles, 3 unknown) female wild turkeys during 2014–2021. We removed 107 nesting attempts that were incubated <3 days since we were unable to isolate incubation behaviors from nests of such short duration. We used 585 nesting attempts (initial attempts = 407, renesting attempts = 178) by 435 females to quantify whether females were revisiting clustered laying patches. We identified 31,145 recess movements during incubation, of which 56.9% (SD = 22.2, median = 58.7) were made to clustered laying patches (Figure 2.2). The random effect of individual had a variance of 1.44 ± 0.63. Mean number of clustered laying patches used during laying that were visited during incubation recesses was 5 (SD = 1.9, range = 0-17 patches). The proportion of recess movements to clustered laying patches had no effect on nest fate (μ of posterior distribution with 95% credible interval -0.0, -0.01-0.01, pd = 61.6%). However, as the number of clustered laying patches used during incubation recesses increased there was a positive impact on nest fate (μ of posterior distribution with 95% credible interval 0.19, 0.06-0.37, pd = 99.8%), where the probability of nest success increased by 2.8% for every additional clustered laying patch visited (Figure 2.3).

For our RSF, we used 16,278 GPS locations from recess locations that were to clustered laying patches. Our top-ranking model was the global model (w_i = 1.00; Table 2.1). The random effect of individual had a variance of 1.84 (SD = 1.36). Female wild turkeys selected for areas closer to hardwoods (β = -0.27, SE ± 0.031), water (β = -0.48, SE ± 0.037), mixed pine-hardwoods (β = -0.10, SE ± 0.025), secondary roads (β = -0.39, SE ± 0.051), shrub/scrub (β = -0.16, SE ± 0.583), and areas closer to the nest (β = -2.04, SE = 0.020; Figure 2.4). Female wild turkeys avoided areas closer to open treeless areas (β = 0.27, SE ± 0.030) and pine (β = 0.06, SE ± 0.022; Figure 2.4).

DISCUSSION

Prospecting behavior before the onset of incubation has been found to occur in a variety of avian species (Reed et al. 1999). Presumably, species rely on prospecting to determine areas capable of conferring greater nest success (Doligez et al. 2002) and profitable patches ensuring availability of resources (Pärt and Doligez 2003). Although prospecting behavior has been shown to occur in avian species, information on how prospecting behavior could function during the laying period is unavailable. Using prospecting movements to identify recursive locations, our results indicate that ~57% of incubation recess movements were to patches visited during laying. Our findings support contemporary research demonstrating that wild turkeys increase daily movements during laying, indicative of a lack of site familiarity (Schofield 2019). Similar behaviors have been described in waterfowl (*Anas* sp.) that visit future brood-rearing ponds prior to hatching (Casazza et al. 2020), ruff (*Philomachus pugnax*) and black grouse (*Tetrao tetrix*) where females visit leks prior to the breeding season (Beehler and Foster 1988) and is presumed to occur in sage grouse (*Centrocercus urophasianus*) prior to incubation (Dudko et al. 2019).

We observed that nest fate was not influenced by the number of times a female returned to clustered laying patches, but was affected by how many different clustered laying patches she visited while on incubation recesses. Observational work by Williams and Austin (1988) reported the unpredictability of timing and movement patterns by female wild turkeys during incubation. When wildlife are faced with patchy resource distributions, they become constrained by the spatial distribution of their resources (Sih 2005). Where resources are sparse, prey may have to endure periods of overlap with predators which makes prey more predictable (Sih 2005, Schmitz et al. 2017). Alternatively, when prey are surrounded by multiple safe sites where predators are less efficient, predators may avoid these locations (Sih 1984). Having multiple profitable foraging patches allows prey to be more unpredictable in their movements which favors the prey instead of the predator (Smith et al. 2019). Overall, we found that female wild turkeys that were not confined to repeatedly using the same patches within their incubation ranges had increased nest success.

During nesting, avian species should surround themselves with adequate resources to survive incubation while reducing predation risk (Skutch 1962, Deeming and Reynolds 2015). Wild turkeys are habitat generalists (Porter 1992), so we were not surprised that females used a variety of landcover types during incubation recess movements to sites previously visited during laying. Presumably, females were simply going to places that offered conditions capable of supporting survival. Our results indicated that pine and open-treeless areas were avoided by wild turkeys. Open-treeless areas and pine forest on our sites were typically open pastures dominated by forages planted for livestock, sod-forming grasses, or industrial pine forest. Similar types of open areas and pine forest fail to offer high quality foraging habitats for incubating females relative to other early successional vegetation communities (Backs and Bledsoe 2011, Martin et al. 2012). Likewise, during incubation females often try to avoid other females, hence reducing predation risk (Healy 1992, Schaap et al. 2005, Schofield 2019). Therefore, remaining in forested areas could provide concealment to reduce intraspecific interactions and predation risk. Alternatively, environmental thermal regimes can shape avian behavior (Huey 1991), and in warmer environments, Galliformes have been found to adjust habitat use to select for areas with cooler temperatures (Hovick et al. 2014, Tanner et al. 2017). Specific to wild turkeys, Nelson et al. (2022) found that broods on our study sites avoided pine forests and selected cooler locations as the day progressed. Therefore, avoidance of open-treeless areas and pine forest may be due to thermal regulatory constraints.

Our results emphasize the complexity of how prior behavioral processes can affect future events, such as nesting behavior. Researchers frequently measure and describe vegetative characteristics at and around nest sites, but these characteristics often fail to describe the spatial scale at which nesting is occurring (Deeming and Reynolds 2015, Ulrey et al. 2022) and are not clearly linked to nest success (Crawford et al. 2021, Keever et al. 2023). Our research details a biologically relevant spatial and temporal scale for evaluating nesting vegetation conditions. Specifically, to evaluate nesting vegetation for female wild turkeys, we suggest that focus on identifying resource selection and activities during the laying period would be relevant and appropriate. We suggest future research to gain a more fine-scaled approach of evaluating habitat at patch locations. Furthermore, prospecting behavior has been thought to occur during recess bouts to identify brood-rearing habitat (Dudko et al. 2018). Future research should evaluate how prospecting for brood-rearing habitat may occur prior to or during the incubation period.

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Table 2.1: Akaike's Information Criterion with small sample bias adjustment (AIC*c*), number of parameters (*K*), ΔAIC_c, Akaike weight of evidence (w_i) in support of model, and log-likelihood (LL) for candidate models examining factors influencing incubation recess selection of eastern wild turkeys in across the southeastern, USA, 2014-2021.

Model	*K*	AIC*c*	ΔAIC*c*	w_i	LL
Hardwood +Mixed pine-hardwood + Open treeless + Pine + Shrub/scrub + Water + Distance to nest	10	87122.4	0.00	1.00	-43551.2
Distance to nest	3	87931.1	808.7	0.00	-43962.6
Hardwood:Distance to nest +Mixed pine-hardwood:Distance to nest + Open treeless:Distance to nest + Pine:Distance to nest + Shrub/scrub:Distance to nest + Water:Distance to nest	9	102698.5	15576.1	0.00	-51340.3
Hardwood +Mixed pine-hardwood + Open treeless + Pine + Shrub/scrub + Water	9	104452.8	17330.3	0.00	-52217.4
(.)	2	105214.4	18092.0	0.00	-52605.2

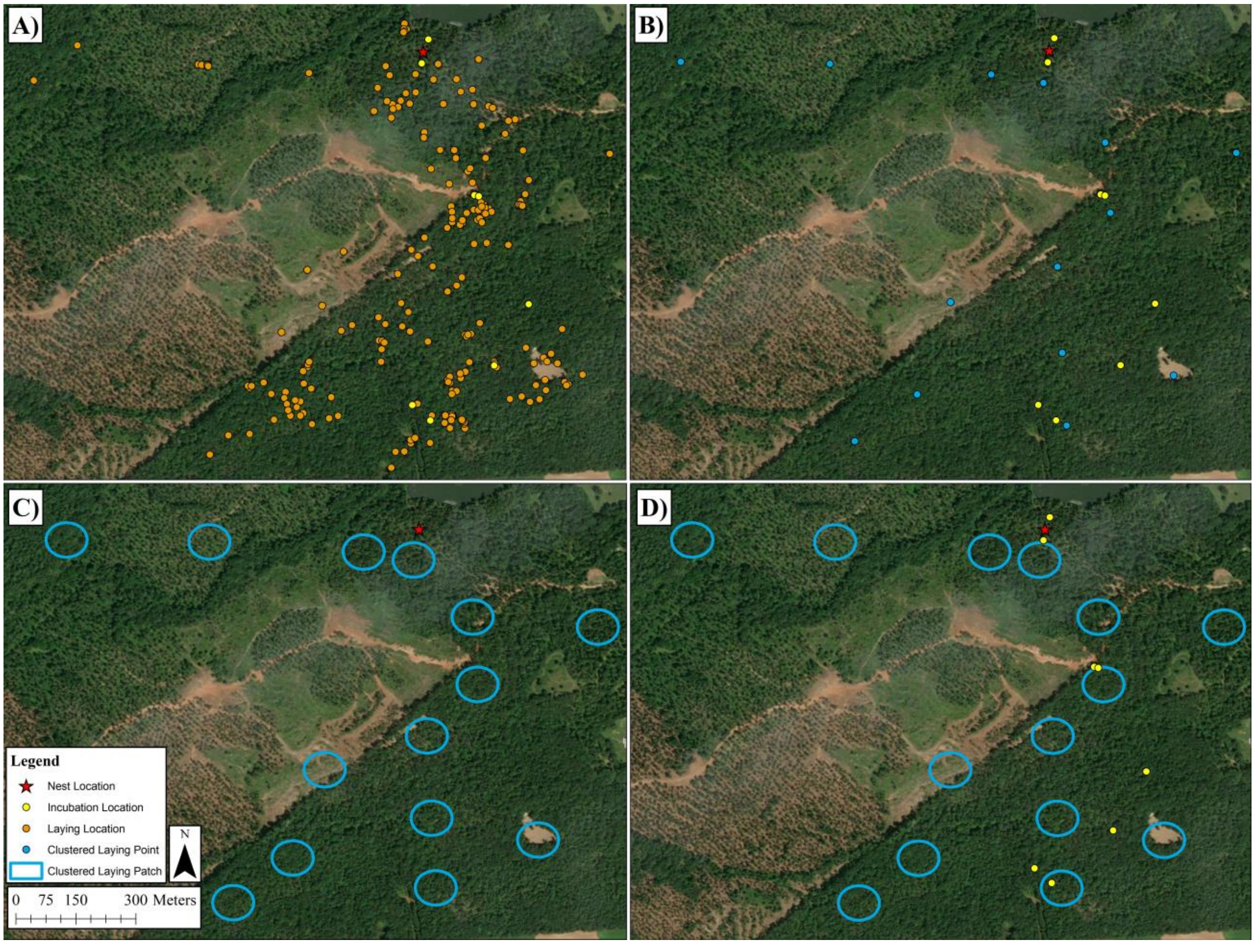

Figure 2.1: GPS locations of a female eastern wild turkey depicting how we determined the clustered laying patch covariate and number of incubation recesses. A) Laying and incubation movements used for the analysis with a star showing the nest location. B) Clustered laying period GPS locations created from the cluster analysis (150 m radius buffer; hereafter, clustered laying patch). C) The clustered laying patch with a 45 m radius buffer determined from how far a female travels during incubation. D) Any incubation point that fell within a clustered laying patch contributed to the proportion of recesses made to a laying period location. Any clustered laying patch that contained an incubation location was considered a clustered laying patch that was used.

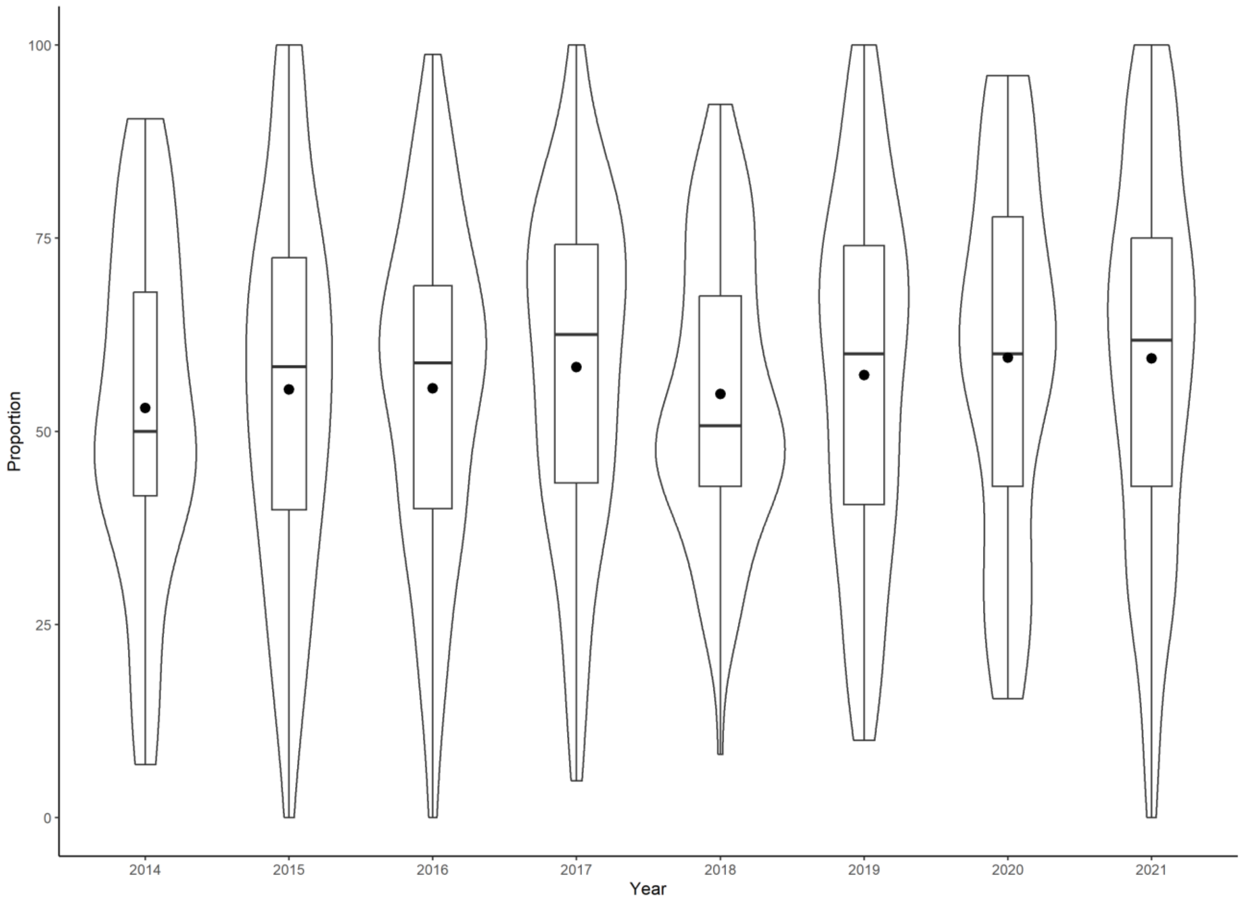

Figure 2.2: Proportion of incubation recess movements made to clustered laying patches for 585 nesting attempts made by 435 female eastern wild turkeys (*Meleagris gallopavo silvestris*) across the southeastern United States during 2014-2021. Violin plots are the distribution of the data with corresponding boxplot inside. The solid line identifies the median and the dot corresponds with the average proportion.

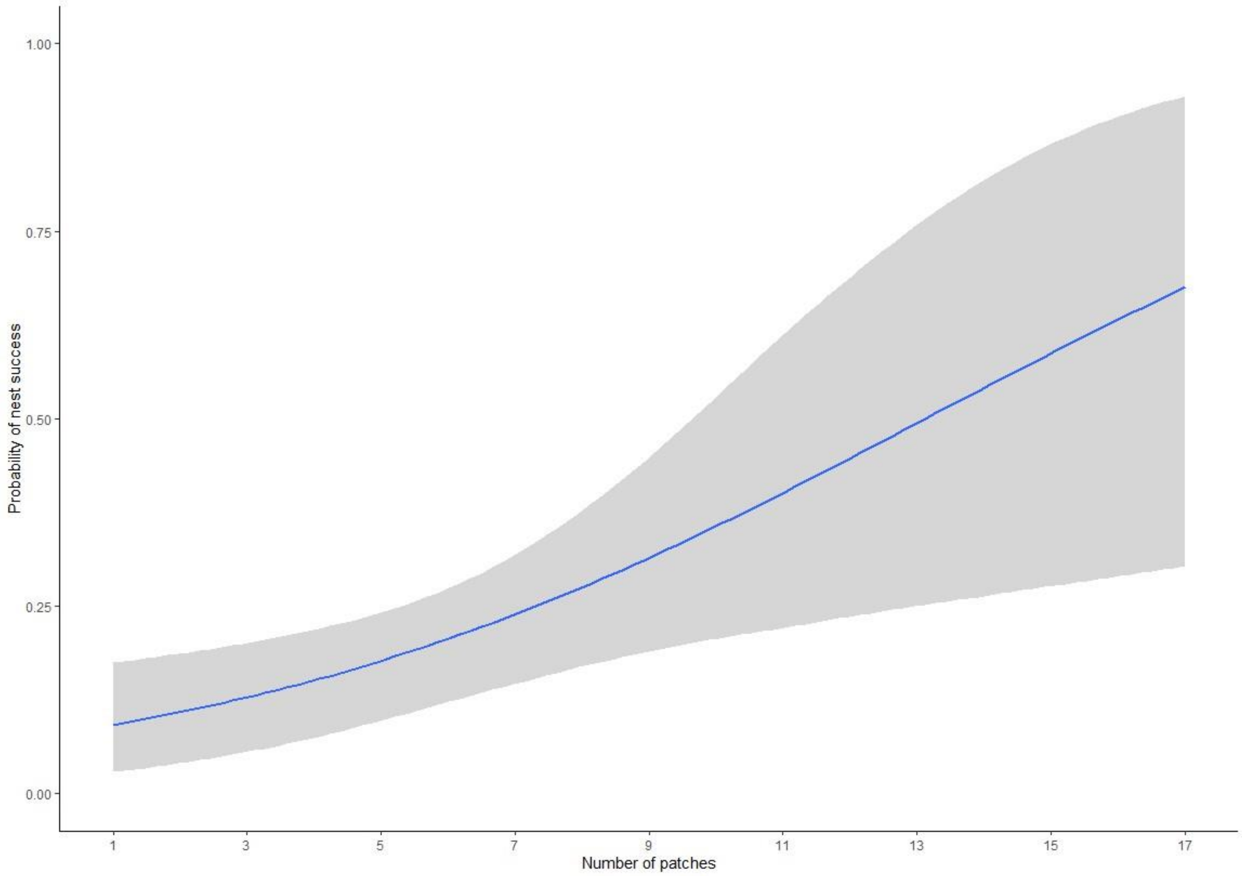

Figure 2.3: Probability of nest success as a function of the number of clustered laying patches visited during incubation recesses for 585 nesting attempts made by 435 female eastern wild turkeys (*Meleagris gallopavo silvestris*) across the southeastern United States during 2014-2021. Gray shading represents the 95% credible intervals.

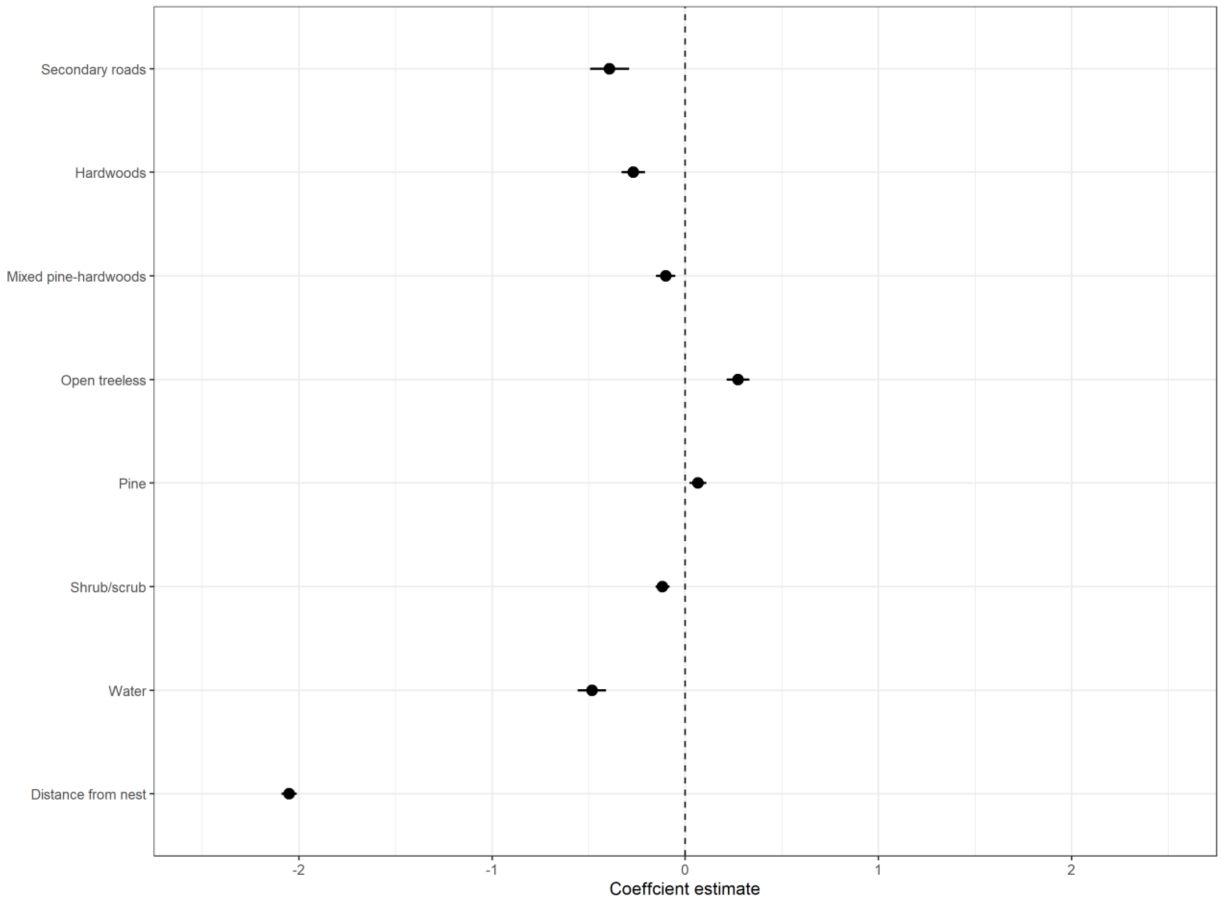

Figure 2.4: Coefficient plot depicting resource selection of eastern wild turkeys (*Meleagris gallopavo silvestris*) during incubation recesses to clustered laying patches across the southeastern United States during 2014-2021. The whiskers depict 95% confidence intervals around regression coefficient estimates.

CHAPTER 3

BEHAVIORAL-DEPENDENT RECURSIVE MOVEMENTS AND IMPLICATIONS FOR RESOURCE SELECTION[1]

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ABSTRACT

Within home ranges, animals repeatedly visit certain areas. Recursive movement patterns are widespread throughout the animal kingdom, but are rarely considered when developing resource selection models. We examined how behavioral state-dependent recursive movements influenced resource selection of eastern wild turkey (*Meleagris gallopavo silvestris*) broods as they aged from day 1 to 28. Because wild turkey broods show more plasticityin behaviors once they begin roosting off the ground, we separated data into ground roosting (1-13 days) and tree roosting (14-28 days). We used Hidden Markov Models to identify 2 behavioral states (restricted and mobile). We extracted state-specific recursive movements based on states and specific step lengths, which we integrated into a step selection analysis to evaluate resource selection. We found that in a restricted state, ground roosting broods spent less time in areas of mixed pine-hardwoods and more time in areas with greater vegetation density. Tree roosting broods revisited areas closer to shrub/scrub landcover types, and areas with greater vegetation density. Tree roosting broods also spent less time near mixed pine-hardwoods, while spending more time in areas with greater vegetation density. We found that in a mobile state, ground roosting broods revisited areas closer to secondary roads and mixed pine-hardwoods, but farther from hardwoods. Tree roosting broods revisited areas farther from secondary roads and with greater vegetation density. Tree roosting broods also spent more time in areas closer to pine. Resource selection varied depending on behavioral state and recursive movements. However, revisitation and residence time impacted selection for both ground and tree roosting broods. Our findings highlight the need to consider how behavioral decisions can influence movement ecology and ultimately resource selection.

INTRODUCTION

Spatial distribution of resources such as forage, water, and shelter influences how animals move across the landscape (Pyke et al. 1984, Owen-Smith et al. 2010). Animals collect resources from patches within home ranges through repeated visitation (Makino & Sakai 2004, Van Moorter et al. 2009, Van Moorter et al. 2016). By revisiting areas that contain resources, animals minimize risks associated with navigating unfamiliar areas which may improve survival and fitness (Börger et al. 2008, Piper 2011, Merkle et al. 2014). Recursive movement patterns are returns to previously visited areas, and are a widespread phenomenon in the animal kingdom (Berger-Tal & Bar-David 2015). Understanding how recursive movement strategies influence behavioral processes is important in examining areas for resource acquisition (Ohashi & Thomson 2005, Berger-Tal & Avgar 2012, Riotte-Lambert et al. 2013, Berger-Tal & Bar-David 2015).

Recursive movement strategies have been documented in a variety of species, typically occurring when individuals are locating resources within a heterogeneous landscape (Bar-David et al. 2009, English et al. 2014, Bista et al. 2022). Path recursions, defined as nonrandom movements in which animals repeatedly return to resource rich locations (Berger-Tal & Bar-David 2015), is a profitable foraging strategy that enables resources to recover (Bar-David et al. 2009, Owen-Smith et al. 2010). Although generality of recursive movements is recognized in how animals select habitat, resource selection analyses often associate movements to availability of resources within individual home ranges (Boyce & McDonald 1999, Boyce et al. 2002, Manly et al. 2002). Including recursion information within a resource selection framework can potentially identify one mechanism driving behavioral decision-making and resource availability within a home range (Buderman et al. 2018, McKeown et al. 2020).

Behavioral decisions can influence the fitness of a species via resource selection (Togunov et al. 2022, Picardi et al 2022, Whittington et al. 2022). Changes in behavior and movement patterns may suggest a response to variation in habitat conditions, such as where an individual goes to acquire resources or avoid risk (Creel & Christianson 2008, Buchholz et al. 2019). Identifying behavioral patterns in resource selection could provide insight as to where individuals choose to travel versus forage (Collier and Chamberlain 2011, Wilson et al. 2012, Ferreira et al. 2022). Failing to incorporate such behavioral patterns in resource selection models can result in biased results, including misidentifying where animals travel and misallocating limits in foraging resources (Roever et al. 2013, Abrahms et al. 2016, Abrahms et al. 2017).

Wild turkeys (*Meleagris gallopavo*) are considered habitat generalists; however, habitat requirements of adults differ from their precocial offspring (Healy 1992). During the first 28 days post-hatch, wild turkey poults experience high mortality risk (Hubbard et al. 1999, Spears et al. 2007, Chamberlain et al. 2020) as they are unable to thermoregulate and must find high quality foraging patches rich in arthropods (Healy 1985, Lafon et al. 2001, Backs & Bledsoe 2011, Nelson et al. 2022). Wild turkey poults grow rapidly during the first month, developing an ability to fly within 2 weeks post-hatch (Barwick et al. 1970, Williams et al. 1973, Pelham & Dickson 1992). Increasing maneuverability facilitates behavioral changes and can alter foraging strategies to exploit areas within their range more efficiently (Barwick et al. 1970, Williams et al. 1973). Hence, resource needs and selection of poults may be more specialized immediately post-hatch and become more generalized as they age (Chamberlain et al. 2020, Nelson et al. 2022).

Wild turkey broods are thought to revisit profitable areas (Healy 1992, Bakner et al. 2022), but whether there are patterns in revisitations remains unknown. Knowledge of revisitation timing to specific sites across the landscape could provide insight to drivers of the selection processes used by broods (Bracis et al. 2018). Therefore, we examined how behavioral state-dependent recursive movements influenced resource selection as broods aged. Our objective was to quantify differences in recursive movements and resource selection of ground versus tree-roosting broods. We used movement behaviors to infer a behavioral state (mobile and restricted) to account for differences in resource selection. We hypothesized that broods would exhibit differential resource selection across behavioral states. We predicted that as broods aged, they would become more plastic in resource selection, but continue to exhibit consistency in recursive movements.

STUDY AREA

We conducted research on 11 sites across the southeastern United States. In Louisiana, we conducted research on the Kisatchie National Forest (KNF), Fort Polk Wildlife Management Area (WMA), and Peason Ridge WMA from January 2014-August 2021. The KNF was owned and managed by the United States Forest Service (USFS), whereas Fort Polk and Peason Ridge WMA was jointly owned by the USFS and the United States Army. Louisiana sites were composed of pine (*Pinus* spp.)-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*). For a detailed description of site conditions on KNF and Fort Polk WMA see Yeldell et al. (2017*a,b*).

We conducted research on Lake Seminole and Silver Lake WMAs located in southwest Georgia from January 2015-August 2016. The Silver Lake WMA was owned and managed by the Georgia Department of Natural Resources-Wildlife Resources Division (GADNR), and the adjacent Lake Seminole WMA was owned by the U.S. Army Corps of Engineers and managed by GADNR. Both sites were predominantly mature pine forests and forested wetlands. Overstory species were predominately longleaf pine, loblolly pine, slash pine (*P. elliottii*), oaks, and sweetgum (*Liquidambar styraciflua*). For a detailed description of site conditions on Silver Lake WMA see Wood et al. (2019).

We conducted research on B.F. Grant and Cedar Creek WMAs located in the Piedmont region of Georgia from January 2017-August 2021. B.F. Grant WMA was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia, and was managed jointly by the GADNR and the Warnell School. B.F. Grant WMA landcover was primarily loblolly pine forest, agricultural lands, mixed hardwood and pine forests, and hardwood lowlands containing mostly oaks, sweet gum, and hickory. Agricultural lands were mostly grazed mixed fescue (*Festuca* sp.) fields and hay fields planted for ryegrass (*Lolium* sp.). Cedar Creek WMA was owned by the USFS and managed in partnership with GADNR. Cedar Creek WMA was composed primarily of loblolly pine uplands, mixed hardwood and pine forests, and hardwood lowlands of similar species composition as B.F. Grant WMA. For a detailed description of site conditions see Wakefield et al. (2020).

We conducted research on 3 contiguous WMAs (Webb, Hamilton Ridge, and Palachucola; hereafter, Webb WMA Complex; January 2014-August 2018) and the Savanah River Site (hereafter, SRS; January 2021-March 2021) in South Carolina. The Webb WMA Complex was owned and managed by the South Carolina Department of Natural Resources (SCDNR). The Webb WMA Complex was dominated by longleaf, loblolly, and slash pine forests with hardwood stands along riparian corridors, and expanses of bottomland hardwood wetlands. The SRS was owned by the United States Department of Energy and managed by USFS. The SRS was primarily forested and consisted of bottomland hardwoods, mixed-pine hardwoods, and planted stands of longleaf pine, loblolly pine and slash pine. For a detailed description of site conditions see Wightman et al. (2019).

METHODS

CAPTURE AND HANDLING

We used rocket nets to capture wild turkeys from January-March of 2014-2021. We aged captured individuals based on presence of barring on the ninth and tenth primary feathers, and identified sex of each individual by the coloration of the breast feathers (Pelham & Dickson 1992). We banded each bird with an aluminum rivet leg band (National Band and Tag Company, Newport, Kentucky; female size = 8, male size = 9) and radio-tagged each individual with a backpack-style GPS-VHF transmitter (Guthrie et al. 2011) produced by Biotrack Ltd. (Wareham, Dorset, UK). We programmed transmitters to record 1 GPS location nightly (23:58:58) and hourly GPS locations from 0500 to 2000 (Standard Time according to the appropriate time zones) until the battery died or the unit was recovered (Cohen et al. 2018). Each transmitter had a mortality switch that was programmed to activate after >23 hours of no movement. We released individuals immediately after processing at the capture location.

NEST AND BROOD MONITORING

We located wild turkeys ≥2 times per week using a 3-element handheld Yagi antenna and receiver to monitor survival based on the presence of a mortality signal, general movements of individuals across their ranges, and nesting activity. We remotely downloaded GPS locations from each turkey ≥1 time per week. In ArcGIS 10.8 (Environment Systems Research Institute, Redlands, California, USA), we spatially projected GPS locations to identify nest locations by determining when a female’s locations became concentrated, which represented the onset of incubation (Conley et al. 2015, Bakner et al. 2019). When GPS locations indicated nest termination, we located the nest site to determine if hatching had occurred (Conley et al. 2016, Yeldell 2017*a*, *b*).

Following standard methods outlined by Chamberlain et al. (2020), we monitored brooding females until brood failure or 28 days after hatch, as most brood mortality occurs during this period (Hubbard et al. 1999). We located females that hatched successfully every 2-3 days post-hatch via VHF to conduct brood surveys, and considered a brood to be present if ≥1 poult was seen or heard with the female (Chamberlain et al. 2020). If we detected a brooding female on the ground prior to sunrise less than 14 days post-hatch, we assumed she was still with a brood as brooding females typically begin tree roosting with poults 14 days post-hatch (Barwick et al. 1970, Healy 1992, Spears et al. 2007). Hence, if we were able to detect a brood during the night, we did not disturb them during the day. Likewise, if we detected a brooding female roosted in a tree prior to 14 days post-hatch and could not detect poults, we assumed the brood was lost. We performed brood surveys up to 28 days after hatch or until we failed to detect any poults during 2 consecutive attempts, at which point we assumed the brood was lost. We defined brood success as the proportion of broods with ≥1 poult surviving to 28 days post-hatch (Chamberlain et al. 2020).

GPS DATA PROCESSING

We processed and cleaned the GPS data by removing fix locations that had dilution of precision values (DOP) > 7. We excluded from analyses females that successfully hatched a nest but were never visually confirmed to have poults. We then removed roosting locations (1 point collected at midnight, 0500 and 0600) as we expected broods would rarely revisit roost sites (Hillestad & Speake 1970, Chamberlain et al. 2020) and our interest was in behaviors most likely to be associated with foraging, loafing, or traveling.

BEHAVIORAL ANALYSIS

We fit a Hidden Markov Model (HMM; Langrock et al. 2012) to define movement trajectories into behavioral states based on step lengths and turning angles (Figure 1). We modeled step lengths using a gamma distribution and turning angles using a Von Mises distribution (Langrock et al. 2012). We defined initial parameter values for 3 states: a stationary movement state with small step lengths (gamma distribution with a mean of 27 m and standard deviation of 27 m) and uniform turning angles (Von Mises distribution with a mean of π and a concentration of 0.1), a restricted movement state with small/moderate step lengths (gamma distribution with a mean of 150 m and standard deviation of 150 m) and uniform turning angles (Von Mises distribution with a mean of 2.5 and a concentration of 0.5), and a travelling movement state with large step lengths (gamma distribution with a mean of 400 m and a standard deviation of 1,000 m) and directed turning angles (Von Mises distribution with a mean of 0.001 and a concentration of 0.99). We used the Viterbi algorithm to assign each step to the most likely behavioral state based on results of the HMM (Zucchini et al. 2017). We conducted our analysis in R (v.4.1.0; R Core Team, 2022) using package momentuHMM (McClintock & Michelot 2018).

RECURSIVE ANALYSIS

We calculated the revisit rate (hereafter, revisitation) as the sum of visits to previously visited locations (Bracis et al. 2018) as follows. We first assigned a unique identification to each female GPS location for the duration of known brooding. To quantify behavioral-specific revisitation, we buffered GPS locations using the mean step-length from our HMMs for restricted and mobile movements (90-m radius and 250-m radius) to identify the area likely used by each brood each hour (Figure 1). We considered revisits to be GPS locations that fell within a spatial buffer for any previous day for the entire period the brood was monitored. Additionally, we calculated residence time, defined as the total elapsed time between successive GPS locations within the circular buffer for all visits during the observed observation period for each brood (i.e., up to 28 days), and return time, defined as the amount of time (days)between visits using the R package recurse (Bracis et al. 2018). For the recursion analyses, we evaluated brooding females independently of one another.

To incorporate the effect of recursive movements on resource selection, we used a modified Brownian bridge approach, the Biased Random Bridge kernel utilization (Benhamou 2011, Benhamou & Riotte-Lambert 2012). We produced a 30-m by 30-m raster to represent behavioral-specific recursive movements for each individual (Figure 3.1). We buffered GPS locations identified from our HMMs as restricted or mobile, using either the 90-m or 250-m radius as noted above. We created a 2-dimensional utilization distribution of each individual's trajectory that represented the relative number of revisits made to each location (Oliveira-Santos et al. 2016). We also assessed the time that a female spent in each area, which provided a biologically relevant measure of intensity of use. Specifically, we used Biased Random Bridge kernel utilization distributions based on residence time to evaluate intensity of use. We converted each behavioral-specific recursion map to a continuous value between 0 and 100, where 0 identified areas that were most strongly associated with the recursive behavior, and values around 100 identified areas not associated with recursive behaviors. We created recursive movement maps using the R package adehabitatHR (Calenge 2006).

ENVIRONMENTAL COVARIATES

We examined resource selection in relation to a set of environmental covariates relevant to ecology of brooding female wild turkeys. We obtained year-specific, 30-m resolution spatial data on landcover from the Cropland Data Layer (Cropscape) provided by the National Agricultural Statistics Service (National Agricultural Statistics Service 2015). We combined landcover classes in R to create 7 unique landcover types (water, pine forest, hardwood forest, mixed pine-hardwood forest, open treeless areas, shrub/scrub, and infrastructure). We then calculated the Euclidean distance in ArcMap 10.8 (Esri, Redlands, CA, USA) to get the distance a GPS location was located from each landcover type. We used 30-m resolution imagery from United States Geological Survey (USGS) Landsat–8 Operational Land Imager to compute a normalized difference vegetation index (NDVI) in ArcMap 10.8 (Esri, Redlands, CA, USA) as an index of vegetation density (Wakefield et al. 2020). Measurements of NDVI allowed us to understand sparseness of vegetation, which has been shown to influence maneuverability, concealment, and foraging ability for poults (Williams et al. 1970, Healy 1985). We used the USGS National Transportation Dataset (https://nationalmap.gov/transport.html) and information provided by the Department of Defense to obtain secondary road layers which was converted to a distance to raster layer.

HABITAT AND MODEL SELECTION

Before analysis, we scaled and centered all variables, so that we could compare effect sizes of variables within individuals on each respective study sites (Schielzeth 2010). We tested for correlation among all continuous predictor variables using Pearson’s correlation and none were highly correlated (correlation coefficient > 0.7). We used a step selection function (SSF; Avgar et al. 2016, Muff et al. 2020) to assess resource selection, where available habitat associated with a given female location was conditional on where the individual occurred at the time of the previous GPS location. We considered a used point as the GPS location of a female, whereas available points were 100 locations that were theoretically available for selection by that female during the hour the GPS location was recorded. We generated available locations using the amt package in R (Signer et al. 2019). To assess temporal resource selection and recursive movement behaviors, we separated data into 2 periods based on whether females with broods were ground (day 1-13) or tree roosting (day 14-28). For each behavioral state (restricted or mobile), we then parameterized 6 models separately. Within each model, we included the logarithm of step length and the cosine of the turning angle as covariates to account for the underlying movement process (Forester et al. 2009). Furthermore, we parameterized a landcover model, which included only landcover and secondary roads. We parameterized 2 models, one of which was based on number of revisits only, and the other based on only residence time. Finally, we parameterized 2 models that contained all covariates and which interacted with either number of revisits or residence time (composite model; Table 3.1).

We used mixed conditional Poisson regression models with stratum-specific intercepts to estimate resource selection (Muff et al. 2020). To account for variability among individuals within our models, we included random slope for each covariate for each unique individual (Duchesne et al. 2010). We did not include random slopes for each interaction of landcover and recursive movement as models failed to converge due to quasi-complete separation. We fitted the SSF using the Poisson formulation where the stratum-specific random intercept variance was fixed to a large value to avoid shrinkage, following Muff et al. (2020). We used the R package glmmTMB to conduct the step selection analysis (Magnusson et al. 2017).

We used second-order Akaike's Information Criteria (AIC*c*) to assess the amount of support for the different candidate models (Akaike 1973, Burnham & Anderson 2002). We calculated ΔAIC*c* values between the AIC*c* value for candidate model *i* and the lowest-ranked AIC value. We also calculated Akaike's weights (w_i) for each model. We then calculated parameter estimates and their standard errors for all covariates in models within 2 ΔAIC*c* units of the lowest-ranked AIC value. To assess how well our SSF models explained the data, we used area under the receiver-operating characteristic curves (AUC) calculated with the pROC package (Zipkin et al. 2012). An AUC value of 0.5 indicated the model provided estimates of no better than random predictions but values greater than 0.7 indicated a better model fit with more accurate predictions.

RESULTS

We captured and radio-marked 993 female wild turkeys during 2014–2021. We monitored 692 nest attempts, 147 (21.2%) of which successfully hatched. We censored data from 10 broods that were presumably lost during or within hours of hatching, as we were not able to visually document poult presence via brood surveys. We censored an additional 26 broods due to GPS failure. Hence, we used 111 broods in our analyses, which we visually monitored until brood failure or 28 days after hatch. Of these 111 broods, 36 (32%) survived to 28 days post-hatch. After removing roosting locations, we used 33,819 GPS locations to use for subsequent analyses.

BEHAVIORAL CLASSIFICATIONS

From our HMM, the step length distribution had an estimated mean of 13.3 m (95% CI = 13.2−13.4 m) and standard deviation of 10.1 m (95% CI = 10.0−10.2 m) for the stationary state, an estimated mean of 92.2 m (95% CI = 90.7−93.8 m) and standard deviation of 74.1 m (95% CI = 72.7−75.5 m) for the restricted state, and an estimated mean of 249.1 m (95% CI = 245.7−252.4 m) and standard deviation of 175.9 m (95% CI = 175.0−177.2 m) for the mobile state (Figure 3.2). The turning angle distribution had an estimated mean of 3.1 (95% CI = 3.1–3.2) and concentration parameter of 0.7 (95% CI = 0.7–0.8) for the stationary state, a mean of 2.4

(95% CI = 0.7–3.1) and concentration parameter of 0.01 (95% CI = −0.01–0.02) for the restricted state, and a mean of −0.1 (95% CI = −0.04−0.01) and concentration parameter of 0.5 (95% CI = 0.5–0.6) for the mobile state (Figure 3.2). For subsequent analyses, we combined the stationary and restricted states as they were both associated with relatively shorter distances moved and sharper turn angles characteristic of foraging bouts. From the HMM, we considered 84.5% of movements restricted whereas 15.5% were mobile.

RECURSIVE MOVEMENTS AND BEHAVIORAL DEPENDENT RESOURCE SELECTION

On average, broods revisited previous locations 9.2 times (SD = 8.1, range = 0−58 visits; Figure 3.2). Mean residence time was 43.2 hr (SD = 47.3 hr, range = 0.1−564.0 hr; Figure 3.3), whereas the return time averaged 1.4 days (SD = 2.2, range = 0−25.9 days; Figure 3.4).

The composite models that included both recursive movements and landcover performed better than those based exclusively on landcover or recursive movements (Table 3.2). Within each model broods revisited and exhibited increased residence time regardless of landcover (Figure 3.5, Figure 3.6). Ground roosting broods in a restricted state spent less time in mixed pine-hardwoods (β = 0.04, 95% CI = 0.00–0.07) and more time at locations with greater vegetation density (β = 0.08, 95% CI = 0.04–0.1). Ground roosting broods selected locations closer to secondary roads (β = −0.33, 95% CI = –0.59– –0.07) but did not revisit or spend time in these areas. Ground roosting broods selected areas farther from pine forest (β = 0.1, 95% CI = 0.04–0.2).

When in a mobile state, ground roosting broods in a mobile state revisited and spent more time at locations closer to secondary roads (β = −0.2, 95% CI = –0.4– –0.1), and mixed pine-hardwoods (β = −0.1, 95% CI = –0.2– –0.02), but farther from hardwoods (β = 0.1, 95% CI = 0.02–0.21; Figure 3.6). Tree roosting broods revisited areas closer to secondary roads (β = −0.1, 95% CI = –0.2– –0.03), and shrub/scrub (β = −0.05, 95% CI = –0.1– –0.01), and with greater vegetation density (β = 0.09, 95% CI = 0.05–0.1) while in a restricted state. Likewise, tree roosting broods in a restricted state spent less time near mixed pine-hardwoods (β = 0.05, 95% CI = 0.005–0.1), but more time in areas with greater vegetation density (β = 0.05, 95% CI = 0.02–0.09). Tree roosting broods in a restricted state selected areas closer to hardwoods (β = −0.1, 95% CI = –0.3– –0.003) and shrub/scrub (β = −0.1, 95% CI = –0.2– –0.03), regardless of revisitation and residence time.

When in a mobile state, tree roosting broods revisited areas with greater vegetation density (β = 0.1, 95% CI = 0.007–0.2) while in a mobile state. Likewise, tree roosting broods spent more time in areas closer to pine forest (β = −0.1, 95% CI = –0.2– –0.04). Tree roosting broods in a mobile state selected areas closer to shrub/scrub (β = −0.2, 95% CI = –0.4– –0.07), regardless of revisitation and residence time.

DISCUSSION

We found that resource selection of wild turkey broods varied depending on behavioral state and recursive movements. Further, we noted that resource selection differed for broods that roosted on the ground (1-14 days old) versus those that roosted off the ground (15-28 days old), although broods exhibited consistent recursive movements regardless of their age. Our approach allowed us to integrate movement behaviors into an improved understanding of resource selection (Fagan et al. 2013, Oded Berger-Tal & Bar-David 2015, Oliveira-Santos et al. 2016). Our SSF indicated that incorporating recursive movements with landcover improved model fit relative to standard SSF approaches, which typically only consider habitat variables and disregard movement behaviors that could influence selection (Fortin et al. 2005, Merkle et al. 2019). Incorporating behavioral states that have potential to influence animal movements and decision-making can increase our ability to understand species movement ecology (Nathan et al. 2008).

Our behavioral analysis identified a restricted state characterized by shorter step lengths and less concentrated turning angles, and a mobile state characterized by longer step lengths and turning angles concentrated around zero, which was not surprising given similar findings in contemporary literature (Picardi et al. 2020, Gonnerman et al. 2022). We observed that broods spent most of their time in a restricted rather than mobile state, consistent with Chamberlain et al. (2020). Restricted movements are often characterized as area-restricted search, loafing, or foraging behaviors (Bennison et al. 2018, Zhang et al. 2019), whereas mobile movements are those such as walking, which represent directional movements away from a patch or along travel corridors (Abrahms et al. 2016, Ferreira et al. 2022). We offer that ignoring behavioral states and how they influence movement could lead to misinterpretation of resource selection models. For instance, mobile movements occur at a much larger spatial scale than restricted movements as individuals are covering more area, and within our analysis we defined availability by step lengths of each state, making selection more representative of the behavior (Avgar et al. 2016, Picardi et al. 2020). Overall, our findings indicate that recursive movements occur in each behavioral state, and resource selection differs by behavioral state whether individuals were ground or tree roosting.

Recursive movements are common across wildlife species (Berger-Tal & Bar-David 2015). We found recursive movements to be important on both a behavioral and temporal scale during brooding. Brooding females are faced with the challenge of finding quality foraging opportunities near vegetative cover that provides concealment (Williams 1974, Rumble & Anderson 1996). Our results support the idea that wild turkey broods increased residence time at locations and develop behaviors that reflect area-restricted searching (Byrne et al. 2014, Chamberlain et al. 2020, Bakner et al. 2022). Area-restricted foraging presumably allows broods to limit movements and space use, which may positively influence foraging success and reduce predation risk (Erikstad & Spidsø 1982, Park et al. 2001, Mainguy et al. 2006). Our results also indicate that recursive movements occur while broods are in a mobile state, suggesting broods were moving through familiar areas. Recursive movements to areas previously visited increases environmental predictability for individuals, which may increase fitness as individuals familiarize themselves with resources on the landscape (Riotte-Lambert & Matthiopoulos 2020). Overall, our results suggest that broods were returning to and spending more time in specific locations, presumably to areas which increase maneuverability and foraging opportunities.

When animals are moving from one resource patch to the next, they may exhibit differential resource selection (Haas 1995, Rosenberg et al. 1997). We observed differences in resource selection between broods that were ground versus tree roosting when they were in a mobile state. When in a mobile state, ground roosting broods were more likely to be closer to secondary roads and mixed pine-hardwoods, while avoiding areas closer to hardwoods. As broods aged and began to roost in trees, they selected pine forest, shrub/scrub, and areas with increasing vegetation density. Traveling and feeding rates of brooding galliforms are impacted by the ability of individuals to maneuver through ground cover (Healy 1985, Giroux et al. 2007). Thus, behavioral strategies in relation to vegetation composition is critical to brooding individuals and will depend on morphological development (Healy 1992, Jin-Min et al. 2015). The differences we observed in resource selection as broods aged provide evidence that selection becomes more plastic as broods age.

In precocial birds, resource requirements and degree of resource specialization may vary due to body size that can influence mobility, thermoregulation, foraging, and responses to predation risk (Brown et al. 2004, Preisser & Orrock 2012). Our findings demonstrate that accounting for underlying behavior and temporal scales as broods age may change assessments of resource selection. For many species, broods are inextricably linked to early successional vegetation communities that offer quality foraging opportunities with reduced predation risk (Novoa et al. 2002, Tirpak et al. 2008, Signorell et al. 2010, Jin-Min et al. 2015). We observed that broods in a restricted behavioral state (i.e., foraging, loafing) selected secondary roads and areas with increased vegetation density during the first 14 days of life when they roosted on the ground. Conversely, after broods reached 14 days of age and began roosting in trees, they selected areas closer to shrub/scrub and hardwood landcover types, and areas with increased vegetation density when they were in a restricted behavioral state. Hence, broods exhibited rapid changes in behavioral plasticity as they aged, which would contribute to the temporal changes in resource selection we observed, and parallel similar observations in contemporary literature on wild turkey broods (Chamberlain et al. 2020, Nelson et al. 2020). Increasing behavioral plasticity as broods age has been reported in other gallinaceous species, in that as broods age their diet breadth (Wegge & Kastdalen 2008, Goddard et al. 2009, Jin-Min et al. 2015) and mobility (Giroux et al. 2007) change, allowing them to exploit more profitable patches within their ranges.

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Table 3.1: Model structure for composite, landcover, and recursive models for ground and tree roosting eastern wild turkey (*Meleagris gallopavo silvestris*) broods during 2014–2021 across 11 study sites distributed throughout the southeastern United States. Each resource covariate was calculated as a distance (m) to metric.

Model	Parameter
Ground roosting	
Restricted state	
Revisit	
Landcover	secondary roads + hardwoods + mixed pine-hardwoods + normalized difference vegetation index + open + pine + shrub/scrub + Cosine of turn angle + logarithm of step length
Recursion-only	Revisitation
Composite	Landcover + Recursion only + Resource * Recursion
Residence time	
Landcover	secondary roads + hardwoods + mixed pine-hardwoods + normalized difference vegetation index + open + pine + shrub/scrub + Cosine of turn angle + logarithm of step length
Recursion-only	Residence time
Composite	Landcover + Recursion only + Resource * Recursion
Mobile state	
Revisit	
Landcover	secondary roads + hardwoods + mixed pine-hardwoods + normalized difference vegetation index + open + pine + shrub/scrub + Cosine of turn angle + logarithm of step length
Recursion-only	Revisitation
Composite	Landcover + Recursion only + Resource * Recursion

Residence time	
Landcover	secondary roads + hardwoods + mixed pine-hardwoods + normalized difference vegetation index + open + pine + shrub/scrub + Cosine of turn angle + logarithm of step length
Recursion-only	Residence time
Compsite	Landcover + Recursion only + Resource * Recursion
Tree roosting	
Restricted state	
Revisit	
Landcover	secondary roads + hardwoods + mixed pine-hardwoods + normalized difference vegetation index + open + pine + shrub/scrub + Cosine of turn angle + logarithm of step length
Recursion-only	Revisitation
Composite	Resource only + Recursion only + Resource * Recursion
Residence time	
Landcover	secondary roads + hardwoods + mixed pine-hardwoods + normalized difference vegetation index + open + pine + shrub/scrub + Cosine of turn angle + logarithm of step length
Recursion-only	Residence time
Composite	Landcover + Recursion only + Resource * Recursion
Mobile state	
Revisit	
Landcover	secondary roads + hardwoods + mixed pine-hardwoods + normalized difference vegetation index + open + pine + shrub/scrub + Cosine of turn angle + logarithm of step length
Recursion-only	Revisitation
Composite	Landcover + Recursion only + Resource * Recursion

Residence time	
Landcover	secondary roads + hardwoods + mixed pine-hardwoods + normalized difference vegetation index + open + pine + shrub/scrub + Cosine of turn angle + logarithm of step length
Recursion-only	Residence time
Composite	Landcover + Recursion only + Resource * Recursion

Table. 3.2: Akaike's Information Criterion with small sample bias adjustment (AIC_c), number of parameters (*K*), ΔAIC_c, adjusted Akaike weight of evidence (w_i) in support of model, log-likelihood (LL), and area under the receiver-operating characteristic curves (AUC) for each final model examining habitat selection within 2 behavioral states by ground and tree roosting eastern wild turkey (*Meleagris gallopavo silvestris*) broods at 11 sites across the southeastern United States during 2014–2021.

Model	*K*	AIC_c	ΔAIC_c	w_i	LL	AUC
Ground roosting						
Restricted state						
Revisit						
Composite	25	298919.7	0.0	1.0	-149434.8	0.73
Recursion-only	4	300157.0	1237.3	0.0	-150074.5	0.71
Landcover	16	309947.2	11027.6	0.0	-154957.6	0.61
Residence time						
Composite	25	295362.2	0.0	1.0	-147656.1	0.76
Recursion-only	4	296202.6	840.4	0.0	-148097.3	0.74
Landcover	16	309955.0	14592.8	0.0	-154961.5	0.61
Mobile state						
Revisit						
Composite	25	35555.5	0.0	1.0	-17752.72	0.82
Recursion-only	4	35693.7	138.2	0.0	-17842.8	0.80
Landcover	16	37618.9	2063.5	0.0	-18793.5	0.69
Residence time						
Composite	25	36061.9	0.0	1.0	-18006.0	0.80

Recursion-only	4	36145.7	83.8	0.0	-18068.9	0.78
Landcover	16	37618.9	1557.0	0.0	-18793.5	0.69
Tree roosting						
<u>Restricted state</u>						
Revisit						
Composite	25	170671.7	0.0	1.0	-85.310.8	0.73
Recursion-only	4	171002.5	330.8	0.0	-85497.3	0.72
Landcover	16	176391.2	5719.5	0.0	-88179.6	0.62
Residence time						
Composite	25	169489.7	0.0	1.0	-84719.9	0.75
Recursion-only	4	169965.3	475.6	0.0	-84978.6	0.74
Landcover	16	176391.2	6901.4	0.0	-88179.6	0.62
<u>Mobile state</u>						
Revisit						
Composite	25	39078.4	0.0	1.0	-19514.2	0.82
Recursion-only	4	39136.4	58.0	0.0	-19564.2	0.81
Landcover	16	41245.0	2166.6	0.0	-20606.5	0.69
Residence time						
Composite	25	39508.7	0.0	1.0	-19729.3	0.80
Recursion-only	4	39587.1	78.4	0.0	-19789.5	0.79
Landcover	16	41245.0	1736.3	0.0	-20606.5	0.69

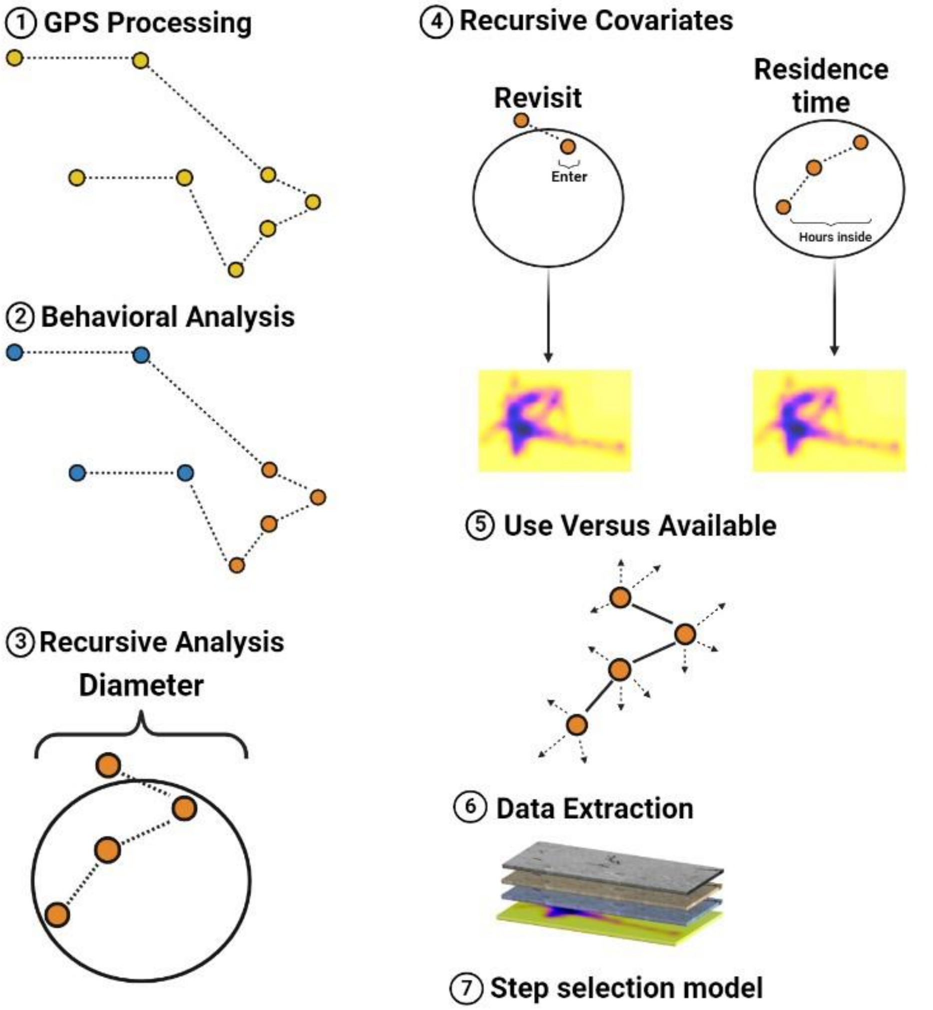

Figure 3.1: Conceptual framework for evaluating resource selection as a response to behavioral dependent recursive movements. This approach relies on standardizing movement data (1) that are used within a hidden Markov model to classify behavioral states (blue: mobile, orange: restrictive; 2). We then used each behavioral state to identify recursive movements based on a diameter appropriate to each behavioral state (star represents the GPS location of interest; 3) and created 2 raster layers representing revisit and residence time (4). We identified used versus available points based on step length and turn angle (5) and extracted environmental and recursive movement covariates (6). Finally, are data was fitted within a step selection function (7) to quantify in resource selection as broods aged.

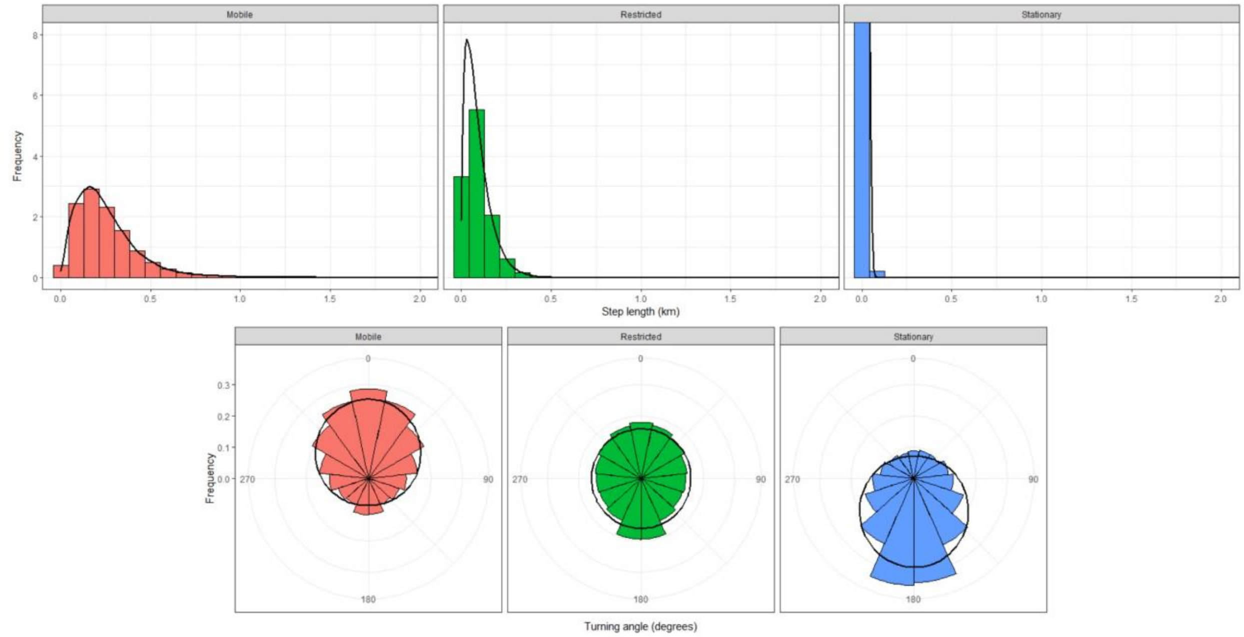

Figure 3.2: Step length and turning angle distributions for movements of eastern wild turkey (*Meleagris gallopavo silvestris*) broods across the southeastern United States during 2014-2021. The black curves depict distributions based on parameter values estimated with a Hidden Markov Model, which are overlaid on histograms of the raw data.

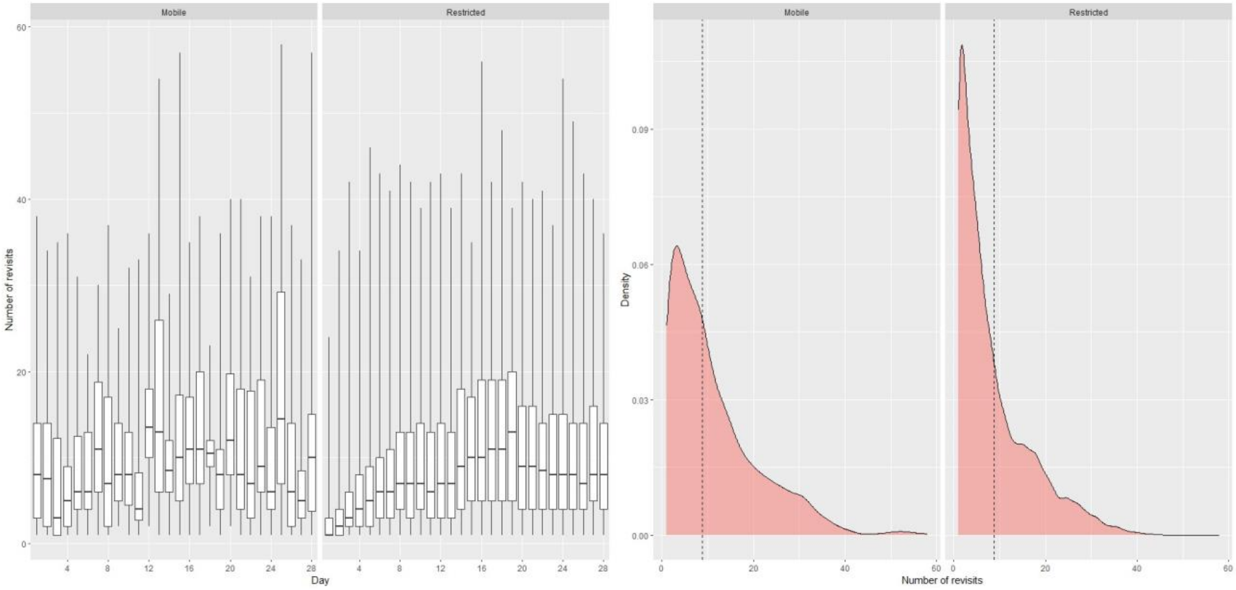

Figure 3.3: Boxplots of daily revisitation events by each behavioral state (mobile and restricted) and density plots showing the distribution of the data for eastern wild turkey (*Meleagris gallopavo silvestris*) broods across the southeastern United States during 2014-2021. The dashed black line in the density plot is the mean of the data.

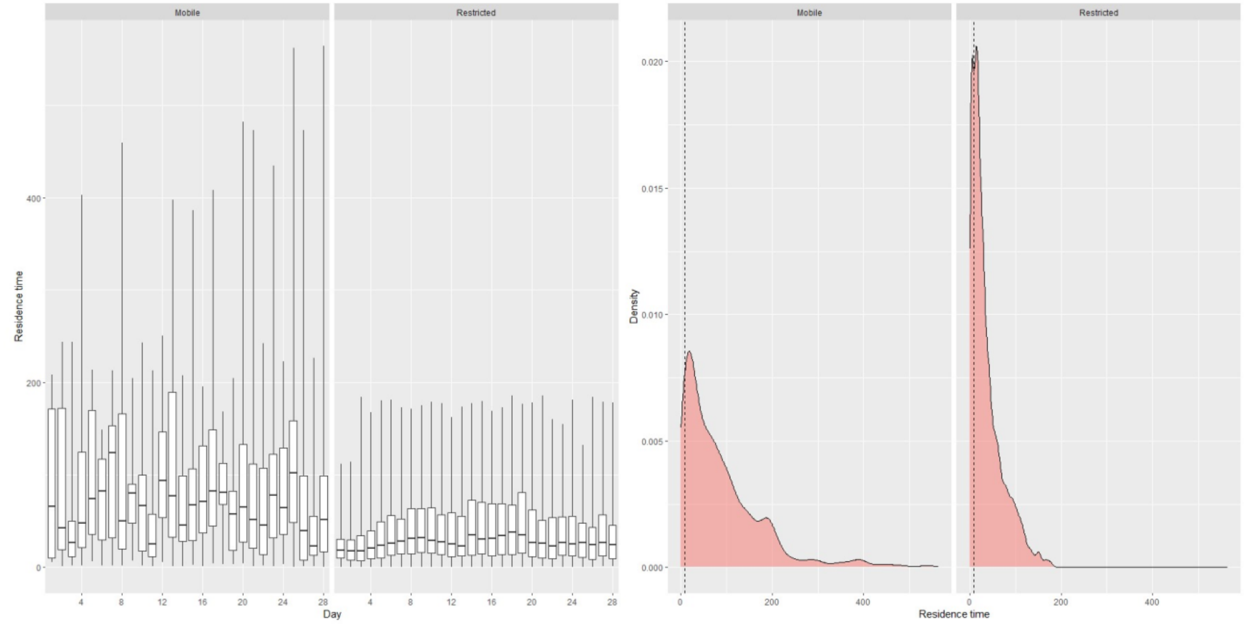

Figure 3.4: Boxplots of daily residence time by each behavioral state (mobile and restricted) and density plots showing the distribution of the data for eastern wild turkey (*Meleagris gallopavo silvestris*) broods across the southeastern United States during 2014-2021. The dashed black line in the density plot is the mean of the data.

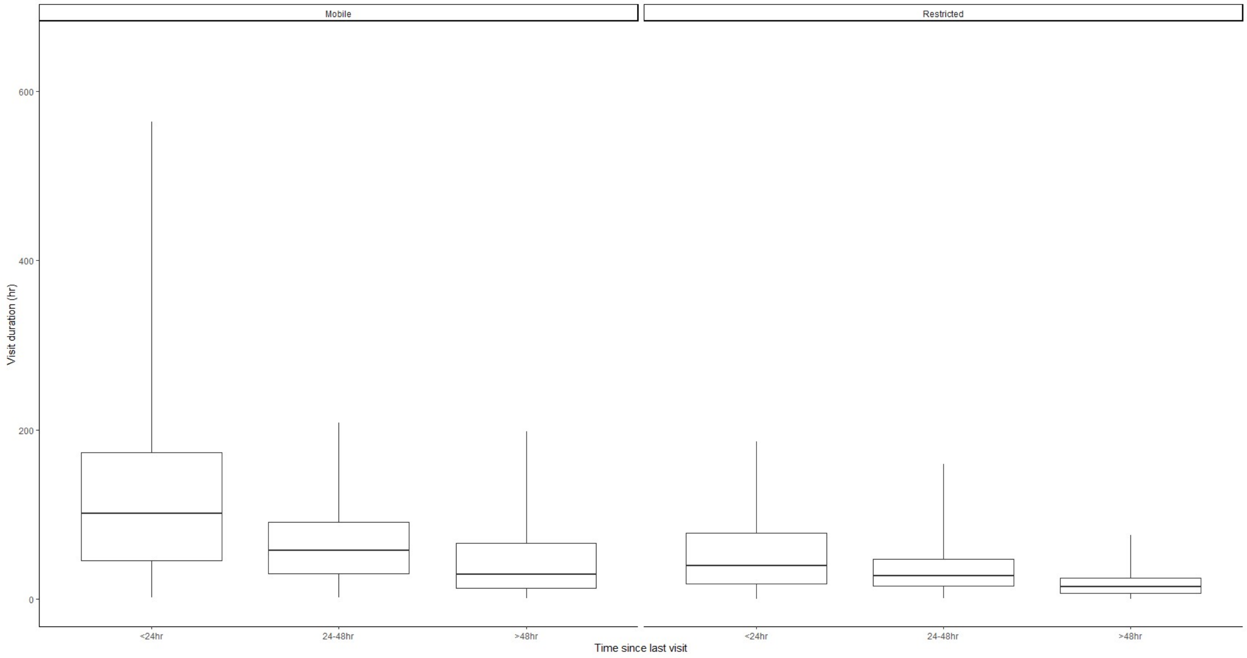

Figure 3.5: Boxplots of time since last visit by each behavioral state (mobile and restricted) of eastern wild turkey (*Meleagris gallopavo silvestris*) broods across the southeastern United States during 2014-2021.

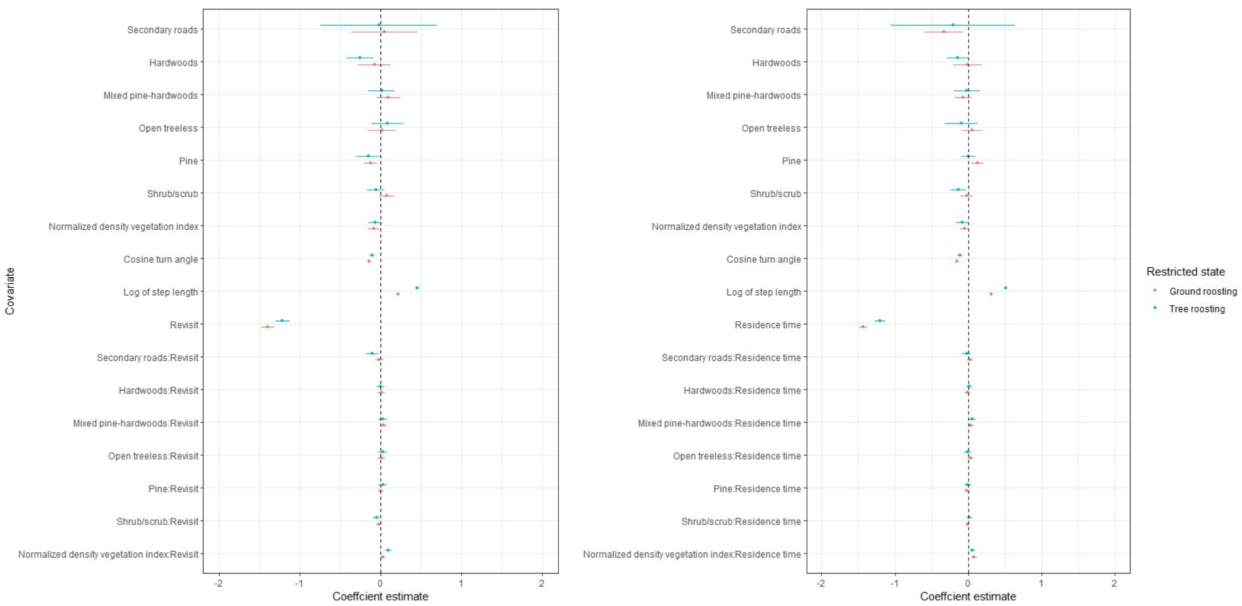

Figure 3.6: Coefficient plot depicting habitat selection of eastern wild turkey (*Meleagris gallopavo silvestris*) broods across the southeastern United States during 2014-2021 while in a restricted behavioral state. The left plot refers to revisit composite model while the right corresponds to the residence composite model. The whiskers depict 95% confidence intervals around mean estimates.

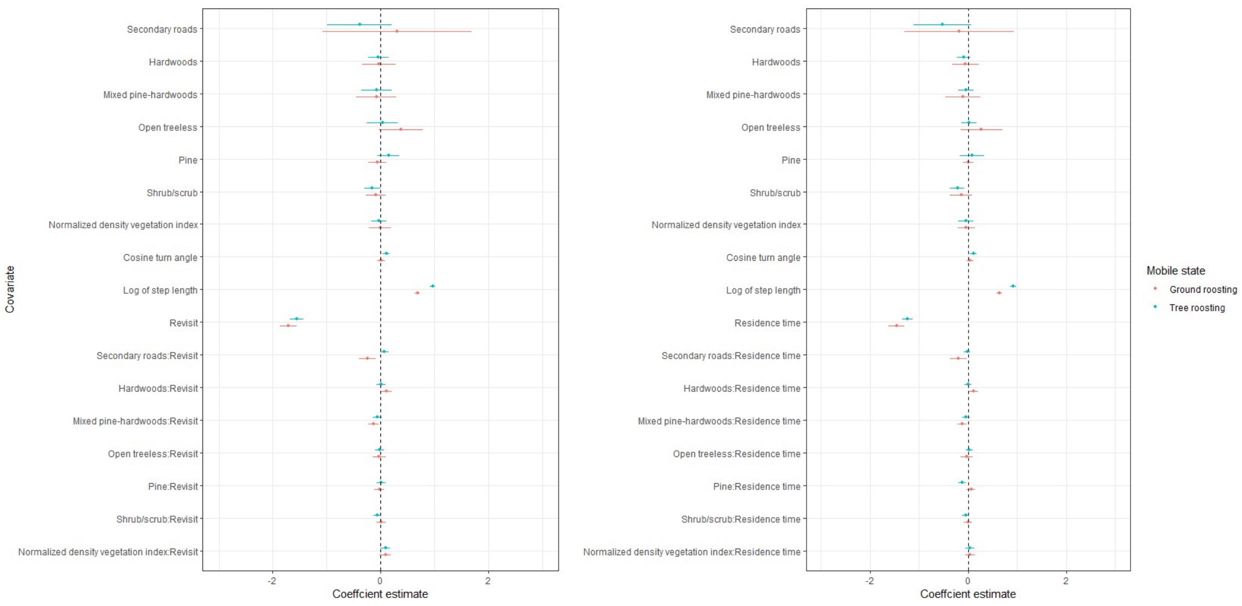

Figure 3.7: Coefficient plot depicting habitat selection of eastern wild turkey (*Meleagris gallopavo silvestris*) broods across the southeastern United States during 2014-2021 while in a mobile behavioral state. The left plot refers to revisit composite model while the right corresponds to the residence composite model. The whiskers depict 95% confidence intervals around mean estimates.

CHAPTER 4

SPATIAL ROOST NETWORKS AND RESOURCE SELECTION OF FEMALE WILD TURKEYS[1]

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[1] Bakner, N. W., E. E. Ulrey, P. H. Wightman, N. A. Gulotta, B. A. Collier, and M. J. Chamberlain. To be submitted to Ornithological Applications.

ABSTRACT

Behavioral decisions impact the demography of wildlife species. Sleep is the most prominent avian behavior, yet our understanding of how sleep behaviors impact diurnal decisions is unknown. Diurnal avian species use roost sites to reduce the cost of thermoregulation, predation risk, and increase foraging efficiency. Often, avian species reuse sleep locations to familiarize themselves with the surrounding area, forming networks within the home range. Here, we used a social network analysis to quantify roost site selection, and structure of roost networks for female wild turkeys during the reproductive season. We estimated site fidelity, identified hub and satellite roost sites, and evaluated landscape features selected at roost sites during different reproductive phases. We identified a scale-free network structure in roosting behavior, with a small percentage of hub roost sites connecting satellite roost sites within the network. Hub roosts were characterized by greater values for betweenness (β = 0.62, SE = 0.02), closeness (β = 0.59, SE = 0.03), and eigenvalue centrality (β = 1.15, SE = 0.05), indicating their strategic importance as connectors and their proximity to the network's functional center. The probability of a roost being a hub roost increased significantly with greater eigenvalue centrality (on scale 0-1; 12.25% for every 0.1 increase), emphasizing the importance of hub roosts in the network. Female wild turkeys consistently selected roost sites at lower elevations ($\bar{x}$ = 82.4 m, SD = 47.6) and with greater topographic ruggedness ($\bar{x}$ = 3.7 m^2, SD = 3.3). The probability of being a hub roost was greater in areas closer to secondary roads, water, and open treeless areas. While ecological studies examining the influence of environmental factors on wildlife spatial networks are limited, our research indicates that female wild turkeys establish a well-organized network of roost sites around hub roosts. Our findings underscore the need for further investigations into how roost site

networks shape conspecific interactions, which could play a role in reproduction and resource utilization for wild turkeys.

INTRODUCTION

Behavioral decisions play a primary role in shaping wildlife demography (Lima and Zollner 1996, Morales et al. 2010). While a substantial body of research delves into the influence of movement choices on survival and fitness (Johnson et al. 1992, Morales et al. 2010), our understanding of the significance of stationarity remains comparatively constrained. When wildlife are confined in their movements, they often become highly susceptible to predation, necessitating strategic adjustments to enhance their chances of survival (Lima et al. 2005). Consequently, the timing and location of stationary behavior in individuals are intricately linked to a diverse array of both social and environmental factors, as well as the anticipated fitness repercussions (Conway and Martin 2000, Lima et al. 2005).

All species engage in sleep or sleep-like behavior (Hartse 1994, Tobler 2000, Rattenborg and Amlaner 2002, Lima et al. 2005). Despite sleep behavior being the most prominent behavioral state, little attention has been dedicated towards understanding aspects of sleep behaviors, such as where an individual chooses to sleep (Zepelin 2000, Lima et al. 2005). Behavioral decisions made while choosing a location to sleep are likely influenced by a host of abiotic and biotic factors as species are most vulnerable during sleep (Amlaner and Ball 1983, Lima et al. 2005). The dangers of sleep due to increased vulnerability to predation are apparent; however, certain strategies can be considered safer than others and are more conducive to diurnal activities (Stiles and Skutch 1989, Amlaner and Ball 1983, Singhal et al. 2007). Thus, where an animal chooses to sleep plays a fundamental role in a species' ecological processes (Lima et al. 2005).

For diurnal species, sleeping sites can have critical consequences for individual fitness, as individuals must select sites that provide access to resources while providing protection from predators or natural elements (Bakken 1992, Singhal et al. 2007). Contemporary literature has noted that behavioral decisions such as sleep site switching (Franklin 2004, Smith et al. 2007) or reuse of sites to familiarize themselves with particular locations may reduce predation risks and presumably influence individual fitness (Di Bitetti et al. 2000, Li et al. 2011).

Social network analysis (SNA) is a tool used to investigate social structure using graph theory (Croft et al. 2008, Newman 2010, Pavlopoulos et al. 2011, Krause et al. 2015). Graphs are comprised of features (nodes) with connection (edges) between them, and a suite of metrics can be used to describe the overall structure of a network. A fundamental premise of SNA is that a node's significance within a network is indicated by the number of connections it possesses (Krause et al. 2015). In the context of scale-free networks, characterized by many nodes with limited connections (satellites) and a small subset of highly connected nodes (hubs), social networks exhibit resilience against random removal of nodes, yet they prove susceptible to deliberate attacks on hubs (Albert et al. 2000, Cohen et al. 2000, Newman 2003). Hence, disturbance of certain sections of a network could reduce fitness and demographic advantage for a species (Watts and Dyer 2018, Prima et al. 2019, le Roux and Nocera 2020).

For diurnal avian species, roost sites are important as they reduce the cost of thermoregulation (Yuan et al. 2018, Woods et al. 2019), decrease predation risk (Cody 1985, Thiel et al. 2007), and increase foraging efficiency (Beauchamp 1999, De-Jun et al. 2011, Zoghby et al. 2016). Drivers of roost site selection are fundamental as an individual must position itself on the landscape in ways that are beneficial for resource acquisition, survival, and reproduction (Skutch 1989). Roost sites are ideally concentrated in core use areas, which may provide individuals with increased access to resources and reduced competition from conspecifics (Rosenberg and McKelvey 1999). Hence, identifying the distribution of roosts within home ranges and how they are positioned relative to other roosts can allow an understanding of important ecological processes (Manfred 2006, Chaverri 2010).

Roosting is an important aspect of wild turkey (*Meleagris gallopavo spp.*) ecology that can influence demography and spatial distribution (Byrne et al. 2015). The primary benefits of roosting are reduced predation risk and protection from adverse weather conditions (Austin and DeGraaf 1975, Vander Haegen et al. 1989). Previous research on wild turkey roosting ecology has focused on roost tree descriptions and associated habitat conditions (Mackey 1984, Flake et al. 1995, Swearingin et al. 2011), and aspects of roost site selection at microhabitat or landscape scales (Chamberlain et al. 2000, Keegan and Crawford 2005, Perlichek et al. 2009, Frary et al. 2011, Phillips et al. 2011). However, microhabitat and landscape characteristics at roosts vary across temporal and spatial scales, suggesting roost site selection may underlie access to receptive mates, foraging habitats, and preferred vegetation cover used during nesting or brooding (Miller 1999, Chamberlain and Leopold 1998, Chamberlain et al. 2000, Byrne et al. 2015, Wakefield et al. 2020).

Reproduction drives wild turkey population trajectories, and female behavioral ecology has been shown to have considerable influence on fitness outcomes (Bakner et al. 2019, Lohr et al. 2020, Chamberlain et al. 2020, Ulrey et al. 2023). During reproductive activities, female wild turkeys face strict spatial constraints, including access to males for breeding opportunities (Schroeder and White 1993, Westcott 1997) and the need to stay near their nesting locations (Bakner et al. 2019, Lohr et al. 2020). During the reproductive period, females transition from pre-laying areas to unfamiliar locations to initiate egg-laying (Conley et al. 2016). Prospecting of unfamiliar areas is used to identify profitable locations during the egg-laying process to ensure there are adequate resources for incubation (Schofield 2019, Bakner et al. In Review). Thus, spatially quantifying roost selection and roost relationships for females throughout the reproductive period could offer insight into how they allocate themselves during sleep periods within this critical biological season.

Here, we used a SNA to evaluate roost site selection and structure of roost site networks for female wild turkeys during the reproductive season. Specifically, we estimated site fidelity and identified hub and satellite roosts during different reproductive phases (i.e., pre-laying, laying, finished nesting, and non-nesting), and we identified relevant landscape features selected at roost sites. We hypothesized that females would select roost sites to optimize their access to resources. Thus, we predicted females would have centralized hub roost sites (higher site fidelity) that exhibit higher degrees of fidelity in closer proximity to areas offering resources important during the reproductive season.

STUDY AREA

We conducted research on 12 sites across the southeastern United States. In Louisiana, we conducted research on the Kisatchie National Forest (KNF), Fort Polk Wildlife Management Area (WMA), and Peason Ridge WMA from January 2014-August 2021. The KNF was owned and managed by the United States Forest Service (USFS), whereas Fort Polk and Peason Ridge WMA was jointly owned by the USFS and the United States Army. Louisiana sites were composed of pine (*Pinus* spp.)-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*). For a detailed description of site conditions on KNF and Fort Polk WMA see Yeldell et al. (2017*a,b*).

Additionally, we conducted research on a broad suite of private and public lands in southeastern Louisiana, including Sandy Hollow WMA in Tangipahoa and Washington Parishes. The region was composed of rolling hills with hardwood riparian zones interspersed with young longleaf pine plantations. Agricultural production included grazing and row crops were the dominant land use. For a detailed description of Sandy Hollow WMA, see Duguay et al. (2017).

We conducted research on Lake Seminole and Silver Lake WMAs located in southwest Georgia from January 2015-August 2016. The Silver Lake WMA was owned and managed by the Georgia Department of Natural Resources-Wildlife Resources Division (GADNR), and the adjacent Lake Seminole WMA was owned by the U.S. Army Corps of Engineers and managed by GADNR. Both sites were predominantly mature pine forests and forested wetlands. Overstory species were predominately longleaf pine, loblolly pine, slash pine (*P. elliottii*), oaks, and sweetgum (*Liquidambar styraciflua*). For a detailed description of site conditions on Silver Lake WMA see Wood et al. (2019).

We conducted research on B.F. Grant and Cedar Creek WMAs located in the Piedmont region of Georgia from January 2017-August 2021. B.F. Grant WMA was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia, and was managed jointly by the GADNR and the Warnell School. B.F. Grant WMA landcover was primarily loblolly pine forest, agricultural lands, mixed hardwood and pine forests, and hardwood lowlands containing mostly oaks, sweet gum, and hickory. Agricultural lands were mostly grazed mixed fescue (*Festuca* sp.) fields and hay fields planted for ryegrass (*Lolium* sp.). Cedar Creek WMA was owned by the USFS and managed in partnership with GADNR. Cedar Creek WMA was composed primarily of loblolly pine uplands, mixed hardwood and pine forests, and hardwood lowlands of similar species composition as B.F. Grant WMA. For a detailed description of site conditions see Wakefield et al. (2020*a*).

We conducted research on 3 contiguous WMAs (Webb, Hamilton Ridge, and Palachucola; hereafter, Webb WMA Complex; January 2014-August 2018) and the Savanah River Site (hereafter, SRS; January 2021-March 2021) in South Carolina. The Webb WMA Complex was owned and managed by the South Carolina Department of Natural Resources (SCDNR). The Webb WMA Complex was dominated by longleaf, loblolly, and slash pine forests with hardwood stands along riparian corridors, and expanses of bottomland hardwood wetlands. The SRS was owned by the United States Department of Energy and managed by USFS. The SRS was primarily forested and consisted of bottomland hardwoods, mixed-pine hardwoods, and planted stands of longleaf pine, loblolly pine and slash pine. For a detailed description of site conditions see Wightman et al. (2019).

METHODS

We used rocket nets to capture eastern wild turkeys (*Meleagris gallopavo silvestris*; hereafter, wild turkeys) from January-March of 2014-2021 (For details on study sites refer to Supplemental Information 1). We aged captured individuals based on presence of barring on the ninth and tenth primary feathers and sexed them by coloration of the breast feathers (Pelham & Dickson 1992). We banded each bird with an aluminum rivet leg band (National Band and Tag Company, Newport, Kentucky; female size = 8, male size = 9) and radio-tagged each individual with a backpack-style GPS-VHF transmitter (Guthrie et al. 2011) produced by Biotrack Ltd. (Wareham, Dorset, UK). We programmed transmitters to record 1 GPS location nightly (23:58:58) and hourly GPS locations from 0500 to 2000 (Standard Time and according to the appropriate time zones) for the duration of the study (Cohen et al. 2018). Each transmitter had a mortality switch programmed to activate after >23 hours of no movement. We released wild turkeys immediately at the capture location after processing. All turkey capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee at the University of Georgia (Protocol #A2019 01-025-R2 and #A2020 06-018-R1) and the Louisiana State University Agricultural Center (Protocol #A2014-013, A2015-07, and A2018-13).

We performed data processing and analysis in program R (v.4.1.0; R Core Team 2023). We processed and cleaned the raw GPS data by removing locations that had dilution of precision values (DOP) > 7. To determine dates of nest initiation (i.e. initiation of laying) and onset of incubation, we mapped our spatial-temporal data using ArcGIS 10.8 (Environment Systems Research Institute, Redlands, California, USA). We identified the onset of incubation as the first time an individual remained on the nest overnight (Bakner et al. 2019, Lohr et al. 2020), and then evaluated hourly locations for the previous 20 days to determine when a female initially visited the nest site (defined as location being < 20 m from the known nest site (Conley et al. 2015, Conley et al. 2016, Schofield 2019). We considered the date of first visit as the date of nest initiation and used it as the beginning of the laying period, as wild turkeys rarely visit nest sites before laying the first egg (Conley et al. 2016, Collier et al. 2019). We removed incubation and brooding locations from analyses because female wild turkeys remain on the ground at the nest. Therefore, we categorized roost locations by pre-laying, laying, post reproduction for each female throughout the reproductive season. If the female never attempted a nest her roosts were classified as non-nesting. These 4 reproductive phases were later used as a covariate in models to describe the temporal aspect of female roost selection (Moscicki et al. 2022; Table 4.1).

Wild turkeys may use specific roosting areas repeatedly but select different trees from one night to the next (Byrne et al. 2015). Therefore, we defined a roost area by running a sensitivity analysis of distance between consecutive roost locations to provide an appropriate cluster radius (250 m) and considered any roost locations that fell within the cluster radius as a single roost area. We used package dbscan (Hahsler et al. 2019) in program R (v.4.1.0; R Core Team 2023) to conduct the cluster analysis. We then estimated roost area fidelity as 1 minus the number of unique roost areas used divided by number of nights within the period [RF=1−(unique roosts/total roosts); Wakefield et al. 2020]. A roost site fidelity value of 1 would indicate that an individuals roosted in the same area every night, whereas values approaching 0 indicated that individuals roosted in a unique area every night. We calculated inter-roost distance between consecutive roosts for each female to identify phenological transitions in roosting behaviors across all birds (Wakefield et al. 2020, Cohen et al. 2022). For each roost location, we quantified elevation, slope, aspect, and topographic ruggedness (degree of irregularity or roughness in the surface of a geographic area) using digital elevation models from the United States Geological Survey National Elevation Dataset (http://lta.cr.us.gs.gov/NED, accessed 10 April 2023; Collier et al. 2019, Bakner et al. 2022). We obtained road data for wildlife management areas (WMAs) from Georgia Department of Natural Resources, Louisiana Department of Wildlife and Fisheries, South Carolina Department of Natural Resources, and the United States Department of Agriculture: Forest Service and used USGS Tiger/Line data (Topologically Integrated Geographic Encoding and Referencing) for roads outside the WMAs. We categorized roads as primary if they were paved/graveled and vehicle access was not limited, whereas secondary roads were unpaved gravel and/or logging roads where vehicle use was reduced (Gerrits et al. 2020). We obtained year-specific, 30-m resolution spatial data on landcover from the Cropland

Data Layer (Cropscape) provided by the National Agricultural Statistics Service (National Agricultural Statistics Service 2015). We recoded and combined landcover in program R (v.4.1.0; R Core Team 2023) to create 2 unique landcover types (open treeless areas, water). We decided to exclude forested habitat in our analyses because wild turkeys will ultimately be in these areas because they roost in trees. Hence, we chose to use open treeless areas and water because these are resources that wild turkeys use for foraging opportunities (Wakefield et al. 2020, Nelson et al. 2021). We then calculated the nearest distance to primary and secondary roads and landcover types using the Euclidean distance tool in ArcGIS 10.8 (Environmental System Research Institute, Inc., Redlands, CA, USA) keeping all raster layers at a 30-m resolution.

NETWORK ANALYSIS

Networks are comprised of nodes connected by edges, which are used to understand network function and structure (Croft et al. 2008, Krause et al. 2015). In our spatial network, we defined nodes as the roost areas and assigned corresponding edges based on visits to different roost areas. Our spatial network was directed, as we were not interested in reciprocated interaction (Croft et al. 2008, Krause et al. 2015). We calculated a suite of metrics describing the nodes and edges for each individual female's network (Table 4.2). The distribution of the node degree can be used to determine the structure of a network, with the node degree being the number of connections one node has to other nodes (Proulx et al. 2005). In the context of roosting behavior, degree is how connected a specific roost site is to the other roost sites within the network. Therefore, we calculated the degree distribution by summing the nodes that had edges and dividing by the total number of nodes. If the degree distribution follows a power law distribution of the form $P(k) = Ak^{-\gamma}$ where the exponent γ typically falls in the range $2 < \gamma < 3$, the network is characterized as scale-free (Newman 2003). Specifically, $P(k)$ is the probability that k takes on a specific value. In the context of a power law distribution, it signifies the probability of a node having a degree (k) in a network. Within power law distribution equation, A is a constant that serves as a normalization factor. It ensures that the probabilities sum up to 1 over the entire range of possible values of k. The exponent γ determines the shape of the distribution. If $\gamma > 1$, it indicates a heavy-tailed distribution where there are relatively more nodes with high degrees compared to nodes with low degrees, opposed to if $\gamma < 1$, which suggests a distribution where most nodes have relatively low degrees.

Scale-free networks are characterized by nodes with few connections (lower degree; satellite roost areas) and those that have many connections (higher degree; hub roost areas). Conversely, a random network would follow a normal distribution, indicating that most nodes (roosts) have a degree distribution close to the average (Bollobas 1985). To investigate potential differences among hub and satellite areas we calculated betweenness, closeness, eigenvalue centrality, and clustering coefficients for each unique roost area using igraph package in program R (v.4.1.0; Csardi and Nepsz 2006, R Core Team 2023; Table 4.2). Betweenness, as defined by Freeman (1988), suggests that a node (in this case, roost area) plays a crucial role in connecting two other nodes within a network. In the context of roost areas, this implies that specific areas have a significant influence on enhancing overall connectivity among different roosting areas. Closeness is a metric used to describe centrality which evaluates the shortest path length between a roost area and all other roost areas within the network (Bavelas 1950). Eigenvalue centrality describes the influence of a roost area by assessing the relative score of connected roosts areas with high-scoring roosts areas providing more importance than connections to low scoring roosts areas (Borgatti and Everett 2006). Eigenvalue centrality is bounded from 0 and 1. The clustering coefficient evaluates cliques within a network, which means it identifies if there are localized communities (group) of roosts areas within the network. Using the 90th percentile values from the degree calculation, we determined whether roost sites were considered hubs or satellites (Newman 2003, Croft et al. 2008). Using the network metrics as covariates, we tested differences between hub and satellite roost areas via a generalized linear model with a binomial response distribution and logit link. Our response was binary (0 = satellite, 1 = hub) to model network parameters at hub and satellite roost areas. We used the R package glmmTMB to conduct our analysis (Magnusson et al. 2017).

RESOURCE SELECTION MODEL

From beginning of pre-laying until post-reproduction, we calculated 95% home ranges by fitting dynamic Brownian bridge movement models (dBBMMs) to the time-specific location data (Cohen et al. 2018) using package move (Kranstauber et al. 2012) in program R. We used an error estimate of 20 m, a moving window size of 7 locations, and a margin setting of 3 locations (Byrne et al. 2014, Cohen et al. 2018).

We used resource selection functions (RSFs) to examine relationships between distance to landcover types, distance to secondary roads, and terrain features to wild turkey roost sites within individual home ranges (3rd-order selection) following a design III approach suggested by Manly et al. (2002). We tested for collinearity between each of our covariates and excluded covariates using Pearson's correlation with a $r > 0.60$ (Dormann et al. 2013). After testing for collinearity, we removed slope and primary roads from our models. We chose to retain topographic ruggedness instead of slope because we believed it to be a more relevant metric as slope varied little across our study sites. We chose to keep secondary roads as they provide connectivity between areas selected by wild turkeys on our study sites and also provide foraging opportunities (Nelson et al. 2023). We did not include interactions of aspect and reproductive phase as models failed to converge due to quasi-complete separation. We compared used points (roost locations) to 5 available points sampled within each range (Benson 2013). We created 4 models which included a global model (i.e., including all covariates), resource model, feature model, and a null model (Table 4.3). Each model included an interaction of reproductive phase for each female (Moscicki et al. 2022). We used a generalized linear mixed model with a binomial response distribution (logistic regression) and logit link to the used-available data (Manly et al. 2002, Johnson et al. 2006). We used the glmmTMB R package (Magnusson et al. 2017) with a binary (0 = available, 1 = used) response variable to model resource selection (Muff et al. 2020). To account for variability among individuals within our models, we included a random effect for each unique individual (Muff et al. 2020). To improve performance, we rescaled all fixed effects by subtracting their mean and dividing by 2 standard deviations prior to modeling (Gelman 2008). Similar to the methodology above, to determine if resource selection differed between hub and satellite roost areas, we used a generalized linear mixed model with a binomial response distribution and logit link to evaluate spatial network data for female wild turkeys. Our response was binary (0 = satellite, 1 = hub) to model resources at hub and satellite roost areas.

We used second-order Akaike's Information Criteria (AIC*c*) to assess the amount of support for the different candidate models (Akaike 1973, Burnham & Anderson 2002). We calculated ΔAIC*c* values between the AIC*c* value for candidate model *i* and the lowest-ranked AIC value. We also calculated Akaike's weights (w_i) for each model. We then calculated parameter estimates and their standard errors for all covariates in models within 2 ΔAIC*c* units of the lowest-ranked AIC value.

RESULTS

We monitored 663 (560 adults, 102 juveniles, 1 unknown) female wild turkeys during 2014–2021. We monitored 689 nesting attempts (initial attempts = 491, renesting attempts = 198) made by 499 females. We identified 66,364 roost locations after removing locations that occurred during incubation and brooding (Table 4.4). Mean site fidelity across all phases was 0.48 (SD = 0.05), with laying being the lowest ($\bar{x}$ = 0.41, SD = 0.20) and the highest was for non-nesters ($\bar{x}$ = 0.54, SD = 0.19; Table 4.4).

Our degree distribution described a scale-free network, with females having few (13.6% total roost areas) hub roost sites within their network (Figure 4.1; Table 4.5). Hub roosts had greater values of betweenness ($\beta = 0.62$, SE = 0.02), closeness ($\beta = 0.59$, SE = 0.03), and eigenvalue centrality ($\beta = 1.15$, SE = 0.05), but lower values of cluster coefficient ($\beta = -0.36$, SE = 0.02) than satellite sites (Figure 4.2). Mean betweenness for hub roosts was 416 (SD = 334; Table 4.5) suggesting that hub roosts served as connections or bridges within the network. Hub roosts were associated with higher closeness values suggesting that hub roosts were positioned near the functional center of the network (Figure 4.3). The probability of the roost site being a hub roost increased 12.25% for every 0.1 increase in eigenvalue centrality, suggesting hub roosts played an important role in structuring the network (Figure 4.2). Our clustering coefficient was lower for hub roost areas suggesting one network rather than multiple communities.

The global model ($w_i = 1.00$; Table 4.6) best fit our data for predicting roost location selection. Females selected for roost locations that were at lower elevations and with greater ruggedness during all reproductive phases (Figure 4.4). During the pre-laying, females selected roost locations closer to water, whereas during laying they selected roost locations farther from secondary roads (Figure 4.4). When females ceased reproductive activities, they selected roost areas closer to open treeless areas and water, but farther from secondary roads (Figure 4.4).

The global model (w_i = 1.00; Table 4.6) best fit our data for predicting selection of hub versus satellite roost areas. During all phases, females selected hub roosts areas that were closer to secondary roads and farther from water (Figure 4.5). Additionally, during pre-laying, laying, and when the reproductive season ceased, females selected for hub roost areas at lower elevations. Non-nesting females selected for hub roost areas with greater ruggedness (Figure 4.5).

DISCUSSION

We observed high site fidelity and lower distances between consecutive roost sites for female wild turkeys during the reproductive season, observations that differ markedly from roost behaviors exhibited by males (Byrne et al. 2015, Wakefield et al. 2020). Our observations are similar to published works on capercaillie (*Tetrao urogallus*), where females displayed increased fidelity to roosts that were closer to lek sites (Gjerde et al. 2000). Hence, remaining at the same roost areas during the breeding season could be a tactic utilized by females to reduce predation risk and increase resource acquisition, which can be directed towards egg-laying and incubation (Gerber et al. 2019).

We found that the roost area network evaluated for individual female wild turkeys exhibited characteristics of a scale-free network (Newman 2003), with few highly centralized hub roosts (~13%) that had many connections, promoting connectivity to other roosts in the network. Maintaining networks with centralized hub sites allows an individual to learn about the location and exploit high quality resources (Spencer 2012, Bracis et al. 2015). Hence, networks exhibiting these characteristics are often associated with resource rich areas (Watts 2018, le

Roux and Nocera 2020), interactions with conspecifics for information (Ruxton 1995, Ruxton and Houston 2002, Dermody et al. 2011), or mate acquisition (Alonso 2000, Gjerde et al. 2000). The level of experience an individual has with the landscape has been attributed with reduced predation risk by identifying refuges and escape routes (Laundré et al. 2010, Gaynor et al. 2019). For example, pheasants (*Phasianus colchicus*) killed by predators were more on the periphery of their home range than towards the center (Heathcote et al. 2023). Hence, female wild turkeys maintaining hub roosts areas centrally located within their reproductive range may facilitate increased vigilance and efficient resource acquisition that positively influences fitness.

Environmental variation across landscapes has potential to influence how species interact with terrain (Whittaker 1967, Chapin et al. 2002). We found that roost locations selected by female wild turkeys were at lower elevation with greater ruggedness regardless of reproductive phase. This is consistent not only with eastern wild turkeys, but Gould's (*M. g. mexicana*), Merriam's (*M. g. merriami*), and Rio Grande (*M. g. intermedia*) wild turkeys that select roosts at lower elevations often associated with riparian corridors (Crockett 1973, Beasom and Wilson 1992, Schemnitz and Zornes 1995, Wakefield et al. 2020). Increased ruggedness is often associated with the irregularity on the outer edges of riparian corridors where the landscape begins to become steep (Chapin et al. 2002). Selecting roosts in areas with greater ruggedness enables avian species to perch at higher elevations, enhancing their ability to better observe their surroundings and increase efficiency of flights (Watson et al. 2014, Domenech et al. 2015). Wild turkeys depend on their vision to detect predators before flying down from their roost in the morning (Pelham and Dickson 1992), so choosing roost areas with increased ruggedness may diminish the risk of predation.

Resource acquisition is necessary for the survival of avian species upon completion of the reproductive period (Deeming et al. 2015). We found that upon the completion of reproduction, female wild turkeys selected to roost closer to open treeless areas and water. Open treeless areas are selected by wild turkeys throughout portions of their annual cycle (Chamberlain et al. 2020, Bakner et al. 2022) and provide the opportunity to increase foraging efficiency while also increasing the detectability of predators, which has similarly been show in various Galliformes (Storch 1994, Aldridge and Boyce 2007). Additionally, selecting roost areas closer to water could buffer thermal extremes common throughout the southeastern United States during summer after reproductive activities cease (Smith et al. 2015, Nelson et al. 2022).

Locations of hub nodes within a network are often affiliated with greater connectivity to other nodes within the network (Krause et al. 2015). Within our network, hub roosts were situated closer to secondary roads, which may provide quality foraging opportunities and opportunity to escape predation threats (Yeldell et al. 2017, Nelson et al. 2022, Nelson et al. 2023) and enhance mobility for females (Bakner et al. 2023). Furthermore, the low-intensity maintenance of trails and secondary roads promotes early successional vegetative communities, which were spatially limited on our study sites. Research on hazel grouse (*Tetrastes bonasia*) has shown that in areas with minimal trail maintenance, individuals may select trails to exploit early successional plant species (Matysek et al. 2020).

Few ecological studies have explored the impact of environmental characteristics and resources on spatial networks of wildlife (le Roux and Nocera 2021). Our findings indicate that wild turkeys develop and maintain a spatial network of roost areas within their reproductive range, with centralized hub roost areas that are ecologically important. The roost area networks used by wild turkeys require further study into how conspecific interactions may occur, as extant literature demonstrates the critical role of networks in breeding (Ryder et al. 2011), resource access (Watts and Dyer 2018, Peignier et al 2019), and disease or parasite transmission (Guimarães et al. 2007, Fortuna et al. 2009, White et al. 2017) among various gregarious species.

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Table 4.1: Descriptions of reproductive phases relative to roost areas election for female eastern wild turkeys (*Meleagris gallopavo silvestris*).

Reproductive Phase	Description
Pre-laying	Movements prior to March 1.
Laying	When a female initially visited the nest site.
Post reproduction	When reproductive activity ceased.
Non-nester	Females that did not make a nesting attempt.

Table 4.2: Descriptions of parameters used to describe spatial networks and the biological context of what information parameters provided for roost sites used by female eastern wild turkeys (*Meleagris gallopavo silvestris*).

Parameters	Description	Biological context
Betweenness	The number of times a node acts as a bridge based on the shortest path between 2 other nodes.	The number of times a roost forms a connection between other roost areas based on the shortest distance them.
Closeness	The mean shortest path between a node and all other nodes.	The shortest distance between a roost area and all other roost areas within the network.
Clustering coefficient	A measure of cliquishness of the network, which is the fraction of a node's immediate neighbor that are themselves neighbors.	A measure of how close a roost area is to other neighboring roost areas. This describes if there are communities of roost areas that are not connected to the entire network.
Degree	The number of links that are connected to a node.	The number of connections to a roost area.
Edge	The interaction between two nodes.	A female wild turkey moving between 2 roost areas.
Eigenvalue centrality	Relative score assigned to nodes to assess their importance based on the connections to other nodes.	Assessment of the importance of a roost area in the network based on connections to other roost areas.
Node	The object in the network.	The roost area.

Table 4.3: Model structure for global, resource, feature, and null models for female eastern wild turkey (*Meleagris gallopavo silvestris*) roost location during 2014–2021 across the southeastern United States. Each covariate within the model had an interaction with reproductive phase (pre-laying, laying, finished nesting, non-nester). The resource covariates were calculated as a distance (m) to metric.

Model	Parameter
Global	secondary roads + open treeless area + water + elevation + ruggedness
Resource	secondary roads + open treeless area + water
Feature	elevation + ruggedness
Null	(.)

Table 4.4: Total and unique number of roost areas, mean site fidelity with associated standard deviations (SD), and mean inter-roost distance in meters with associated standard deviations (SD) by reproductive phase for female eastern wild turkeys (*Meleagris gallopavo silvestris*) across the southeastern United States during 2014-2021.

Reproductive Phase	Total roost locations	Unique roost areas	Mean site fidelity (SD)	Mean inter-roost distance (SD)
Pre-laying	26,455	12,752	0.48 (0.19)	478.07 (505.95)
Laying	7,430	4,242	0.41 (0.20)	554.46 (515.04)
Finished nesting	21,114	9,456	0.50 (0.21)	501.35 (478.68)
Non-nester	11,365	5,383	0.54 (0.19)	547.16 (545.86)

Table 4.5: Descriptive statistics including median, mean, standard deviation, and range for parameters included in a spatial network analysis of roost selection by female eastern wild turkeys (*Meleagris gallopavo silvestris*) across the southeastern United States during 2014-2021.

Parameter	Median	Mean	Standard deviation	Range
Betweenness	30.40	156.53	391.70	0.00-5,323.65
Closeness	0.23	0.24	0.11	0.02-1.00
Clustering coefficient	0.13	0.14	0.07	0.00-1.00
Degree	2.00	4.61	7.54	1.00-153.00
Eigenvalue centrality	0.00	0.04	0.16	0.00-1.00

Table 4.6: Akaike's Information Criterion with small sample bias adjustment (AICc), number of parameters (K), ΔAICc, adjusted Akaike weight of evidence (w_i) in support of model, and log-likelihood (LL) for each model examining roost location selection and selection of hub versus satellite roost areas of female eastern wild turkeys (*Meleagris gallopavo silvestris*) across the southeastern United States during 2014-2021.

Model	*K*	AIC_c	ΔAIC_c	w_i	LL
Roost location selection					
Global	22	353,563.9	0.00	1.00	-176,760.0
Resource	14	354,977.0	1,413.1	0.00	-177,474.5
Feature	10	357,507.3	3,943.4	0.00	-178,743.7
(.)	2	358,816.5	5,252.6	0.00	-179,406.3
Hub versus satellite roost areas					
Global	22	52,304.3	0.00	1.00	-26,130.1
Resource	14	53,324.4	20.4	0.00	-26,148.4
Feature	10	52,944.0	639.7	0.00	-26,462.0
(.)	2	52,960.4	656.1	0.00	-26,478.2

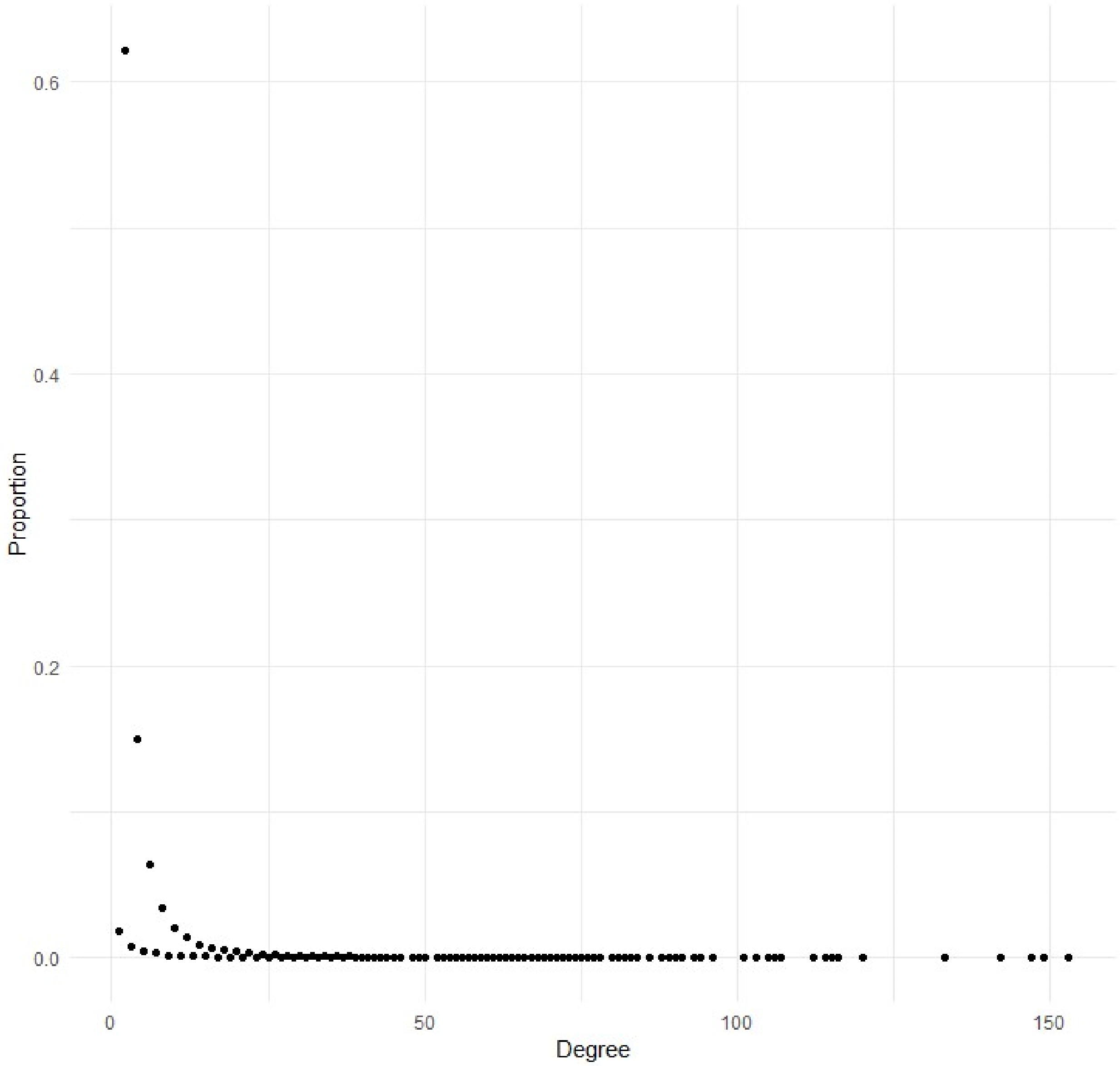

Figure 4.1: Degree distribution characterizing a scale-free network for roost areas of female eastern wild turkeys (*Meleagris gallopavo silvestris*) across the southeastern United States during 2014-2021.

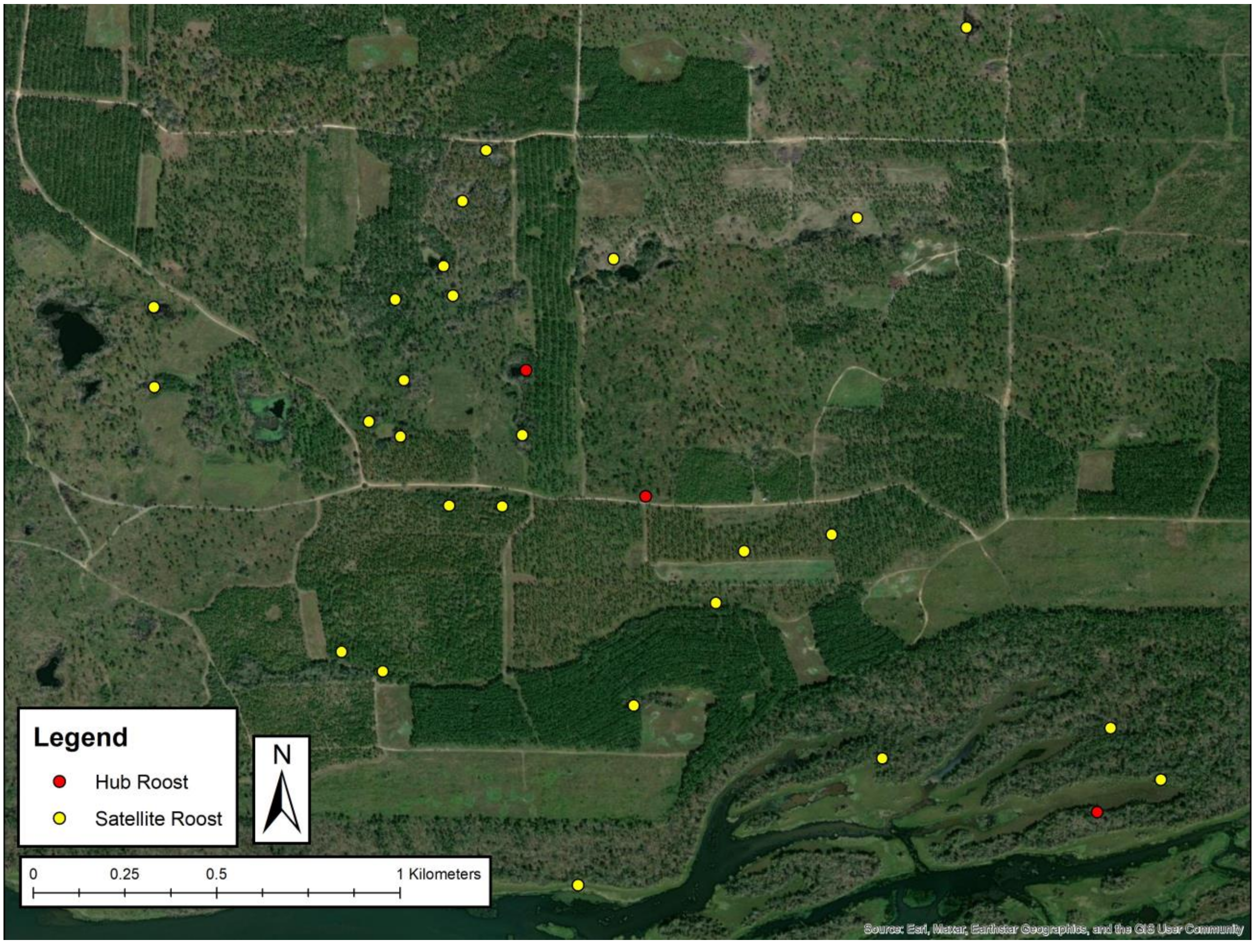

Figure 4.2: An example of a spatial network of roost areas for a female eastern wild turkey (*Meleagris gallopavo silvestris*) across the southeastern United States during 2014-2021.

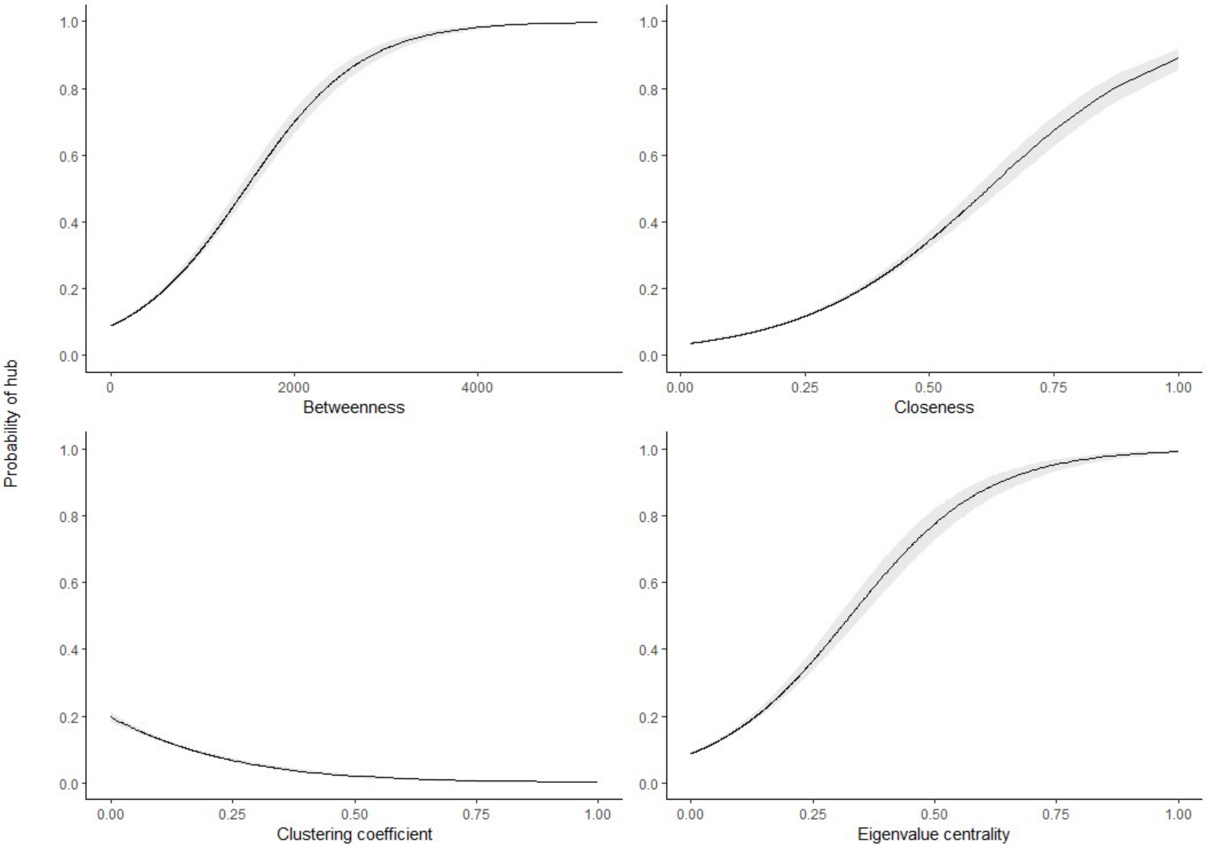

Figure 4.3: Predicted probability of hub roosts relative to betweenness, clustering coefficient, degree, and eigenvalue centrality (solid line) with 95% confidence intervals (dotted line) from the best approximating model for female eastern wild turkeys across the southeastern United States during 2014-2021.

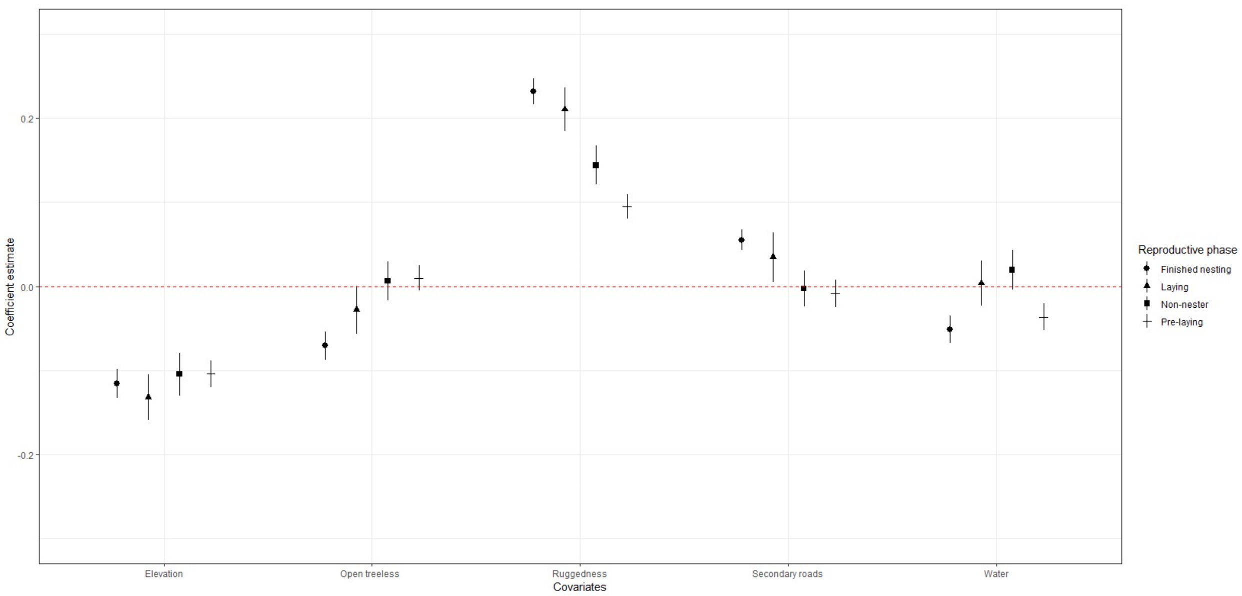

Figure 4.4: Coefficient plot depicting roost location selection during reproductive phases of female eastern wild turkey (*Meleagris gallopavo silvestris*) across the southeastern United States during 2014-2021. The whiskers depict 95% confidence intervals around mean estimates.

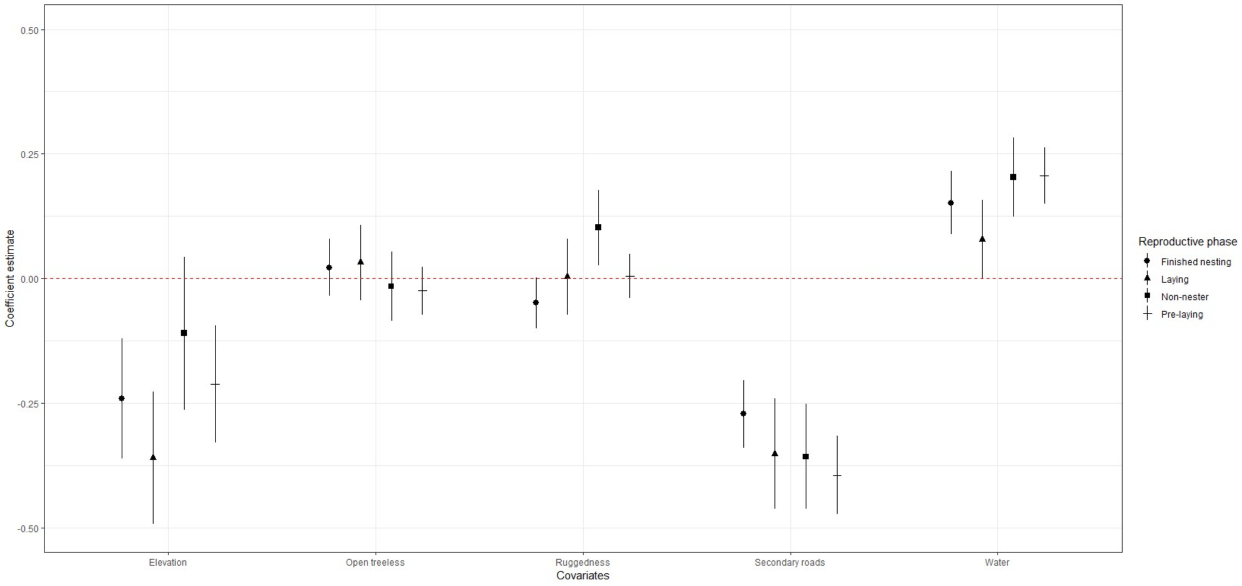

Figure 4.5: Coefficient plot depicting hub versus satellite site during reproductive phase of female eastern wild turkey (*Meleagris gallopavo silvestris*) across the southeastern United States during 2014-2021. The whiskers depict 95% confidence intervals around mean estimates.

CHAPTER 5

BREEDING SEASON SURVIVAL OF FEMALE WILD TURKEYS ACROSS THE SOUTHEASTERN UNITED STATES[1]

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[1] Bakner, N. W., D. L. Bakner, J. A. Martin, N. A. Gulotta, E. E. Ulrey, P. H. Wightman, B. A. Collier, and M. J. Chamberlain. To be submitted to Journal of Wildlife Management.

ABSTRACT

Avian species must balance the trade-off between reproductive effort and individual survival, and female survival is a primary factor influencing population dynamics for gallinaceous birds. Wild turkeys (*Meleagris gallopavo*) are a socially and economically important game species, but over the past 2 decades there have been declines in abundance, recruitment, and spring harvest across significant portions of the species range. We monitored 655 female wild turkeys in the breeding season (March 1 – August 31) using GPS transmitters during 2014-2021 across the southeastern United States to estimate survival. Female survival across the breeding season was 0.79 (95% CI = 0.70 – 0.88). Daily survival probability was significantly lower than the pre-laying period during incubation (log-odds ratio [LOR] = -0.91; 95% CI = -0.89 – -0.93) and brooding (LOR = -0.92; 95% CI = -0.88 – -0.96), while higher for non-nesting females (LOR = 1.01; 95% CI = 1.00 – 1.02). Survival rate across the breeding season was greater across our study sites than rates reported previously. Considering the incurred costs to survival during incubation and brooding, and the observed positive relationship with not engaging in reproductive activities, future research should explore how these relationships affect population trajectories.

INTRODUCTION

Identifying demographic patterns is central to understanding how survival and recruitment contribute to life-history variation and population dynamics in avian populations (Stearns 1992). One of the most prominent ecological trade-offs involves how reproductive effort affects survival (Williams 1966, Erikstad et al. 1998). Avian production is physiologically demanding and exposes individuals to increased levels of predation risks (Martin 1995, Deeming and Reynolds 2015). Due to the constraints on survival associated with reproductive output, avian species must balance current reproductive event against the cost of future reproduction potential (Tuljapurkar et al. 2009). Understanding the cost of reproduction is a primary component to understanding avian population ecology (Clark and Martin 2007).

Female survival is a primary factor influencing population dynamics for gallinaceous birds (Jarvis and Simpson 1978, Sandercock et al. 2008, Taylor et al. 2012), which arises from the extensive maternal investment required in reproduction, such as incubation, brood rearing, and the strategic selection of nesting areas rich in resources (Wiebe and Martin 2000, Deeming and Reynolds 2015). Additionally, females also exhibit behavioral adaptability, often prioritizing their own survival over immediate reproduction (Ghalambor and Martin 2001, Ghalambor and Martin 2002, Fontaine and Martin 2006). This decision-making reflects the delicate balance avian species must achieve between current reproductive endeavors and the potential for future breeding opportunities (Saino et al. 2004, Fontaine et al. 2007). During heightened predation risks in the breeding season, these choices become even more critical for female survival, impacting the overall vitality of avian populations (Fontaine and Martin 2006).

The wild turkey (*Meleagris gallopavo*; hereafter wild turkey), a precocial, ground-nesting, uniparental Galliform, is widely distributed across North America. Over the past 2 decades, managers have noted a concerning trend of declining abundance and recruitment throughout portions of the species' range (Byrne et al. 2015, Chamberlain et al. 2022). Previous research has found female survival (Suchy et al. 1983, Alpizar-Jara et al. 2001), reproductive parameters like nest success and poult survival (Roberts et al. 1995, Pollentier et al. 2014), and a combination of both female survival and reproductive metrics (Vangilder and Kurzejeski 1995, Roberts and Porter 1996, Rolley et al. 1998) to most effect wild turkey population growth. In spring and summer, female wild turkeys engage in solitary reproductive tasks such as incubating eggs and rearing preflight offspring which increases the risk of predation, resulting in reduced survival (Kurzejeski et al. 1987, Roberts et al. 1995, Pollentier et al. 2014). Given the recent decrease in wild turkey productivity (Byrne et al. 2015, Casalena et al. 2015), it is important to discern the factors that limit female survival, as this information constitutes a critical step in understanding potential drivers behind population fluctuations.

We estimated breeding season survival of female wild turkeys across parts of the southeastern United States. Our primary objective was to produce phenological survival estimates of female wild turkeys. Secondarily, we estimated breeding season survival for females that made multiple nesting attempts, as well as survival by age (adult or juvenile) and across years.

STUDY AREA

We conducted research on 12 sites across the southeastern United States. In Louisiana, we conducted research on the Kisatchie National Forest (KNF), Fort Polk Wildlife Management Area (WMA), and Peason Ridge WMA from January 2014-August 2021. The KNF was owned and managed by the United States Forest Service (USFS), whereas Fort Polk and Peason Ridge WMA was jointly owned by the USFS and the United States Army. Louisiana sites were composed of pine (*Pinus* spp.)-dominated forests, hardwood riparian zones, and forested wetlands, with forest openings, utility rights-of-way, 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*). For a detailed description of site conditions on KNF and Fort Polk WMA see Yeldell et al. (2017*a*, *b*).

Additionally, we conducted research on a broad suite of private and public lands in southeastern Louisiana, including Sandy Hollow WMA in Tangipahoa and Washington Parishes.

The region was composed of rolling hills with hardwood riparian zones interspersed with young longleaf pine plantations. Agricultural production included grazing and row crops were the dominant land use. For a detailed description of Sandy Hollow WMA, see Duguay et al. (2017).

We conducted research on Lake Seminole and Silver Lake WMAs located in southwest Georgia from January 2015-August 2016. The Silver Lake WMA was owned and managed by the Georgia Department of Natural Resources-Wildlife Resources Division (GADNR), and the adjacent Lake Seminole WMA was owned by the U.S. Army Corps of Engineers and managed by GADNR. Both sites were predominantly mature pine forests and forested wetlands. Overstory species were predominately longleaf pine, loblolly pine, slash pine (*P. elliottii*), oaks, and sweetgum (*Liquidambar styraciflua*). For a detailed description of site conditions on Silver Lake WMA see Wood et al. (2019).

We conducted research on B.F. Grant and Cedar Creek WMAs located in the Piedmont region of Georgia from January 2017-August 2021. B.F. Grant WMA was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia and was managed jointly by the GADNR and the Warnell School. B.F. Grant WMA landcover was primarily loblolly pine forest, agricultural lands, mixed hardwood and pine forests, and hardwood lowlands containing mostly oaks, sweet gum, and hickory. Agricultural lands were mostly grazed mixed fescue (*Festuca* sp.) fields and hay fields planted for ryegrass (*Lolium* sp.). Cedar Creek WMA was owned by the USFS and managed in partnership with GADNR. Cedar Creek WMA was composed primarily of loblolly pine uplands, mixed hardwood and pine forests, and hardwood lowlands of similar species composition as B.F. Grant WMA. For a detailed description of site conditions see Wakefield et al. (2020*a*).

We conducted research on 3 contiguous WMAs (Webb, Hamilton Ridge, and Palachucola; hereafter, Webb WMA Complex; January 2014-August 2018) and the Savanah River Site (hereafter, SRS; January 2021-March 2021) in South Carolina. The Webb WMA Complex was owned and managed by the South Carolina Department of Natural Resources (SCDNR). The Webb WMA Complex was dominated by longleaf, loblolly, and slash pine forests with hardwood stands along riparian corridors, and expanses of bottomland hardwood wetlands. The SRS was owned by the United States Department of Energy and managed by USFS. The SRS was primarily forested and consisted of bottomland hardwoods, mixed-pine hardwoods, and planted stands of longleaf pine, loblolly pine and slash pine. For a detailed description of site conditions see Wightman et al. (2019).

METHODS

We used rocket nets to capture female wild turkeys from January-March of 2014-2021. We aged captured individuals based on presence of barring on the ninth and tenth primary feathers and sexed them by the coloration of the breast feathers (Pelham & Dickson 1992). We banded each bird with an aluminum rivet leg band (National Band and Tag Company, Newport, Kentucky; size 8) and radio-tagged each individual with a backpack-style GPS-VHF transmitter (Guthrie et al. 2011) produced by Biotrack Ltd. (Wareham, Dorset, UK). We programmed transmitters to record 1 GPS location nightly (23:58:58) and hourly GPS locations from 0500 to 2000 (Standard Time and according to the appropriate time zones) for the duration of the study (Cohen et al. 2018). Each transmitter had a mortality switch that was programmed to activate after >23 hours of no movement. We released wild turkeys immediately at the capture location after processing. All turkey capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee at the University of Georgia (Protocol #A2019 01-

025-R2 and #A2020 06-018-R1) and the Louisiana State University Agricultural Center (Protocol #A2014-013, A2015-07, and A2018-13).

To determine dates of nest initiation (i.e. initiation of laying) and onset of incubation, we mapped our spatial-temporal data using ArcGIS 10.8 (Environment Systems Research Institute, Redlands, California, USA). We identified the onset of incubation as the first time an individual remained on the nest overnight (Bakner et al. 2019, Lohr et al. 2020), and then evaluated hourly locations for the previous 20 days to determine when a female initially visited the nest site (defined as location being < 20 m from the known nest site (Conley et al. 2015, Conley et al. 2016, Schofield 2019). We considered the date of first visit as the date of nest initiation and used it as the beginning of the laying period as wild turkeys rarely visit nest sites before laying the first egg (Conley et al. 2016, Collier et al. 2019). Following methods detailed in Chamberlain et al. (2020), we monitored brooding females until brood failure or 28 days after hatch, as most brood mortality occurs during this period. We located females that hatched successfully every 2–3 days post-hatch via VHF to conduct brood surveys and considered a brood to be present if ≥1 poult was seen or heard with the female (Chamberlain et al. 2020). From the information described above, we were able to determine reproductive phases for each female throughout the reproductive season, which we later used as a covariate in our survival model (Table 5.1).

KNOWN-FATE ANALYSIS

We estimated the daily survival rate (hereafter DSR) of female wild turkeys during the reproductive season, which we considered to start on 1 March and conclude on 31 August. We chose this range as 1 March coincides with the onset of gobbling activity which is considered the beginning of the reproductive period (Chamberlain et al. 2018, Wightman et al. 2019). Gobbling activity increases on our study sites once egg-laying begins (mean egg-laying 14 April, range 7

March – 30 June; Wakefield et al. 2020*b*). Peaks in incubation are known to occur 27 April (range 18 March – 20 July; Bakner et al. 2019, Lohr et al. 2020) and brood rearing occurring late summer depending upon rates of renesting (Chamberlain et al. 2020). To do so, we constructed daily encounter histories for each individual. Our encounter histories represented a chronological record of live-dead observations. Encounter histories began with a 1 on the first day of the breeding season, representing an individual was alive. Some individuals were marked after March 1; these encounter histories contained NA values prior to the first day these individuals were observed. If the individual survived, the encounter history contained a continuous series of 1's for each day they were observed. For individuals that died, the encounter history ended with a 0 for the day mortality occurred. Once individuals died, the remaining portion of the encounter history was filled with NA values. We estimated DSR as a series of Bernoulli trials:

$$y_{i,t} \sim Bernoulli(y_{i,t-1} * \Phi_i),$$

where $y_{i,t}$ is the survival status of individual i at time t, $y_{i,t-1}$ is the survival status of individual i at time $t-1$, and Φ_i is the linear predictor containing the fixed and random effects on the logit scale:

$$logit(\Phi_i) = \beta_0 + \beta_1 * period_{i,t} * day_{i,t} + \beta_2 * age_i + \beta_3 * attempt_i + year_{i,t} + site_i + \varepsilon_i,$$

$$\varepsilon_i \sim Normal(0, \sigma^2)$$

Our linear predictor included reproductive phase, day, age, and nesting attempt as fixed effects. We considered site and year as a random effect in our model. We chose uninformative priors by specifying distributions for both model coefficients and site and year random effects as Normal(0, 0.001), where 0 and 0.001 are the distribution's mean and precision (1/σ2), respectively. We assigned individuals to one of the reproductive phases. For individual i the day variable represented the amount of time an individual was within that phase. We assigned the age variable to each individual as being an adult or juvenile. Nesting attempts were either a 0 for no nesting, 1 for first nesting attempts, or 2 for all renesting attempts. We constructed a Bayesian hierarchical survival model (Royle and Dorazio 2008) using the runjags package (Denwood 2016) in R (v. 4.3.1; R Core Team 2023) to estimate female survival. To obtain samples of posterior distributions of model parameters, we ran 3 chains simultaneously for up to 5,000 iterations for each model. We discarded values prior to convergence as burn-in (1,000) and then used the remaining iterations to calculate posterior parameter estimates. We used both Gelman-Rubin diagnostic (Gelman and Rubin 1992) and visual inspection of chains using package mcmcplots (Curtis et al. 2018) in program R (v. 4.3.1; R Core Team 2023) to determine when convergence had been reached. We concluded that coefficients were different from 0 if 95% credible intervals (CI) did not overlap 0.

RESULTS

We monitored 663 (560 adults, 102 juveniles, 1 unknown) female wild turkeys during 2014–2021. We monitored 689 nesting attempts (initial attempts = 491, renesting attempts 198) initiated by 499 females. We censored 8 individuals that lacked GPS data during the monitoring period. We used 655 individuals (558 adults, 97 juveniles) for subsequent analyses. During the monitoring period, we observed 161 mortalities, of which 62 (39%) occurred during incubation, 12 (7%) during brooding, 39 (24%) while females were not nesting, and for 48 (30%) non-nesting females (Figure 5.1).

Annual survival for females across the breeding season was 0.79 (95% CI = 0.70 – 0.88). Daily survival probability was significantly lower during incubation (LOR = -0.91; 95% CI = -0.89 – -0.93; Figure 5.2) and brooding (LOR = -0.92; 95% CI = -0.88 – -0.96) than the pre-laying period, whereas non-nesting females had greater survival (LOR = 1.01; 95% CI = 1.00 –

1.02; Figure 5.3) than the pre-laying period. There was no significant difference between Julian days within the breeding season or age class (Table 5.2).

DISCUSSION

Over the past 2 decades, there has been a noticeable decline in wild turkey recruitment and spring harvest across a significant portion of the species range (Byrne et al. 2015, Casalena et al. 2015, Chamberlain et al. 2022). Due to these concerning trends, we conducted an extensive evaluation of female wild turkey survival during the breeding season, a critical stage that has substantive influences on population trajectories. We found relatively greater estimates of female breeding season survival than those reported in previous studies on the eastern subspecies (Vangilder and Kurzejeski 1995, Wright et al. 1996, Hubbard et al. 1999, Byrne and Chamberlain 2018, Tyl et al. 2023). Female survival rates in the United States have shown a positive trend over the past few decades, suggesting that turkeys have undergone a historical pattern characterized by substantial declines in per capita productivity, followed by a stabilization in population numbers, along with an improvement in female survival rates (Byrne et al. 2015). We note that survival rates of females may be inversely correlated with per capita reproductive success.

Seasonal variations in survival rates have been observed among female wild turkeys, with the lowest rates often coinciding with reproductive seasons (Vander Haegen et al. 1988, Palmer et al. 1993, Wright et al. 1996). Assuming mortality is not predominantly due to harvesting (legal or illegal), female survival rates can be substantially greater during non-reproductive periods (Pack et al. 1999), aligning with the notion that activities like incubation and brood-rearing render females more susceptible to predation (Bakner et al. 2019, Chamberlain et al. 2020, Lohr et al. 2020). Conversely, females experiencing early nest loss, or those who do not engage in nesting at all, may avoid the risks associated with reproductive activities. Similarly, research on Rio Grande wild turkeys has documented a negative impact of reproductive effort on survival (Collier et al. 2009). Consequently, an increase in the proportion of reproductively unsuccessful females could lead to an overall rise in the population-level survival rate, as the risk of predation outweighs the cost of future reproduction (Sæther 1988, Martin 2004, LaManna and Martin 2016).

The incubation period constitutes one of the most energetically demanding and spatially constrained phenological phases for ground-nesting birds (Deeming and Reynolds 2015). We found that female wild turkeys had significantly lower survival during this phenological state than females that were not nesting. Previous studies have demonstrated that female wild turkeys employ incubation strategies that involve trade-offs between predation risk and reproductive success, suggesting they are more invested in individual survival (Lohr et al. 2020). Our results provide further support for this, as greater than 50% of nests across our study sites are lost by day 6 of incubation (Bakner et al. 2019, Crawford et al. 2021) and DSR is negatively affected on day 10 of incubation. Such findings lend support for weak investment by females into their nest attempts if faced with predation risk or unfavorable nesting conditions (Martin 2004).

Responses to reproductive processes should vary along a gradient; for example, species with greater chances of future reproductive opportunities are less likely to invest in reproductive activities when conditions are unfavorable (Ghalambor and Martin 2001, Martin 2002, Martin 2004). We observed that female wild turkeys that did not nest during the breeding season had a greater probability of survival compared to those that incubated or brooded. Ground-nesting birds incur many costs during incubation, as individuals must balance nest attendance with acquiring resources necessary for their own survival (Webb 1987, Naylor et al. 1988, Fu et al.

2017, Jia et al. 2010). Additionally, during brood rearing females of precocial species make extensive movements to lead their young to sites with adequate food resources and appropriate cover (Atamian et al. 2010, Blomberg et al. 2013, Zhao et al. 2018, Chamberlain et al. 2020). Considering the incurred costs to survival during incubation and brooding, and the observed positive relationship with not engaging in reproductive activities, future research should explore how these relationships affect population trajectories.

Age-specific mortality has been documented throughout previous literature on wild turkeys (Van der Haegen et al. 1988, Little et al. 1990). However, we failed to find links between female age and breeding season survival, which has also been noted in previous works (Roberts et al. 1995, Vangilder and Kurzejeski 1995, Pollentier et al. 2014, Tyl et al. 2023). Although juvenile survival has been found to be lower while incubating (Miller et al. 1998, Tyl et al. 2023), juveniles in our study were poor nesters, contributing little to production, and many did not nest (Crawford et al. 2021). Juvenile wild turkeys are less likely to initiate nesting (Roberts et al. 1995, Pollentier et al. 2014, Crawford et al. 2021), offering at least a partial explanation for greater survival rates than adults during the breeding season as they remain mobile and less vulnerable to predators (Hubbard et al. 1999). This decrease in productivity coupled with greater survival warrants future research to understand how impactful this increase in survival is to the overall population of wild turkey.

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Table 5.1: Descriptions of reproductive phases for female wild turkeys (*Meleagris gallopavo*) monitored during 2014-2021 across the southeastern United States.

Reproductive Phase	Description
Incubation	The 28-30 days a female incubates the eggs.
Brooding	The 28 days after hatch when brood mortality is most pronounced.
Not nesting	Time period in which a female is not incubating, transition between nesting attempts, or post reproduction.
Non-nester	Females that did not make a nesting attempt during the monitored period.

Table 5.2: Population-level mean log-odds ratio (LOR), lower 95% credible interval (CI) level, and upper 95% CI level for each covariate used to model daily survival probability of female wild turkeys (*Meleagris gallopavo*) from March 2014 to August 2021 across the southeastern United States.

Covariate	LOR	Lower CI level	Upper CI level
Incubation phase	-0.91	-0.89	-0.93
Brooding phase	-0.92	-0.88	-0.96
Non-nester	1.01	1.00	1.02
Julian date	-1.00	-1.00	0.99
Adult DSR	2.70	2.70	2.71

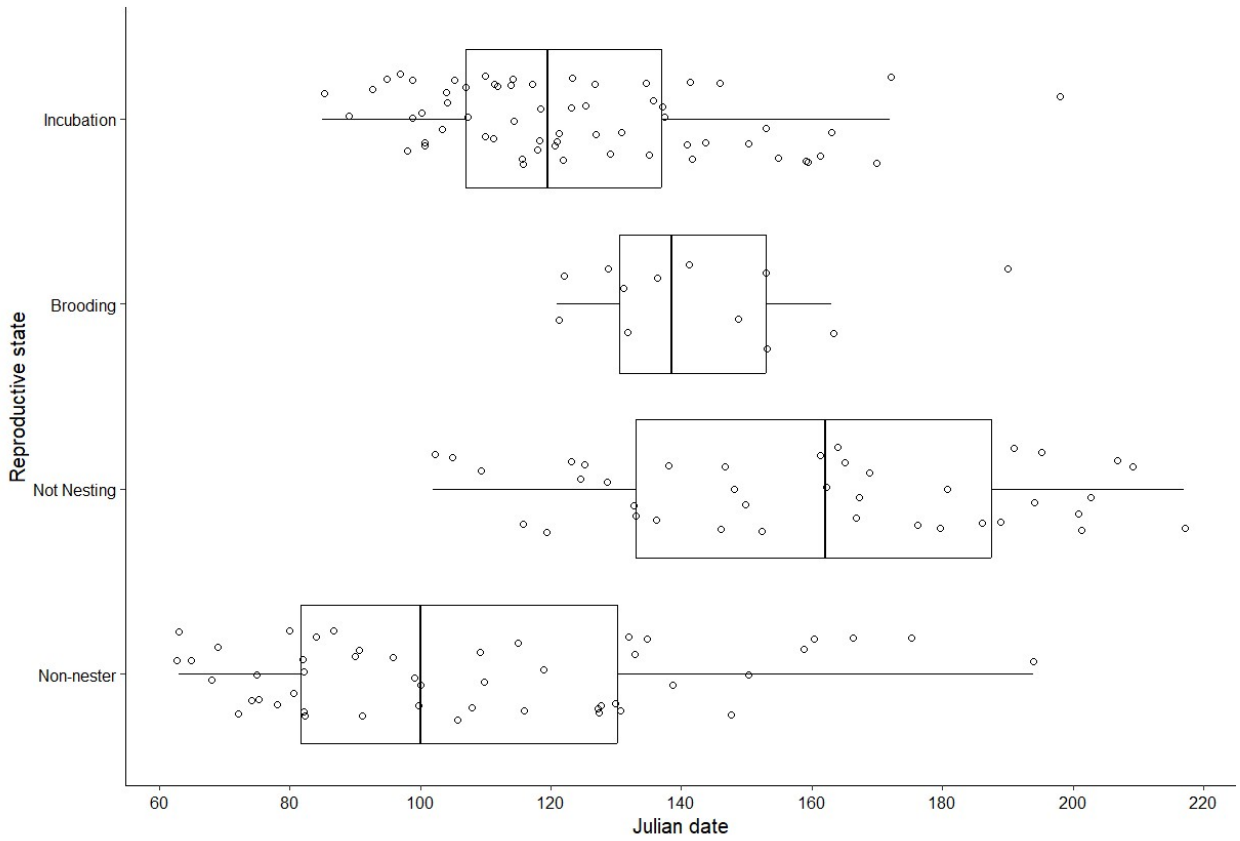

Figure 5.1: Boxplot depicting the distribution of mortalities by Julian date in each reproductive phase for female wild turkeys (*Meleagris gallopavo*) during March 2014 to August 2021 across the southeastern United States.

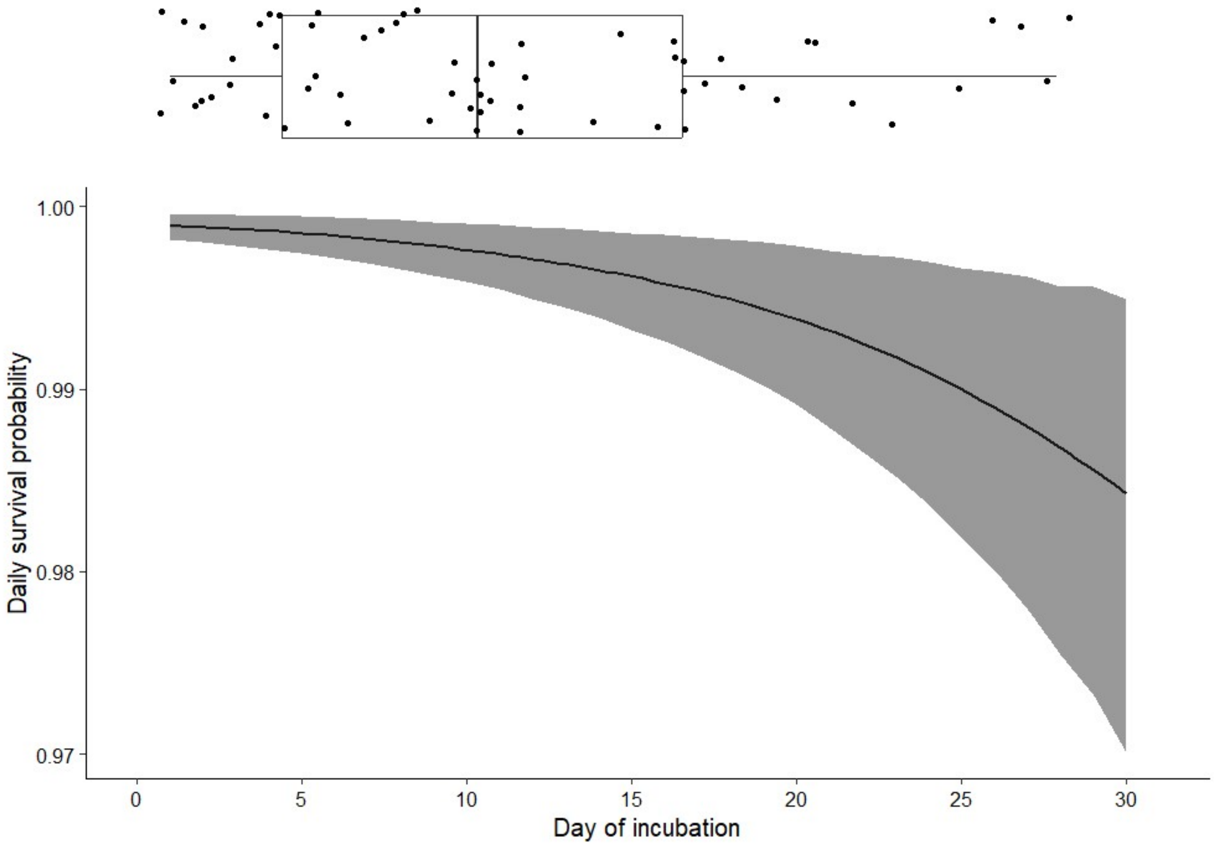

Figure 5.2: Daily survival probability during day of incubation for female wild turkeys (*Meleagris gallopavo*) during March 2014 to August 2021 across the southeastern United States. Black line represents the mean estimate whereas the gray shaded area is the 95% credible intervals.

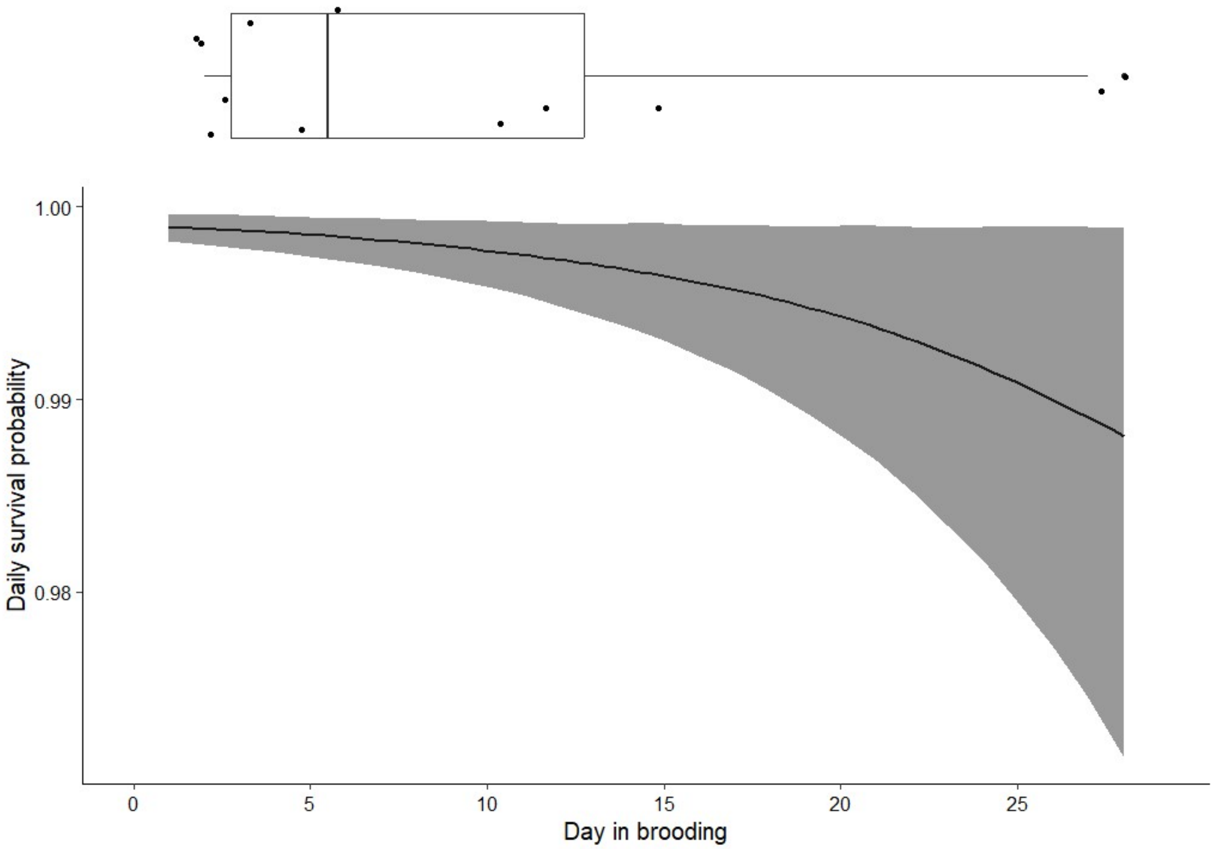

Figure 5.3: Daily survival probability during day of brooding for female wild turkeys (*Meleagris gallopavo*) during March 2014 to August 2021 across the southeastern United States. Black line represents the mean estimate whereas the gray shaded area is the 95% credible intervals.

CHAPTER 6

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

In conclusion, chapter 2 describes the role of prospecting behavior, and how it influences nesting, and ultimately, nest success in female wild turkeys. The number of visits to clustered laying patches did not directly impact nest fate. Instead, total patches used of clustered laying patches visited during incubation recesses influenced nest fate positively. This suggests that a varied selection of profitable foraging patches allows for more unpredictable movements, potentially confounding predators and thereby favoring the prey. This research also emphasizes the importance of considering the spatial and temporal scales at which nesting occurs, as opposed to focusing on vegetative characteristics around nest sites. This provides a more comprehensive understanding of the factors influencing nesting behavior and success. Future research should examine a finer-scaled evaluation of habitat conditions at patch locations and explore the prospecting behavior related to brood-rearing habitat, potentially occurring prior to or during the incubation period.

In chapter 3, I found wild turkey broods altered their behavior and selected for different habitats as they aged. We found that in a restricted state, ground roosting broods spent less time in areas of mixed pine-hardwoods and more time in areas with greater vegetation density. Tree roosting broods revisited areas closer to shrub/scrub landcover types, and areas with greater vegetation density. Tree roosting broods also spent less time near mixed pine-hardwoods, while spending more time in areas with greater vegetation density. We found that in a mobile state, ground roosting broods revisited areas closer to secondary roads and mixed pine-hardwoods, but farther from hardwoods. Tree roosting broods revisited areas farther from secondary roads and with greater vegetation density. Tree roosting broods also spent more time in areas closer to pine. Resource selection varied depending on behavioral state and recursive movements. However, revisitation and residence time impacted selection in both ground and tree roosting broods. My findings highlight the need to consider how behaviors can influence movement decisions and ultimately resource selection.

In summary, chapter 4 provides valuable insights into the roosting behavior of female wild turkeys during the reproductive season. Unlike male wild turkeys, females exhibited high site fidelity and maintained shorter distances between consecutive roost sites. This behavior is likely an adaptive strategy aimed at reducing predation risk and optimizing resource acquisition for egg-laying and incubation. The roost area network exhibited characteristics of a scale-free network, with a small number of centralized hub roosts that had numerous connections. This network structure facilitates information exchange, resource exploitation, and potentially mate acquisition. Additionally, maintaining hub roosts centrally within their reproductive range may enhance vigilance and resource acquisition, positively influencing fitness. The selection of roost locations at lower elevations with greater ruggedness is consistent with previous research and suggests that these features offer advantages in terms of observation and flight efficiency. Post-reproductive roosting selected for open treeless areas and water. This could be to increase foraging efficiency and mitigate thermal stress. The association of hub roosts with secondary roads could be to provide additional foraging opportunities and escape routes. Overall, there is an importance of considering spatial networks in understanding the behavior and ecology of wild turkeys. Future research should examine conspecific interactions, resource access, and disease transmission within these networks.

Chapter 4 provides research on female wild turkey survival during the breeding season providing insight into the factors influencing population dynamics. We observed higher estimates of female breeding season survival compared to previous studies, indicating a positive trend in survival rates over the past few decades. This suggests a potential stabilization in population numbers, coupled with improved female survival, which may be inversely correlated with per capita reproductive success. My findings highlight the challenges that female wild turkeys face during the incubation period. Survival rates were significantly lower for females engaged in incubation and brood rearing compared to those that did not nest. This highlights the trade-offs involved in reproductive activities, where individuals must balance nest attendance with acquiring resources necessary for their own survival. Additionally, my research indicates that juvenile wild turkeys are less likely to initiate nesting, offering a potential explanation for their higher survival rates compared to adults during the breeding season. Understanding the relationships between reproductive activities, survival rates, and age-specific mortality provides valuable insights for conservation strategies. Future research should explore the impact of increased survival on the overall population dynamics of wild turkeys. Additionally, continued monitoring of reproductive success and survival rates will be crucial for assessing the long-term viability of wild turkey populations.