Research Article

Behavior and Movement of Wild Turkey Broods

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ABSTRACT Behavioral and movement ecology of broods are among the most poorly understood aspects of wild turkey (*Meleagris gallopavo*) reproductive ecology. Recent declines in wild turkey productivity throughout the southeastern United States necessitate comprehensive evaluations of brood ecology across multiple spatial scales. We captured and marked 408 female wild turkeys with global positioning system (GPS)-transmitters across 9 pine (*Pinus* spp.)-dominated study sites in the southeastern United States during 2014–2019. We evaluated various aspects of the behavioral and movement ecology of 94 brood-rearing females until brood failure or 28 days after hatch (i.e., when poults are classified as juveniles). We found that 34 (36.2%) females had broods (≥1 poult) survive to 28 days after hatch. Broods moved >500 m away from nest sites the day after hatching, and then moved progressively farther away from nest sites over time. Daily movements increased markedly the first 3 days after hatching, and broods moved >1,000 m/day on average thereafter. Females roosted broods an average of 202 m away from nest sites the first night after hatching, but distances between consecutive ground or tree roosts were variable thereafter. Daily core areas increased from 0.8 ha the day of hatch to 4.6 ha by day 28, and range sizes increased from 6.9 ha to 27.9 ha by day 28. Broods tended to consistently select open land cover types, whereas selection for other land cover types varied temporally after hatch day. Broods spent 89% of their time foraging. Predicted daily survival for broods decreased rapidly with increasing distance moved during the initial 3 days after hatching and showed less variation during the subsequent 2 weeks post-hatch. Our findings parallel previous researchers noting that the most critical period for brood survival is the first week after hatch day. Previous researchers have attempted to identify vegetative communities used by broods under the assumption that these communities are a primary factor influencing brood success; however, our results suggest that brood survival is influenced by behavioral decisions related to movements during early brooding periods. © 2020 The Wildlife Society.

KEY WORDS behavioral state, brood, *Meleagris gallopavo*, movements, southeastern United States, space use, survival, wild turkey.

Wild turkeys (*Meleagris gallopavo*) are an economically and socially important species throughout their geographic range (Kennamer et al. 1992). Restoration of wild turkeys is among the most successful conservation stories in North America, but within the past decade populations of eastern wild turkeys (*M. g. silvestris*) have declined across eastern and midwestern North America (Tapley et al. 2011, Eriksen et al. 2015). The primary factor influencing population declines is reduced reproductive success. Byrne et al. (2015*a*) noted a long-term, consistent decline in productivity across the southeastern United States, characterized in part by an increasing proportion of females observed without broods.

Previous researchers have noted the importance of early successional vegetation communities to broods (Speake

et al. 1975, Sisson et al. 1991*a*) and that broods use a variety of forest stand types (Burk et al. 1990, Jones et al. 2005). At broader spatial scales, cover type interspersion may be an important determinant of landscape suitability for brood-rearing females (Wunz and Pack 1992, Bowling et al. 2015), whereas at the vegetative scale, ground cover availability and height of vegetation are thought to influence brood use (Spears et al. 2007, Streich et al. 2015). Furthermore, poult and brood survival is variable, with extensive poult mortality and brood loss during the first 2 weeks post-hatch (Hubbard et al. 1999). Broods begin roosting in trees at night within 2–3 weeks of hatch (Barwick et al. 1970, Healy 1992), at which point predation risk decreases with increasing poult mobility (Spears et al. 2007).

Although much is known about brood ecology in wild turkeys, significant knowledge gaps remain (Collier and Chamberlain 2011). Brood-rearing females move from nest sites as soon as poults are capable (Healy 1992), but how brood movements change temporally throughout early

brooding periods is unknown. Predation is the primary cause of brood loss (Hubbard et al. 1999), but predation risk influences behavior directly and indirectly (Abrams 1984, Proffitt et al. 2009, Campbell et al. 2012). Hence, brood-rearing females must balance movements and space use with perceived predation risk, which can influence broader reproductive strategies such as breeding activity and habitat selection (Fontaine and Martin 2006). Movements and space use of broods can have direct effects on brood survival in other ground-nesting birds (Erikstad 1985, Park et al. 2001, Kamps et al. 2017), but whether space use or movement of wild turkey broods influence survival is unclear. Likewise, although previous authors have reported coarse-scale assessments of range sizes used by broods (Porter 1977, Miller et al. 1997), how patterns of space use change as broods age is unclear.

Habitat use is a primary mechanism by which individuals acquire resources and reduce predation risk, and ultimately selection influences individual fitness (Orians and Wittenberger 1991, Fontaine and Martin 2006). Wild turkey broods select a variety of vegetative communities both pre- and post-flight, including hardwoods (Phalen et al. 1986, Williams et al. 1997), agricultural areas (Porter 1980), openings and early successional areas (Metzler and Speake 1985, Sisson et al. 1991a), and pine stands with open understories (Burk et al. 1990, Wood et al. 2019). Availability of insects influences habitat use by broods (Healy 1978, 1985) because poults require protein-rich forage to support rapid body growth and feather development (Hamrick and Davis 1971, Blackburn et al. 1975, Hurst and Stringer 1975, Healy 1985). Previous authors have noted that broods must balance movements with foraging requirements because poults require consistent prey consumption to sustain rapid growth (Williams and Austin 1988, Healy 1992). Ultimately, selection of habitat conditions conducive to foraging by broods increases rates of prey consumption by poults. But the use of different land cover types also may influence predation risk and, in turn, individual and population-level fitness (Rosenzweig 1991, Thomson et al. 2006).

Our objectives were to describe daily movements, space use, and habitat selection by wild turkey broods; describe movement behaviors of broods; and assess relationships between these parameters and brood survival across multiple forested landscapes in the southeastern United States. We hypothesized that brooding females would increase movements and space use and alter patterns of resource selection as broods aged, and that brood survival would be inversely related to movements and space use.

STUDY AREA

We conducted research during 2014–2019 throughout the southeastern United States on 9 study sites dominated by pine (*Pinus* spp.)-hardwood forest communities managed with dormant and growing season prescribed fire to manage understory vegetation communities (Fig. 1). Across study sites, mean temperature ranged from 17.9°C to 18.5°C (range = 3–34°C; https://usclimatedata.com/; accessed
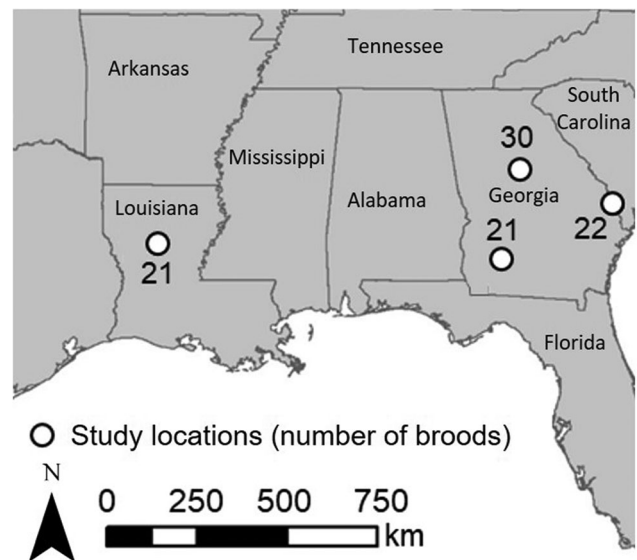
Figure 1. Distribution and number of 94 eastern wild turkey broods monitored across 9 study sites dominated by pine-hardwood forest communities in the southeastern United States, 2014–2019.

15 Feb 2020). Average elevation across our study areas ranged from 25 m to 520 m (https://weatherspark.com/; accessed 15 Feb 2020), and topography ranged from rolling hills to flat coastal plain. Climate on all study sites was characterized by hot, dry summers (Jun–Sep) and cool, wet winters (Nov–Feb). Specifically, we conducted research on Kisatchie National Forest (KNF) and Fort Polk Wildlife Management Area (WMA) in west-central Louisiana, USA. The KNF was owned and managed by the United States Forest Service (USFS) and Fort Polk WMA was jointly owned by the USFS and the United States Army. These sites were composed of pine-dominated forests, hardwood riparian zones, and forested wetlands, with forest openings, utility right-of-ways, and forest roads distributed throughout. Primary overstory species included longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), oaks (*Quercus* spp.), hickories (*Carya* spp.), and red maple (*Acer rubrum*). Prescribed fire was applied on an approximately 3–5-year return interval. Yeldell et al. (2017a) provides a detailed description of site conditions on KNF and Fort Polk WMA.

We also conducted research on 4 sites in Georgia, USA: Cedar Creek, B. F. Grant, Lake Seminole, and Silver Lake WMAs. The Silver Lake WMA (SLWMA) 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 United States Army Corps of Engineers (USACE) and managed by GADNR in southwest Georgia. Both sites were dominated by mature pine forests and forested wetlands. Overstory species were predominately longleaf pine, loblolly pine, slash pine (*P. elliottii*), oaks, and sweetgum (*Liquidambar styraciflua*). Prescribed fire was applied on an approximately 2–3-year return interval. Wood et al. (2019) provide a detailed description of site conditions on SLWMA.

B. F. Grant 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 was dominated by loblolly pine stands, agricultural lands, pine-hardwood forests, and hardwood lowlands containing mostly oaks, sweet gum, and hickory. Agricultural lands were mostly grazed mixed fescue (*Festuca* spp.) fields and hay fields planted for rye grass (*Lolium* spp.). Cedar Creek WMA was owned by the USFS and managed in partnership with GADNR. Cedar Creek was composed primarily of loblolly pine uplands, pine-hardwood forests, and hardwood lowlands of similar species composition as B. F. Grant. Prescribed fire was applied on an approximately 3–5-year rotation. Wakefield et al. (2020) provide a detailed description of site conditions on B. F. Grant and Cedar Creek WMAs.

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

METHODS

We captured female wild turkeys using rocket nets from January–March 2014–2019. We aged captured individuals based on presence of barring on the ninth and tenth primary feathers (Pelham and Dickson 1992). We banded each bird with an aluminum rivet leg band (National Band and Tag Company, Newport, KY, USA) and radio-tagged each individual with a backpack-style GPS-very high frequency (VHF)-transmitter (Biotrack, Wareham, Dorset, UK; Guthrie et al. 2010). We programmed transmitters to record 1 location nightly (2 seconds before midnight) and hourly locations between 0500 and 2000 from 15 February until the battery died or the unit was recovered (Cohen et al. 2018). We released turkeys 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 A2014 06-008-Y1-A0, A3437-01) and the Louisiana State University Agricultural Center (protocol A2018-13, A2014-013, A2015-07).

Nest and Brood Monitoring

We located turkeys ≥2 times/week using handheld Yagi antennas and telemetry receivers to monitor survival and nesting activity. We downloaded GPS locations from each turkey ≥1 time/week, and viewed GPS locations to determine when female locations became concentrated around a single point (Yeldell et al. 2017a, b). Once we suspected females were laying or incubating, we monitored each individual daily. After nest termination, we located and examined the nest site to determine if hatching had occurred (Conley et al. 2016; Yeldell et al. 2017a, b).

After nests hatched, we monitored the brooding female up to 28 days post-hatch because this period represents the time a young wild turkey is known as a poult, after which they are considered juveniles (Hurst 1992). To assess brood survival, we located females that hatched successfully immediately post-hatch (<1 day) and then again every 2–3 days after hatching and conducted brood surveys. For broods that we homed in on via telemetry before sunrise, we approached within 20–30 m and waited to observe the female leave the roost site. For broods monitored later in the day, we homed in on the brood and approached close enough to flush poults or observe them to verify that females still had broods with them. We considered a brood to be present if we saw or heard ≥1 poult with the female. If we detected a brooding female on the ground prior to 14 days, we assumed she was still with a brood because brooding females typically begin tree roosting with poults around 14 days post-hatch (Barwick et al. 1970, Healy 1992, Spears et al. 2007). Likewise, if we detected a brooding female roosted in a tree prior to 14 days post-hatch and we could not detect poults, we assumed the brood was lost. After females began tree roosting with poults, we relied on visual and auditory detection of poults to confirm brood presence. We performed brood surveys up to 28 days post-hatch or until we failed to detect poults during 2 consecutive attempts, at which point we assumed the brood to be lost. We defined brood success as the proportion of broods with ≥1 poult surviving to 28 days post-hatch (Little et al. 2014, Yeldell et al. 2017a). We excluded any individuals that we determined successfully hatched a nest but were not visually confirmed to have poults ≤1 day post-hatch or during the subsequent 2–3-day checks from our analyses. We decided to exclude broods we could not visually confirm because of the encounter history structure used in a ragged telemetry model with daily observations, wherein encounter histories consisting of <1 day of life are invalid (Dinsmore et al. 2002).

We recognize that our estimates of brood survival do not provide individual survival probabilities of poults, as was provided earlier by a number of authors (Sisson et al. 1991a, Peoples et al. 1995, Hubbard et al. 1999, Spears et al. 2007). Some previous studies reported survival estimates that were alarmingly low (Sisson et al. 1991a, Peoples et al. 1995), and marking poults produces biased estimates of survival relative to other less-invasive techniques (Hubbard et al. 1999), likely because of a lack of independence in sibling mortality that causes underestimation of sampling variance (Bishop et al. 2008). Likewise, Barron et al. (2010) noted that marked birds showed significantly increased energy expenditures, and that birds tended to forage less after capture. Therefore, we were concerned with accuracy of individual survival estimates obtained if capturing and marking poults occurred, and because capturing poults necessarily requires disruption to foraging activities and brood cohesion, we chose to estimate brood survival as noted above.

Analyses of Space Use, Movements, and Habitat Selection

Broods generally increase space use as poults age (Hillestad and Speake 1970), but the degree that space use changes daily as broods age is unclear. Therefore, we used a dynamic Brownian Bridge movement model (dBBMM; Kranstauber et al. 2012) to calculate daily utilization distributions (UDs) for each brooding female (Cohen et al. 2018). We calculated daily ranges (99%) and core areas (50%) and manually specified the Brownian motion variance for each step to be equal to that calculated in the entire range (range estimated using all locations for an individual female; Cohen et al. 2018). For estimating the Brownian motion variance, we used a location error of 20 m, and constant window and margin sizes equal to 7 and 3, respectively (Cohen et al. 2018). We used a moving window of 7 to estimate step-specific variance estimates, which we then used to calculate the mean variance for the current time step (Kranstauber et al. 2012). We used a margin size of 3 because dynamic Brownian bridge variance estimates require a minimum of 3 locations under which no change point analysis (Gurarie et al. 2009) could be conducted. We performed all UD calculations using the R package move (Kranstauber et al. 2018) and conducted our analysis in R version 3.6.1 (R Core Team 2019).

Once we created daily UDs for each female, we evaluated habitat selection of broods within daily ranges and core areas. We used 30-m resolution imagery from United States Geological Survey (USGS) Landsat–8 Operational Land Imager to delineate primary land cover types on our study areas during May 2014–2019, excluding images with ≥10% cloud cover. We chose imagery from May because that was the midpoint of the nesting season when broods were beginning to move about the landscape. We used an unsupervised classification in Earth Resources Data Analysis System (ERDAS) Image software (version 16.00.0000.00199, Hexagon Geospatial, Peachtree Corners Circle, Norcross, GA, USA) with 30 classes, and recoded and combined classes to create 6 unique land cover classes (water, pine, hardwood, mixed pine-hardwood, open treeless areas, and infrastructure). We removed water and infrastructure from subsequent analyses because these represented non-useable areas for broods. Within each daily UD, we estimated the proportion of each land cover type to provide an assessment of habitat selection by broods.

We examined daily third-order habitat selection (Johnson 1980) in a use versus availability framework similar to Manly et al. (2002) study design III. Because availability relies on quantifying the area known by an animal, we defined available habitat as the area within each brood's daily range, whereas used habitat was within each daily core area. We calculated selection ratios for each land cover type by dividing the proportion of daily core area containing that land cover type by proportion of that habitat in the daily range. We pooled daily selection ratios of each brood to calculate a mean selection ratio across broods for each day post-hatch. We set $\alpha = 0.05$ and estimated 95% confidence intervals around selection ratios. We considered ratios with 95% confidence intervals excluding 1.0 to be biologically informative. Within this framework, a selection ratio approximately equal to 1.0 indicated use proportional to availability (i.e., random use), whereas a ratio >1.0 indicated selection of land cover types, and a ratio <1.0 indicated avoidance.

Existing literature on movements of wild turkey broods has focused primarily on reporting average distances moved, or describing distances moved away from nest sites (Hillestad and Speake 1970, Williams et al. 1970). To describe daily movements of brooding females and broods as they aged, we calculated daily distance traveled by summing the distance between consecutive GPS locations for each day. Likewise, we evaluated if fidelity to the nesting location changed as broods aged by calculating the average daily distance (m) from the nest site for each female from the daily location data. Wild turkey poults are constrained to roost on the ground until they are capable of flight, at which point they begin roosting above ground (Healy 1992). Furthermore, previous researchers noted that brood roosts were clustered in areas (Barwick et al. 1970), and site familiarity may be an important determinant of roost selection and individual survival (Rumble 1992, Byrne et al. 2015*b*). Hence, we calculated average distance (m) between consecutive roost sites for use in evaluating brood survival.

Behavioral Analysis

Accurately discerning behaviors and understanding environmental factors mediating those behaviors is important to making valid management decisions (Cooke 2008). Likewise, quantifying behaviors provides information on where and when animals forage and rest while using their ranges, which can be used by managers as a basis for conservation decisions (Hulbert 2001). Early research on behavior of broods noted that most time was spent foraging (>86% of time) because poults require nearly constant food intake, and that broods changed directions frequently while foraging (Healy 1985, 1992). Other authors noted that broods remained stationary for extensive periods throughout the day, presumably while foraging or loafing (Williams et al. 1970).

We quantified how brood movement behaviors changed daily from day after hatch until 28 days thereafter. We modeled turkey behavior using behavioral change point analysis (BCPA), a likelihood-based method allowing identification of changes in movement parameters underlying locational time-series data. The BCPA uses a sweeping window analysis and temporal autocorrelation associated with telemetry locations to detect changes in movement parameter values, specifically speeds and relative turn angles (RTAs), and then estimates the most likely change point (i.e., location where shift in movement parameters occur) within each window according to Bayesian Inference Criterion (BIC; Gurarie et al. 2009). We used BCPA to identify and interpret movement behaviors because it can reveal behavioral structure in animal-tracking data without any prior assumptions

regarding the distributions of movement parameters (Gurarie et al. 2009, 2016).

We calculated speed and RTA between all sequential locations for the full movement paths collected for each turkey (i.e., from capture until transmitter failure), which included brooding and nonbrooding locations. Using the full movement path of the turkeys ensured a better quantification of behavioral states, and allowed us to compare the frequency of behaviors between when females were nonbrooding and brooding. We used a smoothed BCPA analysis in the R package bcpa (Gurarie 2014), and tuned our analysis using a window size of 30 sequential locations and sensitivity (K) of 1 (Gurarie 2014, Gurarie et al. 2016). Our settings allowed us to identify changes in behavior at the smallest temporal scale possible while still meeting the minimum sample size required for BIC model selection (Gurarie et al. 2009). We hereafter refer to segments of trajectories between the change points identified by BCPA as bouts. Because the distribution of velocity and RTA values were positively skewed, we calculated median values for these metrics.

We assessed within-group sum of squares and serial classification of bouts using Krzanowski and Lai's (1988) hierarchical clustering method to determine the number of distinct behavioral states for each turkey based on combinations of median speed and RTA (Zhang et al. 2015). Specifically, we used k-means clustering (Hartigan and Wong 1979) in packages cluster (Maechler et al. 2018) and fpc (Hennig 2019) to classify movement bouts into mutually exclusive behavioral states based on combinations of median speed and RTA. This allowed us to categorize bouts identified by BCPA into unique behavioral states based on similarities in patterns of movement. We chose to limit our k-means clustering to 2 behavioral states (Zhang et al. 2015): a resting or restricted search behavior, in which movements would have relatively higher RTA but lower speeds as broods foraged, and a directional movement behavior, in which movements would have lower RTA but higher speeds as presumably broods walked through an area (Zhang et al. 2015, Gurarie et al. 2016). We then assigned GPS locations falling within each bout to the same behavioral state (foraging or walking).

Because we were interested in how female behaviors potentially changed when brooding, we evaluated how behaviors differed between locations taken while females were brooding and those taken while females were not brooding. To discern these differences, we calculated the proportion of locations spent in each behavioral state for each female during these 2 phases, and then calculated the mean and standard error of these proportions across females. Because we were interested in how brooding behaviors potentially changed through time as broods aged to day 28, we evaluated how behaviors differed from 1 to 28 days post-hatch. To discern these differences, we described female behavior by calculating the daily proportion of locations spent in each behavioral state for each brood in a given day post-hatch, and then calculated the mean and standard error of these proportions across broods for each day post-hatch.

Survival Analysis

Survival of broods influences population productivity and wild turkey population dynamics at multiple spatial scales (Roberts and Porter 1998, Byrne et al. 2015a). We estimated daily brood survival (i.e., the probability that ≥1 poult within a brood survived) using the aforementioned brood checks that allowed an assessment of the presence or absence of poults with the brooding female. We modeled changes in daily brood survival temporally and evaluated time-specific covariates tied to movements and habitat use. We used a nest survival approach (Dinsmore et al. 2002) via a known fate model implemented in Program MARK (White and Burnham 1999) to estimate daily brood survival using telemetry data (Rotella et al. 2004, Mong and Sandercock 2007, Collier et al. 2009).

To estimate daily survival, we structured an encounter history for each brooding female across the 28-day period after hatch. We recorded the last day each radio-tagged female was with ≥1 poult, if the brood was still active at the end of the study, and brood fate (survived or failed). We used an information-theoretic approach to select the most parsimonious model, and assessed model support using Akaike's Information Criterion corrected for sample size (AIC$_c$), ΔAIC$_c$, and Akaike's weights (w_i; Burnham and Anderson 2002). We considered models within 2 units of the lowest ΔAIC$_c$ to be equally plausible. We developed a set of candidate models (Table 1) to evaluate if various metrics of movement and habitat selection influenced daily brood survival. We included time-dependent covariates (Collier et al. 2009) for the daily habitat selection ratios (pine, hardwood, mixed, open), average daily distance moved by broods, average daily distances from brood locations to the nest from which they were hatched, daily core (50%) and range (99%) utilization distributions (Cohen et al. 2018), and distance between consecutive roost sites. We also developed time-specific trend models for the aforementioned covariates, which assumed that the effect of each covariate was constant over time (Franklin 2001). Because only 2 broods failed past day 17 (1 on day 18 and 1 on day 22), we restricted our use of time-dependent covariates to the first 17 days, and held daily survival constant from day 18–28. Additionally, for candidate models that included daily time dependence, 2 extrinsically non-identifiable parameters could not be estimated via standard maximum likelihood estimation or data cloning with profile likelihood confidence intervals. Therefore, we fixed parameters for days 10 and 13 to 1 for all fully time-dependent analyses.

RESULTS

We captured and radio-marked 408 (346 adult, 62 juvenile) female wild turkeys, of which 323 (79.2%) attempted ≥1 nest. Including renests, we monitored 475 nest attempts, and 104 (21.9%) successfully hatched. Of those 104, 10 broods were presumably lost during or immediately after hatching, and never visually documented via brood surveys. Therefore, 94 successfully hatched and produced a

Table 1. Candidate models, along with number of parameters (K), deviance, difference from lowest second-order Akaike's Information Criterion (ΔAIC_c), and Akaike's model weights (w_i), used to examine the effects of time-dependent habitat selection ratios for pine, mixed pine-hardwoods, open, and hardwood, daily distances moved by brooding females, distances between consecutive roost sites, day-specific estimates of distance from nests, and estimates of space use (50% and 99% utilization distributions [UD]) on daily survival rates (DSR) of eastern wild turkey broods from multiple study sites in the southeastern United States, 2014–2019.

Model notation	K	Deviance	ΔAIC_c	w_i
DSR (Time-dependent nest distance, DSR[a] for days 18–28 constant)[a]	17	416.90	0.00	0.959
DSR (Days 1–17 constant, days 18–28 constant, differed between both periods)	2	455.11	7.75	0.019
DSR (Time-dependent daily roost distance, DSR for days 18–28 constant)[a]	17	426.54	9.63	<0.01
DSR (Time-dependent mixed pine-hardwood, DSR for days 18–28 constant)[a]	17	428.07	11.16	<0.01
DSR (Time-dependent open, DSR for days 18–28 constant)[a]	17	428.21	11.31	<0.01
DSR (Time-dependent pine, DSR for days 18–28 constant)[a]	17	428.92	12.01	<0.01
DSR (Time-dependent hardwood, DSR for days 18–28 constant)[a]	17	429.07	12.16	<0.01
DSR (Time-dependent 99% UD, DSR for days 18–28 constant)[a]	17	431.12	14.21	<0.01
DSR (Time-dependent 50% UD, DSR for days 18–28 constant)[a]	17	432.68	15.77	<0.01
DSR (Time-dependent daily distance moved, DSR for days 18–28 constant)[a]	17	436.16	19.26	<0.01
DSR (Decreasing DSR trend [days 1–17], DSR For days 18–28 constant)[a]	2	472.88	25.52	<0.01
DSR (Fully parameterized time-specifc model)	27	425.94	29.72	<0.01
DSR (Time-dependent daily distance moved, constant over time)	2	485.48	38.12	<0.01
DSR (Time-dependent open, constant over time)	2	486.72	39.36	<0.01
DSR (.)	1	490.82	41.45	<0.01
DSR (Time-dependent pine, constant over time)	2	489.02	41.66	<0.01
DSR (Time-dependent 99% UD, constant over time)	2	490.03	42.67	<0.01
DSR (Time-dependent mixed pine-hardwood, constant over time)	2	490.28	42.92	<0.01
DSR (Time-dependent nest distance, constant over time)	2	490.54	43.18	<0.01
DSR (Time-dependent 50% UD, constant over time)	2	490.61	43.25	<0.01
DSR (Time-dependent daily roost distance, constant over time)	2	490.72	43.36	<0.01
DSR (Time-dependent hardwood, constant over time)	2	490.80	43.44	<0.01

[a] Model includes 2 fixed values for extrinsically non-identifiable parameters.

brood we visually documented (Fig. 1), and we monitored each of these 94 broods until 28 days of age or brood failure. Three females produced 2 broods during a single nesting season, and in these instances we considered each brood to be independent. We observed that 34 (36.2%) broods survived to 28 days post-hatch, hence 7.2% of nests we monitored successfully produced ≥1 poult that survived to 28 days post-hatch.

Mean size of daily core areas increased from 0.8 ± 0.1(SE) ha the day of hatch to 2.4 ± 0.2 ha by day 5, but thereafter only increased to 4.6 ± 0.6 ha by day 28 (Fig. 2A). Likewise, mean daily range size increased from 6.9 ± 1.9 ha to 14.4 ± 1.5 ha from hatch to day 5, and gradually increased to 27.9 ± 4.7 ha by day 28 (Fig. 2B). Females moved broods >200 m on average away from nests the day after hatching, and within 3 days had moved broods an average of 808 ± 58 m away from nests (Fig. 2C). Within 5 days of hatching, broods had moved an average of $1,126 \pm 85$ m away from nests and distance continued to increase as poults aged (Fig. 2C). Broods moved an average of 517 ± 37 m the day after hatching, and >1,000 m daily thereafter (Fig. 2D). On the night after hatch, broods roosted an average of 202 ± 107 m away from the nest site, and roosts on successive nights thereafter were typically on average >300 m (range = 299–742 m) from the previous night (Fig. 2E).

Brood habitat selection changed temporally (Fig. 3). Broods did not select for hardwoods during the first 14 days after hatching, but between days 14 and 21 selection of hardwoods increased and thereafter waned (Fig. 3A). Broods did not tend to select for mixed pine-hardwood or pine forests (Figs. 3B and C). Broods exhibited strong

selection for open land cover types (Fig. 3D), although the strength of this selection varied. Broods tended to most strongly select for open areas during the first 10 days after hatching. Broods exhibited 2 distinct modes of behavior in their movement trajectories (Fig. 4). One behavioral state was characterized by fast (median velocity = 207.2 ± 12.4 m/hr) and comparatively straight (median RTA = $40.2 \pm 4.5°$) movement trajectories. We interpreted this behavior as a directional movement and considered individuals in this state to be walking. A second behavioral state had slow velocity speeds (median velocity = 73.7 ± 10.2 m/hr) and high turn angles (median RTA = $113.7 \pm 2.3°$). We interpreted this to be an area-restricted search or loafing behavior, and considered individuals in this state to be foraging. When evaluating behavioral states across the entire sample of females using only locations when females were not brooding, we found that walking accounted for 1.1–34.4% of locations ($\bar{x} = 12.3 \pm 0.7\%$), whereas foraging behaviors accounted for 65.6–98.9% ($\bar{x} = 87.7 \pm 0.7\%$). Behavioral states differed when females were brooding; walking accounted for $11.3 \pm 0.6\%$ of locations, whereas foraging behaviors accounted for $88.7 \pm 0.6\%$ (Fig. 5).

Our best-fitting candidate model for daily survival of broods suggested that daily brood survival was most influenced by distances from where broods were located on the landscape relative to the nest from which they hatched (Table 1). We found no support for models that constrained survival probability to be constant or to have time-dependent trends. Predictions for the time-dependent effect of distance from nest for the 15 estimable periods indicated
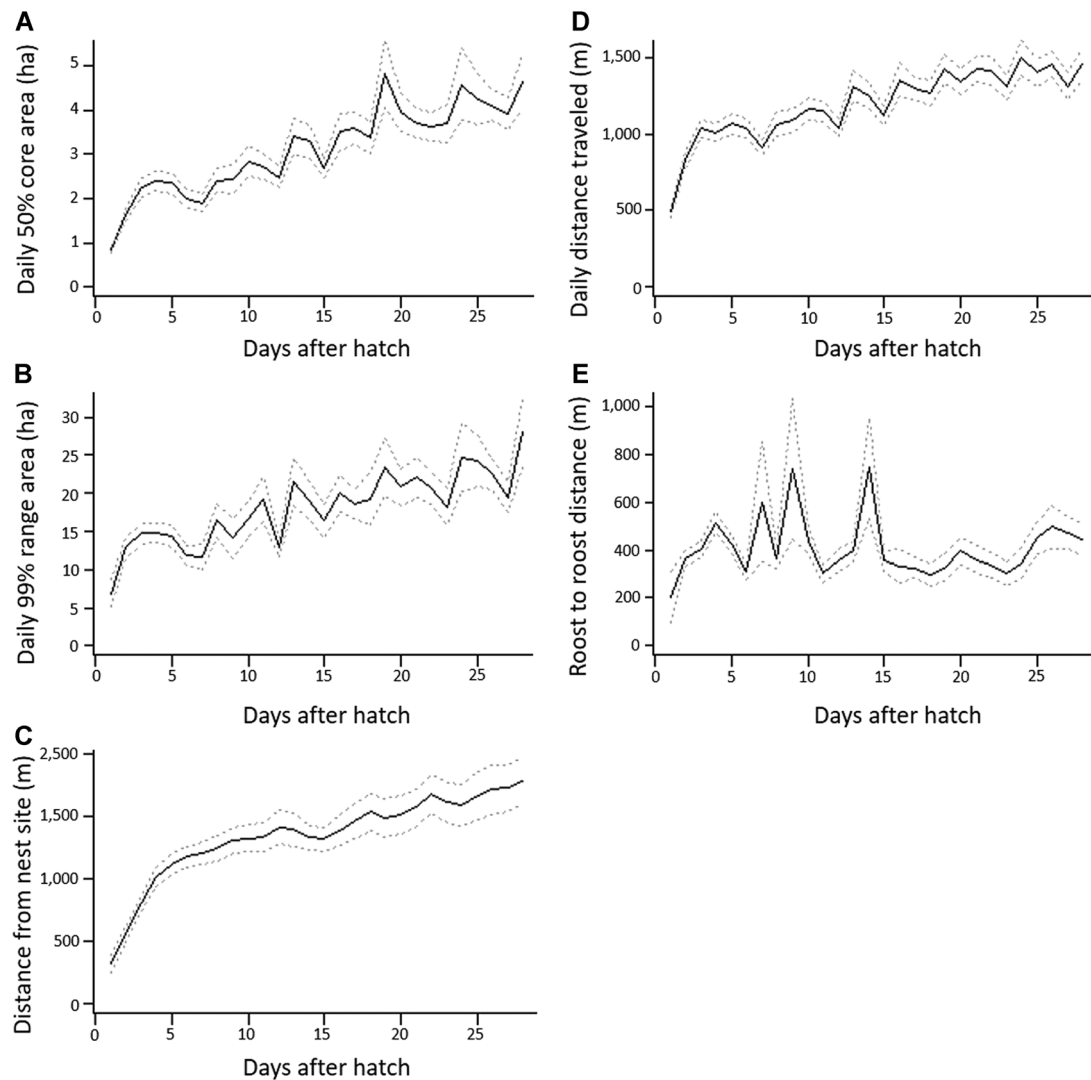
Figure 2. Metrics of daily space use (50% [A] and 99% [B] daily dynamic Brownian bridge movement model) and movement (m; daily distance from nest site [C], daily distance traveled [D], daily distance between consecutive roosts [E]) across days after hatch date for 94 eastern wild turkey broods across multiple study sites in the southeastern United States, 2014–2019. Solid black lines indicate means and dashed grey lines are ±1 standard error.

that when broods were generally closer to nests during the first 3 days after hatching, survival tended to be greater (Fig. 6). Thereafter, the influence of distance from nest on daily survival was variable and likely biologically irrelevant (Table 2). Daily survival for the 10-day period after day 17 was high (0.994 ± 0.004), indicating that daily brood survival was effectively 1 once broods began roosting in trees. Collectively, the estimated probability of a brood surviving the monitoring period, given the mean of each time-dependent covariate, was 0.38 ± 0.05 (95% CI = 0.28–0.48).

DISCUSSION

We observed that nearly 80% of female wild turkeys initiated incubation but that nest success was relatively low (~22%) compared to other species with comparable reproductive strategies, such as greater sage grouse (*Centrocercus urophasianus*) and willow ptarmigan (*Lagopus lagopus*; Holloran et al. 2005, Wilson et al. 2007). We documented 3 females producing 2 broods in a single

reproductive season, an observation not readily found in the literature (Sisson et al. 1991*b*, Morgan and Schweitzer 2001, Yeldell et al. 2017*a*). We also observed that brood survival was approximately 36%, and daily survival of broods was positively associated with shorter distances moved away from nest sites during early brooding periods (first 3 days after hatch). Likewise, broods that were intact 17 days after hatching remained so through day 28, but only 7% of nests produced poults that survived until 28 days post-hatch. Broods spent most time foraging, and space use and movements generally increased as broods aged, findings that parallel extant literature on behavior of wild turkey broods (Porter 1977, Healy 1992). Conversely, we observed notable differences in estimates of space use, daily movements, and resource selection by broods relative to previous studies (Hillestad and Speake 1970, Phalen et al. 1986). For instance, Hillestad and Speake (1970) noted that broods failed to increase daily ranges as poults aged, and Phalen et al. (1986) reported that open, treeless
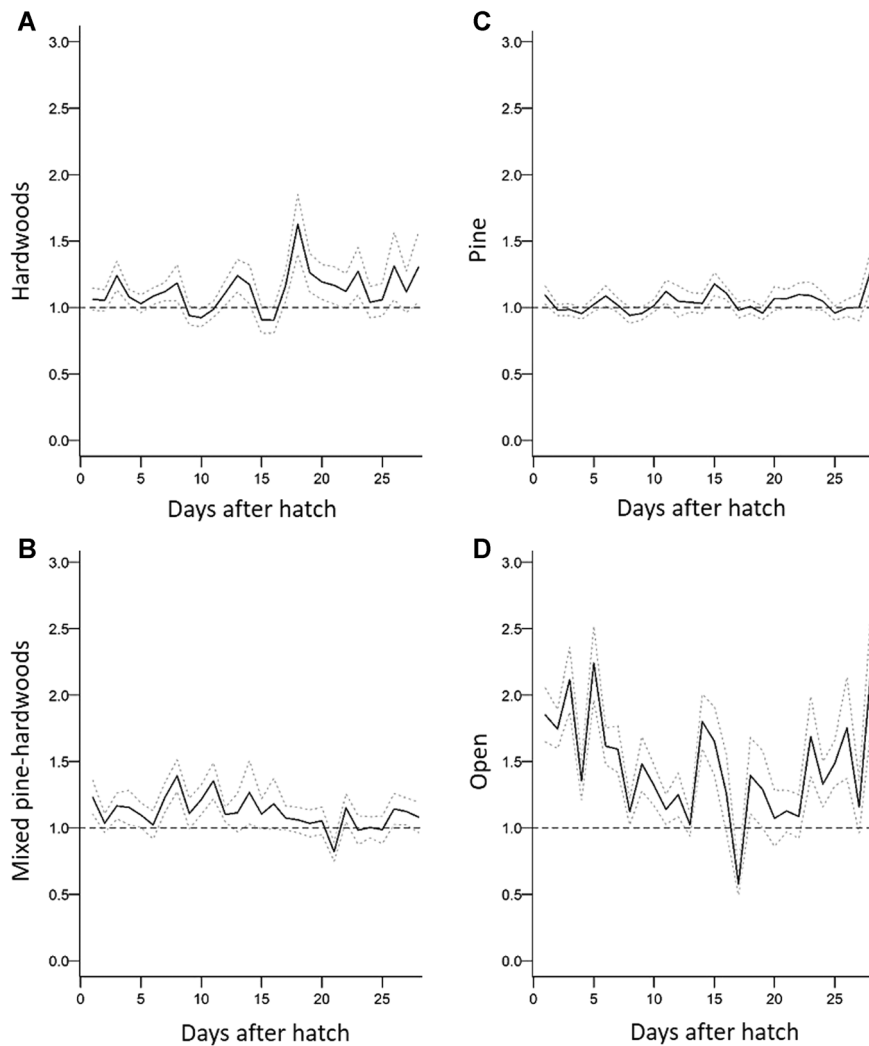
Figure 3. Selection ratios (solid line) and 95% confidence intervals (dotted line) of 94 eastern wild turkey broods during the 28 days after hatching across multiple study sites in the southeastern United States, 2014–2019. Estimates <1 indicate avoidance, estimates = 1 represent selection in proportion to availability (i.e., no selection or avoidance), and estimates >1 indicate selection, with deviation from 1 indicative of effect size. Land cover types included A) hardwood, B) mixed pine-hardwood, C) pine, and D) open, early successional areas (open).

areas were not used by broods in a pine-dominated system in Mississippi, USA, whereas hardwood forests were preferred. We offer that these differences were a function of more robust sample sizes in the current study, and improved methodological approaches (Collier and Chamberlain 2011, Cohen et al. 2018) that allowed us to assess spatial behaviors of broods at finer resolutions than previous researchers.

Our collective knowledge of wild turkey brood behavior is based on observations of imprinted poults (Healy 1985), field observations of broods monitored via VHF-telemetry (Hillestad and Speake 1970, Williams and Austin 1988, Spears et al. 2007), or triangulated locations obtained via VHF monitoring (Phalen et al. 1986, Burk et al. 1990, Sisson and Speake 1994), with the exception of recently published findings detailed in Wood et al. (2019). The advent of GPS-transmitters suitable for wild turkeys (Collier and Chamberlain 2011, Guthrie et al. 2011) allowed us to detail various aspects of brood behavior more precisely than previously possible. For instance,

previous authors observed that broods moved an average of 514 m/day, and considered daily movements >1,200 m extraordinary (Hillestad and Speake 1970). Daily movements considered extraordinary in earlier studies approximated the mean daily distance moved by broods on our study sites (but see Hon et al. 1978), and that distances moved were fairly consistent several days after hatching to approximately 1 month post-hatch. Likewise, we found that daily core area and range sizes gradually increased as poults aged, which contradicts earlier works describing daily space use of broods (Hillestad and Speake 1970).

Wild turkey broods, similar to other Galliformes, are inextricably linked to open, early successional vegetation communities that offer quality foraging opportunities with reduced predation risk (Storch 1994, Aldridge and Boyce 2007). Previous authors have noted that broods often selected open areas within forested landscapes (Williams and Austin 1988, Sisson et al. 1991a, Peoples et al. 1995), but considerable literature also has detailed plasticity in
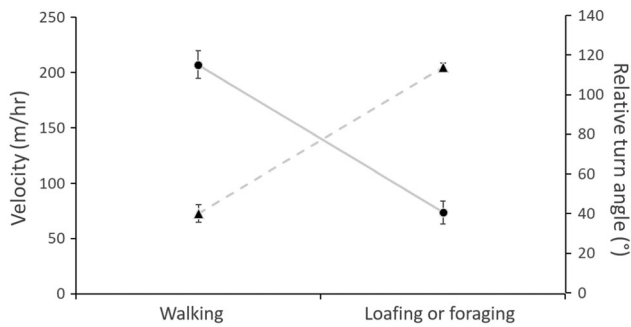
Figure 4. Statistical definitions of behavioral states inferred for global positioning system (GPS) locations of 94 female eastern wild turkeys who successfully hatched nests and started brooding. Behaviors were classified by sequential use of behavioral change point and *k*-means clustering analyses, based on combinations of between-fix speeds (solid line) and relative turn angles (dotted line). Broods exhibited 2 distinct modes of behavior in their movement trajectories: one behavioral state was characterized by fast and comparatively straight movement trajectories, which we interpreted as a walking behavioral state, and a second behavioral state had slow velocity speeds and high turn angles, which we considered to be a foraging behavioral state. Circles and triangles represent the mean value, and vertical bars represent the standard error.

habitat selection by broods across multiple landscapes (Rumble and Anderson 1996, Keegan and Crawford 1997). Similarly, we observed that broods generally selected open land cover types, but selection varied markedly temporally. We also observed a modest increase in the selection of hardwood areas as broods aged, consistent with some previous works that detailed habitat use by broods in pine-dominated forests (Phalen et al. 1986, Williams et al. 1997). Wild turkey poults are capable of roosting in trees within 2–3 weeks after hatch but begin roosting above ground in shrubs sooner (Barwick et al. 1973, Streich et al. 2015). Likewise, poults can exhibit short flights within a week of hatching, which facilitate predator avoidance (Williams 1974, Healy et al. 1975). Hence, broods exhibit rapid changes in behavioral plasticity as they age, which would contribute to the temporal changes in habitat selection we observed.

Reproductively successful ground-nesting birds are faced with the need to balance movements post-hatch to identify and exploit brood habitats with the potential that such movements could increase predation risk (Mainguy et al. 2006*b*). For many species, broods are conferred greater survival probabilities if they maintain smaller ranges during early brood development (Park et al. 2001), attributable to hatchlings maximizing growth while reducing predation risk (Mainguy et al. 2006*a*). Godfrey and Norman (1999) reported that brood movements failed to influence survival of individual poults, but we observed that brood survival was negatively influenced by increased daily movements within the first 3 days after hatching. Similarly, Erikstad (1985) reported reduced survival in willow ptarmigan broods that maintained larger ranges and moved greater distances, and similar relationships have been observed for ring-necked pheasant (*Phasianus colchicus*; Hill 1985), red grouse (*Lagopus lagopus scotica*; Park et al. 2001), and northern bobwhite (*Colinus virginianus*; Kamps et al. 2017). In precocial birds, increased daily movements initially after hatching can result in reduced time spent foraging and brooding (Erikstad and Spidsø 1982), increased predation and abandonment (Leonard et al. 1996, Goddard and Dawson 2009), and increased energy demands (Mendenhall and Milne 1985). Active small-bodied birds require more energy than active large-bodied birds, and require more energy relative to body size during periods of heightened activity (Bennett and Harvey 1987). Wild turkey poults and similar precocial hatchlings require consistent forage intake with minimal energy expenditure for days after hatching (Healy 1985); hence, it is logical that stressors associated with increased daily movements within 3 days of hatching would negatively influence brood survival.

Precocial chicks develop the ability to forage quickly after hatching, which places high energetic demands on broods while they locate and exploit foraging areas (Starck and Ricklefs 1998, Schekkerman et al. 2001). Likewise, differences in allometric scaling between brooding females and newly hatched young creates challenges for broods, requiring access to abundant high energy foods that are easily secured by rapidly developing young (Teather and Weatherhead 1994). Healy (1992) noted that wild turkeys poults were capable of leaving the nest within hours of
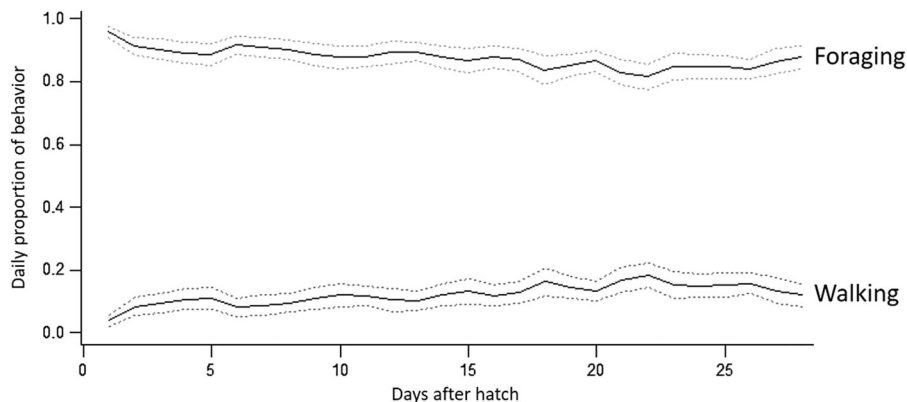
Figure 5. Predicted probability of eastern wild turkey broods engaging in walking and foraging behavior (solid line) ± standard error (dotted line) during 28 days after hatching across multiple study sites in the southeastern United States, 2014–2019.
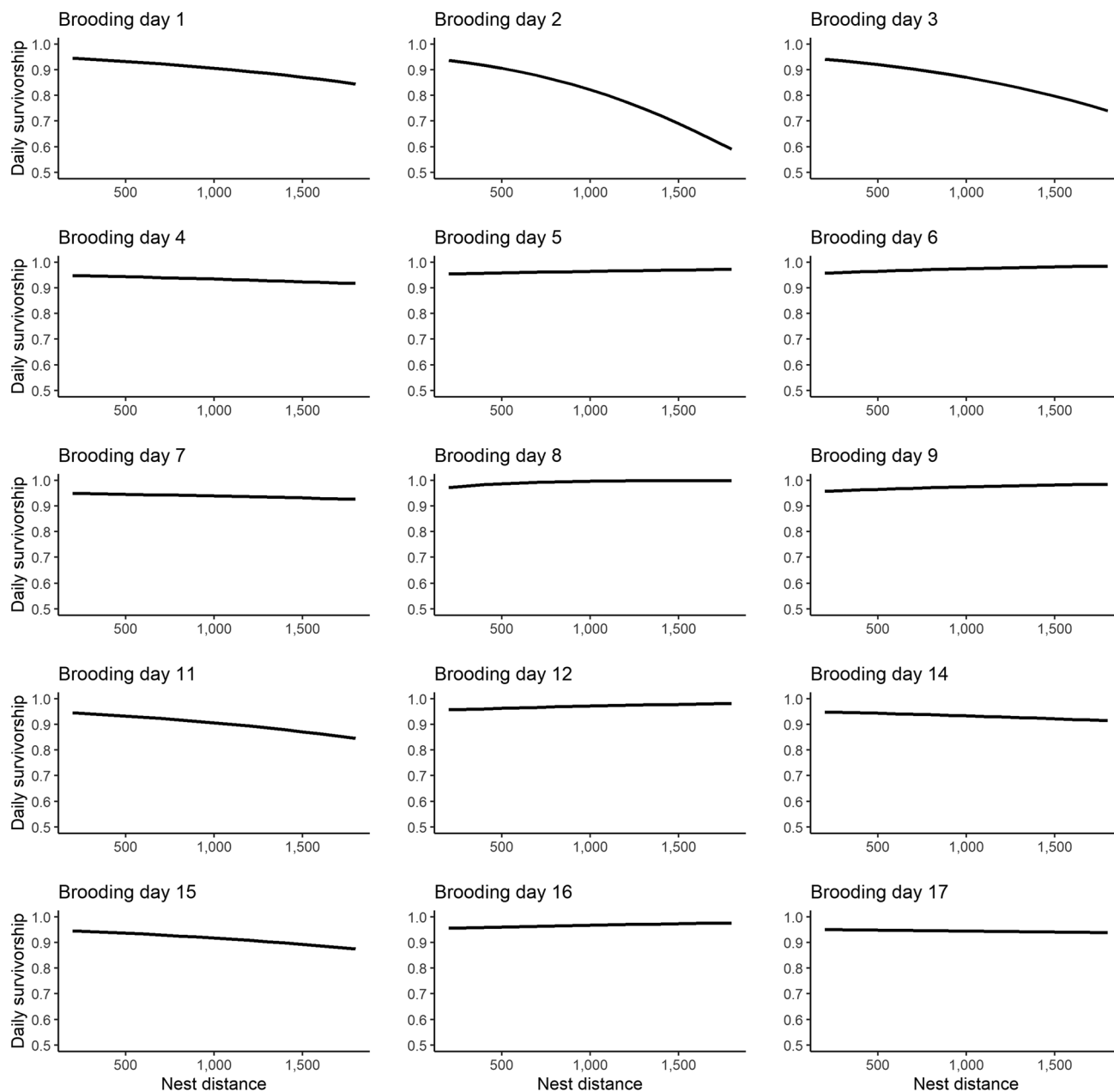
Figure 6. Predicted daily survival rate of eastern wild turkey broods relative to distance (m) from the nests from which they were hatched throughout the first 17 days after hatching across multiple study sites in the southeastern United States, 2014–2019. Day 10 and 13 had no events and were fixed at 1 for analysis.

hatching, could walk with brooding females at a normal pace within hours of leaving the nest, and traveled 200 m/hour while foraging. We categorized brood movements into 2 behavioral states and found that broods spent considerable time in a foraging state. Broods in the behavioral state we classified as walking moved an average hourly distance of approximately 200 m. Therefore, we recognize that broods classified as walking could have also been foraging, consistent with observations of imprinted poults that foraged constantly when active (Healy 1992). Regardless, our findings suggest that wild turkey broods exhibit extended periods of behavior reflective of area-restricted searching or loafing, which has been reported previously

(Williams et al. 1970). We suspect that extended bouts of movements mimicking area-restricted searching were reflective of concentrated foraging in areas with available prey resources (Kareiva and Odell 1987) because wild turkey poults require nearly constant food intake (Healy 1985), whereas periods of loafing and self-maintenance are less pronounced within daily activity budgets (Healy 1992).

After hatching, female Galliformes typically move broods away from nest sites presumably to locate secure foraging areas and reduce predation risk (Rumble and Anderson 1996, Signorelli et al. 2010). In wild turkeys, until poults are flighted they brood at night under females at ground roosts, which are often located in areas offering concealment

Table 2. Parameter estimates for the best-supported model including a time-dependent effect of daily distance from nests on daily survival of eastern wild turkey broods during the first 17 days after hatching and a constant parameter for days 18–28 on multiple study sites in the southeastern United States, 2014–2019. We fixed parameters for days 10 and 13 because both parameters were non-identifiable given our data, and could not be estimated via standard maximum likelihood estimation or data cloning with profile likelihood confidence intervals.

Parameter	β	SE
Intercept	2.9923	0.26339
β (day 1)	−0.0072	0.00356
β (day 2)	−0.0014	0.00465
β (day 3)	−0.0010	0.00391
β (day 4)	−0.0032	0.00428
β (day 5)	0.0032	0.00635
β (day 6)	0.0069	0.00801
β (day 7)	−0.0024	0.00408
β (day 8)	0.0027	0.00274
β (day 9)	0.0068	0.00774
β (day 10)	Fixed	
β (day 11)	−0.0071	0.00262
β (day 12)	0.0055	0.00732
β (day 13)	Fixed	
β (day 14)	−0.0034	0.00424
β (day 15)	−0.0058	0.00403
β (day 16)	0.0040	0.00770
β (day 17)	−0.0014	0.00473
β (days 18–28)	5.1474	0.70915

(Lehman et al. 2010, Streich et al. 2015). We found that after hatching, initial ground roosts were approximately 200 m from nest sites, and thereafter were typically separated by 300 m on consecutive nights. Previous authors have reported similar distances to first roost sites, although these distances may be variable (Williams et al. 1970, Hon et al. 1978). Furthermore, Barwick et al. (1970) observed that wild turkey broods did not return to roosts on consecutive nights but instead aggregated roost sites within portions of their range. Contemporary literature has noted that male wild turkeys exhibit low fidelity to roost sites, instead using a strategy of roosting in different parts of their ranges on consecutive nights (Byrne et al. 2015b, Wakefield et al. 2020). Roost lability may be influenced by many factors, including predator avoidance, disturbance, microclimate, and the need to locate near foraging areas (Lewis 1996, Béchet et al. 2010). Regardless, we offer that roost lability is likely an important aspect of eastern wild turkey ecology designed to minimize predation risk in landscapes where available roosts are widespread, consistent with other species that distribute roost sites throughout their ranges (Lewis 1995).

MANAGEMENT IMPLICATIONS

Our results are relevant to managers of forested landscapes throughout the range of the eastern wild turkey. We observed that wild turkey broods extensively selected open, treeless land cover types while also exhibiting plasticity in habitat selection as they aged. We recommend managers in forest-dominated landscapes consider strategies to maintain and enhance open, treeless areas, primarily through efforts to promote early successional vegetation communities. These strategies could include various forms of disturbance (e.g., prescribed fire, mechanical techniques) that enhance early successional vegetation. Likewise, our findings suggest that as broods age, diversity of cover types within their daily ranges become increasingly more important. Therefore, we recommend managers consider the importance of maintaining diverse cover types in pine-dominated forests, such as hardwood and mixed pine-hardwood forests. Our results indicate that greater movements away from nest sites within 3 days after hatching contributes to reduced brood survival, and presumably females exhibit such movements to locate and exploit areas they perceive as offering foraging opportunities while minimizing predation risk. We recommend that managers seek ways of ensuring that areas offering nesting cover be juxtaposed to open, treeless areas selected by broods during the initial 3 days after hatching. On average broods moved approximately 800 m away from nest sites within 3 days of hatching; therefore, juxtaposing nesting cover <800 m to open, treeless cover types is warranted.

LITERATURE CITED

Abrams, P. A. 1984. Foraging time optimization and interactions in food webs. American Naturalist 124:80–96.

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Barron, D. G., J. D. Brawn, and P. J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods in Ecology and Evolution 1:180–187.

Barwick, L. H., D. H. Austin, and L. E. Williams, Jr. 1970. Roosting of young turkey broods during summer in Florida. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 25:231–243.

Barwick, L. H., W. M. Hetrick, and L. E. Williams, Jr. 1973. Foods of young Florida wild turkeys. Proceedings of the Southeastern Association of Game and Fish Commissioners 27:92–102.

Béchet, A., J. F. Giroux, G. Gauthier, and M. Bélisle. 2010. Why roost in the same place? Exploring short-term fidelity in staging snow geese. Condor 112:294–303.

Bennett, P. M., and P. H. Harvey. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. Journal of Zoology 213:327–344.

Bishop, C. J., G. C. White, and P. M. Lukacs. 2008. Evaluating dependence among mule deer siblings in fetal and neonatal survival analysis. Journal of Wildlife Management 72:1085–1093.

Blackburn, W. E., J. P. Kirk, and J. E. Kennamer. 1975. Availability and utilization of summer foods by eastern wild turkey broods in Lee County, Alabama. National Wild Turkey Symposium 3:86–96.

Bowling, A. C., C. J. Parent, M. V. Schiavone, D. M. Williams, W. F. Porter, and B. L. Swift. 2015. Brooding over broods: regional impacts of habitat quality on wild turkey productivity. National Wild Turkey Symposium 11:315–328.

Burk, J. D., D. R. Smith, G. A. Hurst, B. D. Leopold, and M. M. Melchoirs. 1990. Wild turkey use of loblolly pine plantations for nesting and brood rearing. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 44:163–170.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Byrne, M. E., M. J. Chamberlain, and B. A. Collier. 2015a. Potential density dependence in wild turkey productivity in the southeastern United States. National Wild Turkey Symposium 11:329–351.

Byrne, M. E., B. A. Collier, and M. J. Chamberlain. 2015b. Roosting behavior of male eastern and Rio Grande wild turkeys. National Wild Turkey Symposium 11:175–185.

Campbell, E. W., A. A. Yackel Adams, S. J. Converse, T. H. Fritts, and G. H. Rodda. 2012. Do predators control prey species abundance? An experimental test with brown treesnakes on Guam. Ecology 93:1194–1203.

Cohen, B. S., T. J. Prebyl, B. A. Collier, and M. J. Chamberlain. 2018. Home range estimator method and GPS fix schedule affect selection inferences for wild turkeys. Wildlife Society Bulletin 42:150–159.

Collier, B. A., and M. J. Chamberlain. 2011. Redirecting research for wild turkeys using global positioning system transmitters. National Wild Turkey Symposium 10:81–92.

Collier, B. A., K. B. Melton, J. B. Hardin, N. J. Silvy, and M. J. Peterson. 2009. Impact of reproductive effort on survival of Rio Grande wild turkey *Meleagris gallopavo intermedia* hens in Texas. Wildlife Biology 15:370–379.

Conley, M., N. Yeldell, M. J. Chamberlain, and B. A. Collier. 2016. Do movement behaviors identify reproductive habitat sampling for wild turkeys? Ecology and Evolution 6:7103–7112.

Cooke, S. J. 2008. Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. Endangered Species Research 4:165–185.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Eriksen, R. E., T. A. Brown, K. B. Scott, T. W. Hughes, M. D. Akridge, and C. S. Penner. 2015. Status and distribution of wild turkeys in the United States: 2014 status. National Wild Turkey Symposium 11:7–18.

Erikstad, K. E. 1985. Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. Ornis Scandinavica 16:181–190.

Erikstad, K. E., and T. K. Spidsø. 1982. The influence of weather on food intake, insect prey selection, and feeding behaviour in willow grouse chicks in northern Norway. Ornis Scandinavica 13:176–182.

Fontaine, J. J., and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters 9:428–434.

Franklin, A. B. 2001. Exploring ecological relationships in survival and estimating rates of population change using program MARK. Pages 290–296 in R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. Wildlife, land, and people: priorities for the 21st century. The Wildlife Society, Bethesda, Maryland, USA.

Goddard, A. D., and R. D. Dawson. 2009. Factors influencing the survival of neonate sharp—tailed grouse *Tympanuchus phasianellus*. Wildlife Biology 15:60–67.

Godfrey, C. L., and G. W. Norman. 1999. Effect of habitat and movement on wild turkey poult survival. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 53:330–339.

Gurarie, E. 2014. bcpa: behavioral change point analysis of animal movement. https://CRAN.R-project.org/package=bcpa. Accessed 1 Jul 2019.

Gurarie, E., R. D. Andrews, and K. L. Laidre. 2009. A novel method for identifying behavioural changes in animal movement data. Ecology Letters 12:395–408.

Gurarie, E., C. Bracis, M. Delgado, T. D. Meckley, I. Kojola, and C. M. Wagner. 2016. What is the animal doing? Tools for exploring behavioural structure in animal movements. Journal of Animal Ecology 85:69–84.

Guthrie, J. D., M. E. Byrne, J. B. Hardin, C. O. Kochanny, K. L. Skow, R. T. Snelgrove, M. J. Butler, M. J. Peterson, M. J. Chamberlain, and B. A. Collier. 2011. Evaluation of a global positioning system backpack transmitter for wild turkey research. Journal of Wildlife Management 75:539–547.

Hamrick, W. J., and J. R. Davis. 1971. Summer food items of juvenile wild turkeys. Proceedings of the Southeastern Association of Game and Fish Commissioners 25:85–89.

Hartigan, J. A., and M. A. Wong. 1979. Algorithm AS 136: A k-means clustering algorithm. Applied Statistics 28:100–108.

Healy, W. M. 1978. Feeding activity of wild turkey poults in relation to ground vegetation and insect abundance. Dissertation, West Virginia University, Morgantown, USA.

Healy, W. M. 1985. Turkey poult feeding activity, invertebrate abundance, and vegetation structure. Journal of Wildlife Management 49:466–472.

Healy, W. M. 1992. Behavior. Pages 46–65 in J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Healy, W. M., R. O. Kimmel, and E. J. Goetz. 1975. Behavior of human-imprinted and hen-reared wild turkey poults. National Wild Turkey Symposium 3:97–107.

Hennig, C. 2019. fpc: flexible procedures for clustering. https://CRAN.R-project.org/package=fpc. Accessed 1 Jul 2019.

Hill, D. A. 1985. The feeding ecology and survival of pheasant chicks on arable farmland. Journal of Applied Ecology 22:645–654.

Hillestad, H. O., and D. W. Speake. 1970. Activities of wild turkey hens and poults as influenced by habitat. Proceedings of the Southeastern Association of Game and Fish Commissioners 24:244–251.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Hon, T., D. P. Belcher, B. Mullis, and J. R. Monroe. 1978. Nesting, brood range, and reproductive success of an insular turkey population. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 32:137–149.

Hubbard, M. W., D. L. Garner, and E. E. Klaas. 1999. Wild turkey poult survival in south-central Iowa. Journal of Wildlife Management 63:1999–203.

Hulbert, I. A. R. 2001. GPS and its use in animal telemetry: the next five years. Pages 69–72 in A. M. Sibbald and I. J. Gordon, editors. Tracking animals with GPS. The Macaulay Land Use Research Institute, Aberdeen, United Kingdom.

Hurst, G. A. 1992. Foods and feeding. Pages 66–83 in J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Hurst, G. A., and B. D. Stringer. 1975. Food habits of wild turkey poults in Mississippi. National Wild Turkey Symposium 3:76–85.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, B. C., J. E. Inglis, and G. A. Hurst. 2005. Wild turkey brood habitat use in relation to prescribed burning and red-cockaded woodpecker management. National Wild Turkey Symposium 9:209–215.

Kamps, J. T., W. E. Palmer, T. M. Terhune, G. Hagan, and J. A. Martin. 2017. Effects of fire management on northern bobwhite brood ecology. European Journal of Wildlife Research 63:27.

Kareiva, P., and G. Odell. 1987. Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. American Naturalist 130:223–270.

Keegan, T. W., and J. A. Crawford. 1997. Brood-rearing habitat use by Rio Grande wild turkeys in Oregon. Great Basin Naturalist 57:220–230.

Kennamer, J. E., M. C. Kennamer, and R. Brenneman. 1992. History. Pages 6–17 in J. G. Dickson, editor. The wild turkey: biology and management. Stackpole, Mechanicsburg, Pennsylvania, USA.

Kranstauber, B., R. Kays, S. D. LaPoint, M. Wikelski, and K. Safi. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. Journal of Animal Ecology 81:738–746.

Kranstauber, B., M. Smolla, and A. K. Scharf. 2018. Package 'move': visualizing and analyzing animal track data. <http://computational-ecology.com/main-move.html> Accessed 8 Aug 2018.

Krzanowski, W. J., and Y. Lai. 1988. A criterion for determining the number of groups in a data set using sum-of-squares clustering. Biometrics 44:23–34.

Lehman, C. P., D. J. Thompson, and M. A. Rumble. 2010. Ground roost resource selection for Merriam's wild turkeys. Journal of Wildlife Management 74:295–299.

Leonard, J. P., M. G. Anderson, H. H. Prince, and R. B. Emery. 1996. Survival and movements of canvasback ducklings. Journal of Wildlife Management 60:863–874.

Lewis, S. E. 1995. Roost fidelity of bats: a review. Journal of Mammalogy 76:481–496.

Lewis, S. E. 1996. Low roost-site fidelity in pallid bats: associated factors and effect on group stability. Behavioral Ecology and Sociobiology 39:335–344.

Little, A. R., M. M. Streich, M. J. Chamberlain, L. M. Conner, and R. J. Warren. 2014. Eastern wild turkey reproductive ecology in frequently-burned longleaf pine savannas. Forest Ecology and Management 331:180–187.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2018. cluster: cluster analysis basics and extensions. https://cran.r-project.org/web/packages/cluster/cluster.pdf. Accessed 1 Jul 2019.

Mainguy, J., G. Gauthier, J. F. Giroux, and J. Bêty. 2006a. Gosling growth and survival in relation to brood movements in greater snow geese (*Chen caerulescens atlantica*). Auk 123:1077–1089.

Mainguy, J., G. Gauthier, J. F. Giroux, and I. Duclos. 2006b. Habitat use and behaviour of greater snow geese during movements from nesting to brood-rearing areas. Canadian Journal of Zoology 84:1096–1103.

Mendenhall, V. M., and H. Milne. 1985. Factors affecting duckling survival of eiders *Somateria mollissima* in northeast Scotland. Ibis 127:148–158.

Metzler, R., and D. W. Speake. 1985. Wild turkey poult mortality rates and their relationship to brood habitat structure in northeast Alabama. National Wild Turkey Symposium 5:103–111.

Miller, D. A., B. D. Leopold, and G. A. Hurst. 1997. Seasonal home ranges of wild turkeys in central Mississippi. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 51:414–425.

Mong, T. W., and B. K. Sandercock. 2007. Optimizing radio retention and minimizing radio impacts in a field study of upland sandpipers. Journal of Wildlife Management 71:971–980.

Morgan, J. J., and S. H. Schweitzer. 2001. Eastern wild turkey hatching two clutches during the same breeding season. Wilson Bulletin 113:335–337.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29–S49.

Park, K. J., P. A. Robertson, S. T. Campbell, and R. Foster. 2001. The role of invertebrates in the diet, growth, and survival of red grouse (*Lagopus lagopus scoticus*) chicks. Journal of Zoology 254:137–145.

Pelham, P. H., and J. G. Dickson. 1992. Physical characteristics. Pages 32–45 *in* J. G. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Peoples, J. C., D. C. Sisson, and D. W. Speake. 1995. Mortality of wild turkey poults in coastal plain forests. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 49:448–453.

Phalen, P. S., G. A. Hurst, and W. J. Hamrick. 1986. Brood habitat use and preference by wild turkeys in central Mississippi. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 40:397–404.

Porter, W. F. 1977. Home range dynamics of wild turkeys in southeastern Minnesota. Journal of Wildlife Management 41:434–437.

Porter, W. F. 1980. An evaluation of wild turkey brood habitat in southeastern Minnesota. National Wild Turkey Symposium 4:203–212.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. Journal of Wildlife Management 73:345–356.

R Core Team. 2019. R: a language and environment for statistical computing. Version 3.6.1. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, S. D., and W. F. Porter. 1998. Influence of temperature and precipitation on survival of wild turkey poults. Journal of Wildlife Management 62:1499–1505.

Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. American Naturalist 137:S5–S28.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recent developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.

Rumble, M. A. 1992. Roosting habitat of Merriam's turkeys in Black Hills, South Dakota. Journal of Wildlife Management 56:750–759.

Rumble, M. A., and S. H. Anderson. 1996. Feeding ecology of Merriam's turkeys (*Meleagris gallopavo merriami*) in the Black Hills, South Dakota. American Midland Naturalist 136:157–171.

Schekkerman, H., G. H. Visser, and C. Blem. 2001. Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. Auk 118:944–957.

Signorelli, N., S. Wirthner, P. Patthey, R. Schranz, L. Rotelli, and R. Arlettaz. 2010. Concealment from predators drives foraging habitat selection in brood-rearing Alpine black grouse *Tetrao tetrix* hens: habitat management implications. Wildlife Biology 16:249–257.

Sisson, D. C., and D. W. Speake. 1994. Spring burning for wild turkey brood habitat: an evaluation. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 48:134–139.

Sisson, D. C., D. W. Speake, and J. L. Landers. 1991a. Wild turkey brood habitat use in fire-type pine forests. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 45:49–57.

Sisson, D. C., D. W. Speake, and J. T. Landers. 1991b. An incidence of second brood production by an Eastern wild turkey. Wilson Bulletin 103:303–305.

Speake, D. W., T. E. Lynch, W. J. Fleming, G. A. Wright, and W. J. Hamrick. 1975. Habitat use and seasonal movements of wild turkeys in the southeast. National Wild Turkey Symposium 3:122–129.

Spears, B. L., M. C. Wallace, W. B. Ballard, R. S. Phillips, D. P. Holdstock, J. H. Brunjes, R. Applegate, M. S. Miller, and P. S. Gipson. 2007. Habitat use and survival of preflight wild turkey broods. Journal of Wildlife Management 71:69–81.

Starck, J. M., and R. E. Ricklefs. 1998. Avian growth and development: evolution within the altricial-precocial spectrum. Oxford University Press, New York, New York, USA.

Storch, I. 1994. Habitat and survival of Capercaillie *Tetrao urogallus* nests and broods in the Bavarian Alps. Biological Conservation 70:237–243.

Streich, M. M., A. R. Little, M. J. Chamberlain, L. M. Conner, and R. J. Warren. 2015. Habitat characteristics of eastern wild turkey nest and ground-roost sites in 2 longleaf pine forests. Journal of the Southeastern Association of Fish and Wildlife Agencies 2:164–170.

Tapley, J. L., R. K. Abernethy, M. Hatfield, and J. E. Kennamer. 2011. Status and distribution of the wild turkey in 2009. National Wild Turkey Symposium 10:19–30.

Teather, K. L., and P. J. Weatherhead. 1994. Allometry, adaptation, and the growth and development of sexually dimorphic birds. Oikos 71:515–525.

Thomson, R. L., J. T. Forsman, F. Sarda-Palomera, and M. Mőnkkőnen. 2006. Fear factor: prey habitat selection and its consequences in a predation risk landscape. Ecography 29:507–514.

Wakefield, C., J. A. Martin, P. H. Wightman, B. T. Bond, D. K. Lowery, B. S. Cohen, B. A. Collier, and M. J. Chamberlain. 2020. Hunting activity effects on roost selection by male wild turkeys. Journal of Wildlife Management 84:458–467.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Supplement 46:120–138.

Wightman, P. H., J. C. Kilgo, M. Vukovich, J. R. Cantrell, C. R. Ruth, B. S. Cohen, M. J. Chamberlain, and B. A. Collier. 2019. Gobbling chronology of Eastern wild turkeys in South Carolina. Journal of Wildlife Management 83:325–333.

Williams, L. E. 1974. Flight attainment in wild turkeys. Journal of Wildlife Management 38:151–152.

Williams, L. E., and D. H. Austin. 1988. Studies of the wild turkey in Florida. University of Florida Press, Gainesville, USA.

Williams, L. E., D. H. Austin, T. E. Peoples, and R. W. Phillips. 1970. Observations on movement, behavior, and development of turkey broods. National Wild Turkey Symposium 2:79–99.

Williams, M. W., D. B. Gibbs, T. H. Robert, and D. L. Combs. 1997. Habitat use by eastern wild turkey broods in Tennessee. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 51:457–466.

Wilson, S., K. Martin, and S. J. Hannon. 2007. Nest survival patterns in willow ptarmigan: influence of time, nesting stage, and female characteristics. Condor 109:377–388.

Wood, J. W., B. S. Cohen, L. M. Conner, B. A. Collier, and M. J. Chamberlain. 2019. Nest and brood site selection of eastern wild turkeys. Journal of Wildlife Management 83:192–204.

Wunz, G. A., and J. C. Pack. 1992. Eastern turkey in eastern oak–hickory and northern hardwood forests. Pages 232–264 *in* J. G. Dickson, editor. The wild turkey: biology and mangement. Stackpole, Mechanicsburg, Pennsylvania, USA.

Yeldell, N. A., B. S. Cohen, A. R. Little, B. A. Collier, and M. J. Chamberlain. 2017*a*. Nest site selection and nest survival of eastern wild turkeys in a pyric landscape. Journal of Wildlife Management 18:1073–1083.

Yeldell, N. A., B. S. Cohen, T. J. Prebyl, B. A. Collier, and M. J. Chamberlain. 2017*b*. Use of pine-dominated forests by female eastern wild turkeys immediately after prescribed fire. Forest Ecology and Management 398:226–234.

Zhang, J., K. M. O'Reilly, G. L. W. Perry, G. A. Taylor, and T. E. Dennis. 2015. Extending the functionality of behavioural change-point analysis with *k*-means clustering: a case study with the little penguin (*Eudyptula minor*). PLoS ONE 10:e0122811.

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