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Fine-scale resource selection and behavioral tradeoffs of eastern wild turkey broods

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Abstract

Resource heterogeneity across the landscape prompts animals to make behavioral tradeoffs to survive and reproduce. Behavioral thermoregulation can buffer organisms from thermal extremes but may conflict with other essential activities such as predator avoidance or foraging, and necessitate tradeoffs among resource requirements. We evaluated patterns of habitat selection relative to thermal conditions, forage availability, and concealment cover for female eastern wild turkeys (*Meleagris gallopavo silvestris*) with broods to assess potential tradeoffs among resource requirements. We quantified air temperature (°C), vegetation characteristics (e.g., visual obstruction), and arthropod biomass (g/m^2) at locations used by broods across 5 study sites in the southeastern United States during May–July 2019–2020. We used conditional logistic regression to estimate brooding female resource selection at the second (home range) and third (within home range) orders. Specifically, we identified differences in selection between brooding and non-brooding females (second order), and factors influencing selection of sites used by brooding females during the day (when loafing and foraging) and night (roosting; third order). Brooding females selected sites with cooler temperatures (β = −0.22; 95% CI = −0.338−−0.102) and greater ground cover vegetation (β = 0.02; 95% CI = 0.013−0.033) than non-brooding females. Additionally, biomass of large prey (Orthoptera) was positively

related to ambient temperature, suggesting that use of thermal refuge by brooding females may limit availability of large prey. Brooding females appeared to balance the tradeoff between thermal refuge and forage availability by altering habitat selection patterns within home ranges. Brooding females selected for herbaceous areas that provided greater biomass of large arthropods during the day, and avoided areas dominated by woody vegetation during both the day and night. We did not observe brooding females using locations where woody cover exceeded 27% of understory vegetation. Thermal refuge is an important component of brood habitat, but within thermally suitable areas brooding females can select sites with greater availability of large prey to meet energetic demands of broods. Evaluation of multiple spatial scales is key when assessing tradeoffs among resource needs and determining the potential of behavioral thermoregulation to buffer an organism's thermal environment and allow persistence in a warming climate.

Spatiotemporal heterogeneity in resource distribution across a landscape forces animals to make behavioral tradeoffs to maintain fitness (Nonacs and Dill 1990, Pecor and Hazlett 2005, Zub et al. 2009). Behavioral tradeoffs can be influenced by energetic expenditures, forage availability, predation risk, and environmental stressors (Schradin et al. 2010, Pollentier et al. 2017, Gaynor et al. 2019) but are predicated on meeting resource requirements (Nonacs and Dill 1990, McShea 2000, Verdolin 2006). Resource requirements vary spatially and temporally based on individual phenology, which in turn affects resource selection (Nedergaard et al. 1990, Parrish 2000, Yeldell et al. 2017b) and the scale of selection (McShea 2000, Davis et al. 2014). For instance, reproductive phenology may influence the relative value of different vegetation characteristics for the individual; females raising offspring are often limited in mobility and may value vegetation structure with more cover to reduce predation risk (Benson and Chamberlain 2007, Pearson and Knapp 2016), whereas non-reproductively active females may value vegetation with greater forage availability (Smereka et al. 2020). Thus, the value of vegetation characteristics may vary based on phenology, resulting in different resource selection patterns and tradeoffs (Blomberg et al. 2013, Gibson et al. 2016).

In addition to vegetation-driven tradeoffs, variation in abiotic conditions can influence the distribution and behavior of a species (Sims et al. 2004, Londe et al. 2021). For example, when local thermal conditions exceed internal individual body temperature, accumulated heat loads must be dissipated via behavioral or physiological mechanisms (Scheffers et al. 2014; Smith et al. 2015, 2017). Despite the value of thermoregulatory behaviors in maintaining body temperature (Broders et al. 2012, Martin et al. 2015, Londe et al. 2021), thermoregulation may conflict with other essential activities such as predator avoidance or foraging, thereby necessitating tradeoffs amongst resource requirements (Aublet et al. 2009, Cunningham et al. 2015, Edwards et al. 2015). Specifically,

foraging efficiency may decrease under extreme temperature conditions, which can negatively affect body mass, growth, and fitness (du Plessis et al. 2012, van de Ven et al. 2019). As climate change is predicted to increase temperatures in many regions (Intergovernmental Panel on Climate Change 2013), tradeoffs between foraging and thermoregulation may become more important to fine- and large-scale distribution and demographics as animals alter thermoregulatory behaviors.

Eastern wild turkeys (*Meleagris gallopavo silvestris*; turkeys) across the southeastern United States are experiencing declines in productivity and poult recruitment (Byrne et al. 2015). Declines in recruitment have drawn attention to the availability and composition of quality brooding habitat (Byrne et al. 2015, Eriksen et al. 2015). After hatching, poults are flightless for 2 weeks and brood on the ground (Williams 1974). During this 2-week flightless period, broods suffer high predation rates (Hubbard et al. 1999, Spears et al. 2007). Turkey poults are also vulnerable to exposure because they are poor thermoregulators in the first weeks of life owing to their incomplete feather and physiological development (Dickson 1992). Brood habitat is typically characterized by early successional vegetation communities that provide foraging opportunities and concealment cover (Metzler and Speake 1985, Porter 1992, Spears et al. 2007), and areas with increased herbaceous cover may be associated with increased brood survival (Metzler and Speake 1985, Spears et al. 2007).

Arthropod abundance is an important component of brood habitat, but there remains ambiguity as to the importance of total arthropod versus larger-bodied arthropod availability (Healy 1985). To facilitate rapid growth and feather development, poults depend on protein-rich invertebrates (Hamrick and Davis 1971, Hurst 1978, Chitwood et al. 2017) such as Orders Orthoptera, Hymenoptera, Coleoptera, and Araneae (Iglay et al. 2005, McCord et al. 2014) and spend most of the day foraging (Chamberlain et al. 2020). The breeding currency hypothesis (Greenberg 1995) posits avian habitat selection is a function of large-bodied arthropod abundance when a high-protein diet is required because large-bodied arthropods are seasonally limited and highly profitable, suggesting that a subsection of available large-bodied arthropod taxa would be most important to poults. In contrast, Healy (1985) suggested that total arthropod availability, particularly of small arthropods, would be more important to poults than fewer larger arthropod food items.

Understory vegetation is important for providing concealment cover from visual predators and foraging opportunities for poults (Randell 2003, Backs and Bledsoe 2011). The value of vegetation is likely distinguishable by birds at 2 scales (Reiley and Benson 2019): a coarser scale where overall 3-dimensional structure provides cover in the form of concealment and shade (Rakowski et al. 2019), and a finer scale where species-specific understory communities affect locomotion and forage (Healy 1985, McCord et al. 2014). Therefore, habitat selection of turkey broods may be affected by vegetation structure and composition but also availability of thermal refuge and arthropods; however, an optimal combination of these features may not concurrently occur at sites across the southeastern United States. For example, open herbaceous landscapes may have high arthropod abundances (Hamrick and Davis 1971, Healy 1985, Backs and Bledsoe 2011) but could be prohibitively warm (Carroll et al. 2018, Rakowski et al. 2019). Forested sites could be thermally suitable (Rakowski et al. 2019) but with greater meso-mammal predator densities (Chamberlain et al. 2003, Godbois et al. 2003) and lower arthropod availabilities (Backs and Bledsoe 2011).

We monitored brooding and non-brooding female turkeys during May–July when peaks in brooding activity occur across our study populations (Chamberlain et al. 2020) to identify habitat selection and evaluate behavioral tradeoffs by turkey broods. Specifically, our objectives were to evaluate influence of temperature, arthropod biomass, and vegetation on site selection by brooding females; compare selection between brooding and non-brooding females; and determine the relative importance of thermal conditions, forage availability, and concealment cover in habitat selection to understand potential behavioral tradeoffs in resource selection. We hypothesized that brood site selection was influenced by temperature, arthropod biomass, and vegetation. We predicted that brooding females would select sites with cooler thermal profiles during the day when temperatures peak, but because of mild temperatures at night brooding females would be indifferent to temperature when selecting roost sites. Similarly, we predicted that brooding females would select sites with greater arthropod biomass during the

day to meet energetic demands for growth (Healy 1985, Lafon et al. 2001, Backs and Bledsoe 2011), but arthropod biomass would not influence selection of roost sites. Lastly, we predicted that brooding females would select sites with greater herbaceous vegetation and less woody vegetation. We hypothesized that selection would differ based on reproductive phenology, and predicted that brooding females would select cooler sites than non-brooding females. Because the use of thermal cover may limit access to food or reduce foraging efficiency (Beever et al. 2017), we hypothesized there would be a tradeoff between forage availability and thermal refuge. We predicted that brooding females would prioritize selection of sites with cooler temperatures over sites that provide greater available forage or cover resources.

STUDY AREA

We conducted research on 5 study sites across Georgia and Louisiana, USA (Figure 1) in 2019–2020. Mean daytime temperature during 30 April–31 July averaged 25.9°C (range = 13–37.5°C) across our study areas based on data collected as detailed herein. We conducted research on B. F. Grant Wildlife Management Area (WMA) and Cedar Creek WMA in Georgia. The B. F. Grant WMA, a 4,613-ha area located in Putnam County, Georgia, was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia (UGA) and managed cooperatively with the Georgia Department of Natural Resources (GADNR) Wildlife Resources Division. The property consisted of managed forest, predominately loblolly pine (*Pinus taeda*) and mixed hardwood pine forests (*Pinus* spp.), and experimental agricultural grazing land for livestock. The understory was dominated by eastern redbud (*Cercis canadensis*), sweet gum (*Liquidambar styraciflua*), muscadine (*Vitis rotundifolia*), and briars (*Rubus* spp.). Cedar Creek WMA was 16,187 ha located in Jasper, Jones, and Putnam counties, Georgia. Cedar Creek WMA was owned by the United States Forest Service (USFS) and managed in partnership with GADNR. The Cedar Creek WMA study site also included adjacent private property where a majority of broods were raised. The site was composed of loblolly pine forests and mixed hardwood pine forests with similar understory composition to B. F. Grant WMA. Forest management on both sites was primarily through patch cuts, thinning, and prescribed fire
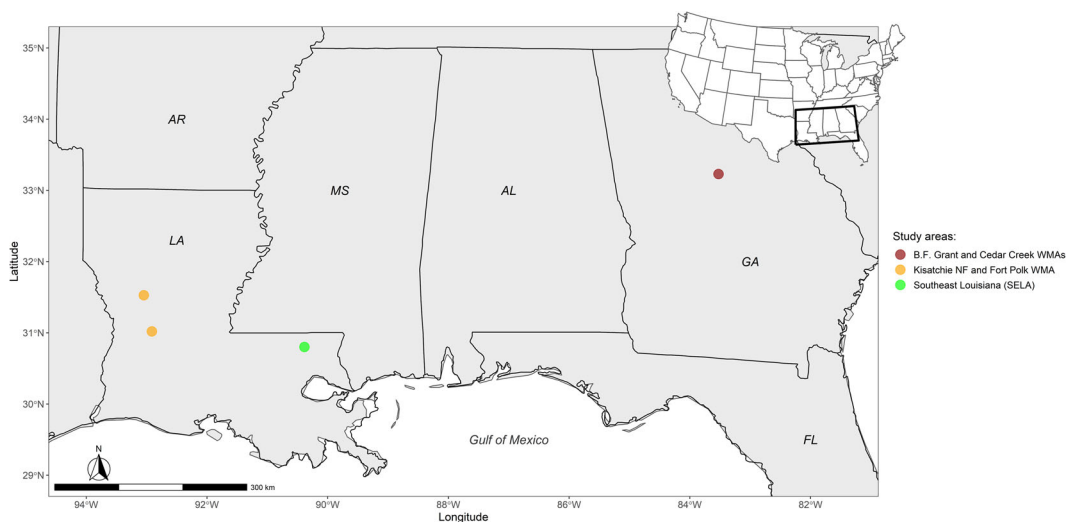
FIGURE 1 Study areas where we monitored eastern wild turkey brooding and non-brooding females and sampled temperature, arthropod biomass, and vegetation metrics, Georgia and Louisiana, USA, May–July 2019–2020. Study areas included B. F. Grant Wildlife Management Area (WMA), Cedar Creek WMA, southeast Louisiana (SELA), Kisatchie National Forest (NF) and Fort Polk WMA.

applied on an approximately 3–5-year rotation. Areas surrounding B. F. Grant and Cedar Creek WMAs were predominately pine forests and agricultural fields for livestock, and average elevation was 520 m (https://weatherspark.com/, accessed 15 Oct 2019). The climate for B. F. Grant and Cedar Creek WMAs was characterized by hot, dry summers and cool, wet winters. Wakefield et al. (2020) provide a detailed description of B. F. Grant and Cedar Creek WMAs.

We also conducted research on the Kisatchie National Forest (KNF) and Fort Polk WMA in west-central Louisiana. The KNF was divided into 5 districts encompassing over 244,000 ha in Rapides, Vernon, Grant, Winn, Natchitoches, Webster, and Claiborne parishes, and was owned and managed by the USFS. Fort Polk WMA was located in Vernon Parish and jointly owned by the USFS (39,710 ha within KNF) and the United States Army (managed 40,000 ha of land). Both sites were composed of pine-dominated forests, hardwood riparian zones, and forested wetlands, with forest openings, utility rights-of-way, and forest roads distributed throughout. Average elevation for KNF and Fort Polk WMA was 60 m. The understory of KNF and Fort Polk WMA was dominated by yaupon (*Ilex vomitoria*), American beautyberry (*Callicarpa americana*), blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), wild grape (*Vitis* spp.), and woodoats (*Chasmanthium* spp.). Prescribed fire was applied on an approximately 3–5-year return interval on both sites. The KNF and Fort Polk WMA were characterized by subtropical climates, with hot, wet summers and cool, wet winters. For a detailed description of site conditions on KNF and Fort Polk WMA, see Yeldell et al. (2017a).

Lastly, we conducted research across a broad suite of private and public lands, including the Sandy Hollow WMA (1,880 ha), in Tangipahoa and Washington parishes in southeastern Louisiana (i.e., the southeastern Louisiana [SELA] site; Figure 1). The region was composed of rolling hills with hardwood riparian zones interspersed with young longleaf pine (*Pinus palustris*) plantations and agricultural production (grazing and row crop) as the dominant private land uses. Mean elevation of SELA was 66 m and was characterized by hot, humid summers and mild to cool winters. For a description of the region, see Duguay et al. (2017).

METHODS

Capture and monitoring

We captured female turkeys using rocket nets from January–March 2019–2020. We sexed individuals based on contour feather color and aged 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 global positioning system-very high frequency (GPS-VHF) transmitter (Guthrie et al. 2011) produced by Biotrack Ltd. (Wareham, Dorset, United Kingdom). We programmed transmitters to record 1 roost location nightly (1 minute before midnight) and daytime hourly locations between 0500 and 2000 from capture until the battery died or the unit was recovered (Cohen et al. 2018). We immediately released turkeys at the capture location after processing.

We located turkeys via telemetry ≥2 times/week using 3- or 5-element handheld Yagi antennas, roof-mounted antennas, R4000 receivers (Advanced Telemetry Systems, Isanti, MN, USA), or Biotrackers (Lotek, NewMarket, ON, Canada) to monitor survival and nesting activity. We downloaded GPS locations from each deployed transmitter ≥1 time/per week and reviewed GPS locations to determine when locations became concentrated around a single point (Yeldell et al. 2017a, b), which we inferred to indicate nesting. Once females were laying or incubating, we monitored each individual daily. We determined date of hatch using visual inspection of nests when the female was off the nest. After nest termination, we located the nest site to determine if hatching had occurred (Conley et al. 2016; Yeldell et al. 2017a, b).

After eggs hatched, we monitored the brooding female up to 28 days post-hatch, as this period represents the time poults are most susceptible to predation and exposure (Hubbard et al. 1999, Chamberlain et al. 2020). We conducted brood surveys every 3 days after females successfully hatched nests. If we detected a brooding female roosting on the

ground prior to 14 days post-hatch, we assumed she was still with a brood as brooding females typically begin tree roosting with poults around 14 days post-hatch (Barwick et al. 1970, Spears et al. 2007). 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. For broods that we located prior to sunrise following 14 days post-hatch, we approached within 20–30 m and waited to observe the female and her brood leave the roost site. For broods monitored later in the day, we located the brood and approached close enough to flush or otherwise detect poults for verification. After females began tree roosting with poults, we relied on visual and auditory detection of poults to confirm brood presence. We considered a brood to be present if we saw or heard ≥1 poult with the female (Chamberlain et al. 2020). We performed brood surveys up to 28 days post-hatch or until we failed to detect poults during 2 consecutive attempts, at which time we assumed the brood was lost. We excluded any females where contact was lost (e.g., transmitter failure or death) or that successfully hatched a nest but were never visually confirmed to have poults.

Sampling locations of turkeys

Resource needs may vary across phenological states and during day or roosting periods (Nedergaard et al. 1990, McShea 2000, Davis et al. 2014). Therefore, we examined brood habitat selection at 3 levels to identify resources critical to turkey broods: between daytime and paired-random locations (day-use site selection), between known ground roost and paired-random locations (roost site selection), and between brooding and non-brooding females across the landscape (brood site selection). Because we only monitored females and not poults, we used the GPS locations of brooding females as a surrogate for brood locations. Therefore, our references to brood refers to decisions made by the female that affected her poults, not decisions by individual poults themselves. We assumed that locations used during the day were those where foraging and loafing occurred compared to locations used at night, which were roost sites (Chamberlain et al. 2020). We randomly selected 3 GPS locations during the day (day-use) and 1 roost location per brood for each 3-day post-hatch interval for a total of 4 locations per 3-day period. We subdivided location data into 3-day intervals to avoid spatial autocorrelation among replicates and because we verified broods were still alive every 3 days. Thus, subdividing location data into 3-day periods ensured our samples were taken when we could confirm broods were alive. We randomly selected 1 day-use location for each day in the 3-day period to ensure our day-use locations were representative of the entirety of daytime hours across our sample. We did not sample brood roost locations >15 days post-hatch because tree roosting occurs after this point (Barwick et al. 1970, Spears et al. 2007).

We paired the randomly selected day-use and ground roost use locations with a random location ≥200 m (range = 210–513 m) away from the use location. We generated paired-random locations by using a random number generator to determine azimuth and distance from the known location but constrained the locations to fall within the 100% minimum convex polygon of all locations up to the date of the known location for that individual female. Finally, we sampled locations of non-brooding females to provide comparisons in resource selection between brooding females and non-brooding females. Because non-brooding females are usually spatially separated from broods (Healy 1992), brood site selection also represents a broader spatial scale of selection (i.e., second-order home range; Johnson 1980) than day-use or roost site selection (i.e., third-order within-home range; Johnson 1980). We paired day-use locations with 3 daytime locations from a non-brooding female monitored during the same 3-day interval to determine if resource selection differed for females in different reproductive states.

Environmental factors

We measured temperature (°C), arthropod biomass (g/m^2), and vegetation metrics at all sampling locations described above to collectively represent environmental conditions at brood and non-brooding female locations.

We measured environmental conditions within 14 days ($\bar{x}$ = 7 days; SD = 3.6) of when the female used the location. We recognize that there could be subtle changes to arthropod abundance and vegetative characteristics from the time females were at these sites until we sampled them. We assumed those changes would be minimal and would not have influenced our results because abundance estimates of arthropods and vegetation characteristics change little within short temporal periods (Montgomery et al. 2021, Nelson 2021). We used air temperature as an indicator of thermal variation and potential thermoregulatory stress, arthropod biomass as a proxy for available forage, and vegetation metrics as an indicator of concealment cover.

Air temperature

We programmed Thermochron iButtons (model: DS1921G, Maxim Integrated Products, Sunnyvale, CA, USA) to record hourly air temperature and placed them in 10-cm-long, 3.81-cm-diameter white polyvinyl chloride (PVC) piping horizontally 0.66 m above ground attached to the north-facing side of a log, shrub, or tree. The PVC piping protected iButtons from rain and direct sunlight while allowing contact with atmospheric conditions. We deployed iButtons at the center of all sampling locations for 4 days to measure variation in daily temperature.

We calculated temperature differences (i.e., iButton temperature–weather station temperature) between sampled locations and nearby local weather stations (<45 km; Georgia source: http://weather.gfc.state.ga.us/Getwxdata/Getwxdata.aspx; Louisiana source: https://mesonet.agron.iastate.edu/ASOS, accessed 26 Oct 2020) because we assumed the relative temperature difference (i.e., whether a sampled location was relatively cooler or warmer than surrounding area) and not the absolute air temperature at sampled locations was more informative. In Georgia, we compared temperatures to a weather station in Milledgeville, which was 33 km from Cedar Creek and 44 km from B. F. Grant WMAs. For the SELA site, we compared temperatures to a weather station at the Hammond Regional Airport, which was 45 km away from the center of the study area. For Fort Polk WMA, we compared temperatures to a weather station inside Fort Polk WMA that was <1 km from the center of the study site. For KNF, we compared temperatures to a weather station that was 27 km away.

Our measure of ambient temperature differences represented a standardized metric for the thermal refuge provided by a location in comparison to other locations at the same site, not an exact temperature at a location (Elmore et al. 2016). For each sampled location, we calculated the average difference in the mean, median, maximum, and minimum daily temperature for the 4 days the iButton was deployed. Thermal refuge from hot temperatures may be important during the day (Rakowski et al. 2019) but may also be important from cooler temperatures at night. To ensure we only compared daytime temperatures for day-use sites and nighttime temperatures for roost sites, we split average daily temperature differences from the weather stations into daytime (0600–2059) and nighttime (2100–0559) differences.

Arthropod biomass

We employed suction sampling using a modified leaf blower-vac (Husqvarna 125BVx 28-cc, Charlotte, NC, USA; Zou et al. 2016) at each sampling location to measure arthropod biomass. Some terrestrial arthropod sampling methods, such as pit-fall traps and sticky traps, are biased towards ground-dwelling arthropods, and sweep-netting targets flying and taller grass or shrub-dwelling arthropods (Cooper and Whitmore 1990, Yi et al. 2012). Suction sampling reduces potential biases, collectively targeting ground-dwelling, herbaceous-dwelling, and flying arthropods (Zou et al. 2016). We approached the site and rapidly placed the receptacle on the ground to reduce the potential bias for underestimating disturbance-sensitive species (Zou et al. 2016). For each sampling location, we sampled arthropods at plot center and in each cardinal direction 15 m from plot center. We collected arthropods in a cylindrical receptacle (66 × 55 cm) with an open bottom and nylon window screening on top. The height of the

receptacle was the approximate height at which females and poults could reach arthropods. When sampling, we placed the receptacle's open side onto the ground over vegetation to prevent arthropods from escaping. We then suctioned arthropods inside the receptacle for 60 seconds. We placed collected arthropods in kill jars and preserved them in 70% ethanol (Ricca Chemical Company, Arlington, TX, USA). We followed taxonomic sorting similar to Chitwood et al. (2017) and sorted arthropods into 7 taxonomic categories: Orders Hymenoptera, Orthoptera, Coleoptera, Lepidoptera, and Araneae, Class Arachnida excluding Araneae, and other (all other arthropods). We chose specific taxonomic categories because they are important food sources for wild turkeys, whereas we combined other taxonomic groups because of their lesser contribution to turkey diets (Healy 1985, McCord et al. 2014, Tebo 2014). After sorting arthropods, we dried them in ovens at 60°C for 24 hours (Dermott and Patterson 1974, Mackey 1977, Johnston and Cunjak 1999) and placed them into a desiccator using anhydrous drierite desiccating agent ($CaSO_4$, stock number 11005, W. A. Hammond Drierite, Xenia, OH, USA) at room temperature to prevent atmospheric moisture uptake and control for standardization among weights. After 24 hours, we removed samples from desiccators, weighed them to the nearest 0.0001 g to quantify dry-weight biomass for each taxonomic category, and converted weights to g/m^2.

Vegetation metrics

After sampling arthropods, we conducted vegetation sampling at the center and in each cardinal direction 15 m from the center of each sampling location (Yeldell et al. 2017a). Because arthropod sampling could disturb vegetation, we measured percent ground cover composition and density, basal area (m^2/ha), percent canopy cover, and vegetation height (cm) immediately adjacent to arthropod sampling. We measured percent ground cover composition and density using a 1-m^2 frame (Daubenmire 1959) placed on the ground. We classified the percentage of understory vegetation in 3 classes: woody, grass, and forb understory. We estimated percent canopy cover of overstory vegetation using a convex spherical densiometer (Lemmon 1956). We placed a 200-cm-tall Robel pole (Robel et al. 1970) at the center and performed readings at 15 m in each cardinal direction towards the center to estimate maximum vegetation height, average vegetation height, and visual obstruction. We measured basal area using a 10-factor prism at the center of each sampling location. Within each sampled location, we averaged measurements from all 5 locations for ground cover composition and density, canopy cover, and vegetation height.

Data analysis

To evaluate the influence of temperature, arthropod biomass, and vegetation on selection of sites by brooding females, we used conditional logistic regression in a matched-pairs case-control design (i.e., design III; Compton et al. 2002, Manly et al. 2002) to estimate resource selection functions (RSFs) for brood site selection, day-use selection, and roost site selection. For brood site selection, we defined used sites as known GPS locations of brooding females and available sites as known GPS locations of non-brooding females, which allowed us to evaluate differences in habitat selection relative to reproductive state of females. For day-use and roost site selection, we defined used sites as known GPS locations of brooding females and available sites as the paired random locations. We estimated beta coefficients and calculated odds ratios for each temperature, arthropod biomass, and vegetation metric. We estimated 95% confidence intervals around the beta estimates and odds ratios.

We calculated Pearson correlations (r) between pairs of explanatory covariates prior to building candidate models because inclusion of highly correlated covariates in models can inflate estimates of variance and hinder data interpretation (Zuur et al. 2010). If covariates were highly correlated ($|r| \geq 0.6$; Zuur et al. 2010), we retained only 1 covariate that had the strongest biological effect based on effect size and associated uncertainty and Akaike's

Information Criterion adjusted for small sample size (AIC$_c$; Burnham and Anderson 2002). We performed conditional logistic regression with case-controlled sampling using package survival (Therneau and Lumley 2016) in program R (version 3.6.3; R Core Team 2020), where cases were used sites and controls were available sites. We stratified data by brooding female to match the conditional pairs. We performed model selection using AIC$_c$ using package AICcmodavg (Mazerolle 2020).

We built a suite of *a priori* candidate models representing our hypotheses of brood resource selection and used a secondary candidate set strategy (Morin et al. 2020), which is a hierarchical approach, to evaluate support for candidate models. We first compared candidate models within each environmental factor (i.e., temperature, arthropod biomass, and vegetation) to determine which covariates most influenced brood, day-use, and roost site selection. Then, we used the covariates from the top model that were biologically relevant (i.e., 95% CIs did not overlap zero) within each environmental factor to create our final candidate model set.

Because our temperature covariates (mean, median, maximum, and minimum differences) were highly correlated, we ran univariate models for the temperature candidate models. Based on the breeding currency hypothesis (Greenberg 1995) and total arthropod hypothesis (Healy 1985), we developed 3 arthropod candidate models. The first model predicted that selection was most influenced by total arthropod biomass (total mass model). The second model predicted that selection was most influenced by the availability of large food items (Orthoptera, large prey items model; Greenberg 1995), whereas the third model predicted that selection was most influenced by availability of small food items (Hymenoptera, Coleoptera, and Araneae; small prey items model; Healy 1985). Next, we developed 3 vegetation candidate models. The first model predicted that selection was most influenced by vegetation height and density (visual obstruction, maximum vegetation height, basal area, ground cover, and canopy cover; vegetation structure model). The second model predicted that specific understory vegetation classes (woody, grass, and forb understory) most influenced selection (vegetation community model; Fettinger et al. 2002, Chitwood et al. 2017, Wood et al. 2019). The third model predicted percentage ground cover that can provide visual concealment most influenced selection (ground cover model).

We compared all candidate model sets for each environmental factor to a null model. We considered models with ≤2 ΔAIC$_c$ units to be equally plausible. We considered covariates within each plausible model to be biologically significant if 95% confidence intervals of the beta estimate did not overlap zero. We then used biologically significant covariates to develop a final candidate model set. If the null model was within 2 AIC$_c$ units of the top model, we assumed the covariates in that top model did not influence selection, and we did not include those covariates in our final candidate model set (Burnham and Anderson 2002).

To determine the relative importance of thermal conditions, forage availability, and concealment cover in brood habitat selection to understand potential behavioral tradeoffs, we developed 7 final candidate models for brood site, day-use, and roost site selection. The 7 models represented every combination of the 3 environmental factors. We considered the model with the lowest AIC$_c$ score and containing the fewest covariates the most parsimonious model and reported beta coefficients, odds ratios, and 95% confidence intervals for that model. Again, we considered covariates to be biologically significant if 95% confidence intervals of the coefficient estimate did not overlap zero. Additionally, we calculated the Pearson's correlation coefficient (r) between the environmental factors to understand potential tradeoffs in thermal conditions, forage availability, and concealment cover.

RESULTS

We captured 155 female wild turkeys during 2019–2020, which resulted in our ability to sample 12 broods at B. F. Grant and Cedar Creek WMAs, 9 broods at the SELA site, and 6 broods at KNF and Fort Polk WMA (Table 1). We recorded environmental conditions at 714 used and available locations (83% day-use locations, 17% roost locations) from the 27 brooding females ($\bar{x}$ = 26 locations/brooding female; range = 6–70) and 295 paired used locations during the day from 31 non-brooding females ($\bar{x}$ = 9 locations/female; range = 3–26). Day-use locations of

TABLE 1 Capture and monitoring sample sizes of brooding and non-brooding eastern wild turkey females in B. F. Grant Wildlife Management Area (WMA) and Cedar Creek WMA in Georgia, southeast Louisiana (SELA), and Kisatchie National Forest (KNF) and Fort Polk WMA in Louisiana, USA, January–March 2019–2020.

Study area (yr)	Number of females trapped	Number of females that initiated a nest	Number of nests attempted (nests initiated)	Number of hatched nests	Number of broods sampled	Number of broods surviving to ≥28 days old	Number of non-brooding females sampled
B. F. Grant and Cedar Creek (2019, 2020)	78	52	68	15	12	6	20
SELA (2020)	47	32	41	19	9	3	6
KNF and Fort Polk (2020)	30	22	34	8	6	3	5

brooding females were characterized by 15% cooler ambient temperatures, 80% greater Orthoptera biomass, and 55% higher percentage of grass understory than available locations (Table 2). Day-use and roost locations had 29% and 32% lower percentage woody understory than paired available locations, respectively (Table 2). Notably, brooding females did not use locations during the day or night with >27% woody understory; only 3% of brooding female locations were in areas with >20% woody understory and <1% of brooding female locations were in areas with >25% woody understory. For non-brooding females, used locations were 27% warmer and had 45% lower percentage of grass understory than locations used by brooding females (Table 2). At all sampling locations, ambient temperature ranged from a minimum of 20.0°C (range = 10.0–25.8°C) to a maximum of 30.8°C (range = 20.6–49.3°C) per day (Figure 2).

Average vegetation height was correlated with visual obstruction ($r = 0.71$) and maximum vegetation height ($r = 0.73$), so we excluded average vegetation height from subsequent modeling. At all sampling locations during the day, Orthoptera biomass increased with greater ambient temperatures ($r = 0.18$) and percent grass understory vegetation ($r = 0.25$). There was no relationship between ambient temperature difference and total arthropod biomass ($r = 0.04$) or percent grass understory ($r = 0.04$).
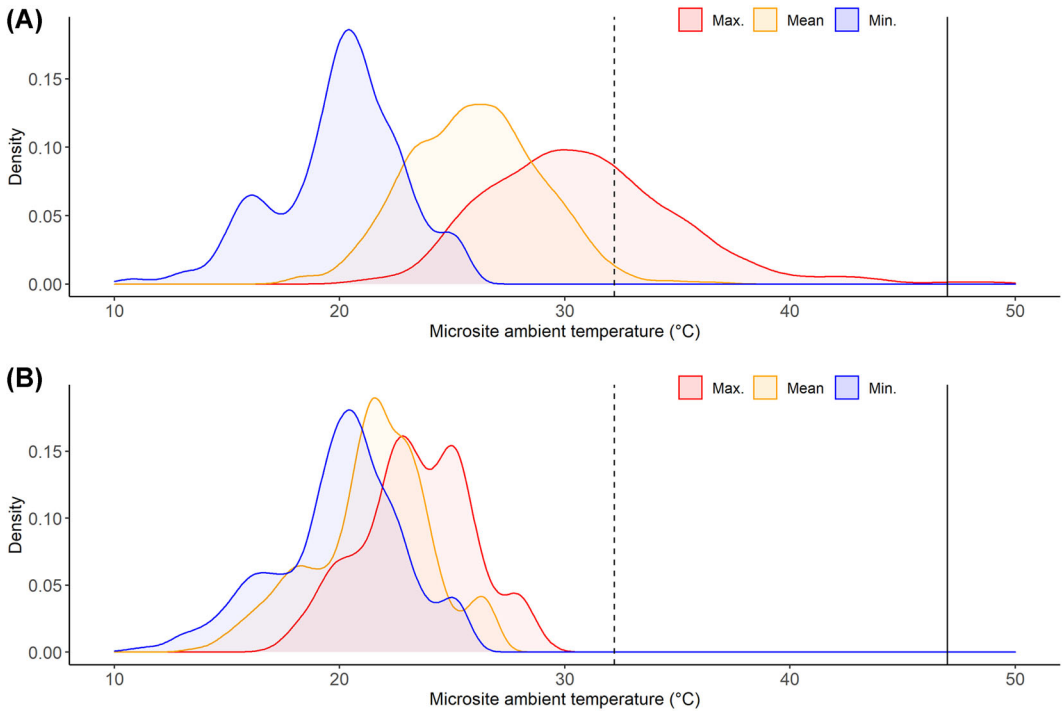
Brood site selection

The top model for temperature was the mean temperature difference model, whereas the top model for vegetation was the vegetation structure model (Table S1, available online in Supporting Information). Basal area, canopy cover, and maximum vegetation height were not biologically significant and thus we excluded them from the final models. The top model for arthropod biomass was the total mass model (Table S1). Therefore, we compared models representing various additive combinations of mean temperature difference, visual obstruction, percentage ground cover, and total arthropod biomass in the final model selection process.

The top model for the final model selection process included temperature, arthropod biomass, and vegetation metrics (Table S2, available online in Supporting Information). Although total arthropod biomass and visual obstruction were in the top model, neither were biologically relevant (Table 3). Brooding females were more likely to use areas with lower ambient air temperature and greater ground cover (Table 3). Brooding females were 1.25 (95% CI = 1.108–1.402) times more likely to select for a site for every 1°C decrease in mean temperature difference (Figure 3A; Table 3) relative to non-brooding females. Brooding females were 1.26 (1.107–1.403) times more likely to select sites with each 10% increase in ground cover (Table 3) relative to non-brooding females.

TABLE 2 Mean (±SE) values of temperature, arthropod biomass, and vegetation variables measured at day-use and roost sites used by eastern wild turkey brooding females and at nearby available sites and by non-brooding females during the day in Georgia and Louisiana, USA, May–July 2019–2020.

Variable	Brood: day-use				Brood: roost				Non-brooding	
	Used		Available		Used		Available		Used	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Air temp										
Mean temp difference (°C)	−1.82	0.118	−1.57	0.102	−0.09	0.130	0.10	0.127	−1.43	0.114
Min. temp difference (°C)	−0.01	0.148	0.15	0.073	0.15	0.144	0.31	0.127	0.24	0.077
Max. temp difference (°C)	−1.51	0.218	−1.10	0.206	−0.33	0.151	−0.09	0.158	−1.04	0.215
Arthropod biomass										
Total (g/m^2)	0.033	0.0029	0.021	0.0024	0.016	0.0030	0.016	0.0035	0.025	0.0025
Orthoptera (g/m^2)	0.014	0.0023	0.006	0.0013	0.003	0.0018	0.006	0.0021	0.012	0.0021
Hymenoptera (g/m^2)	0.001	0.0003	0.001	0.0002	0.0002	0.00008	0.0002	0.0001	0.0005	0.0001
Coleoptera (g/m^2)	0.002	0.0002	0.003	0.0009	0.002	0.0007	0.002	0.0004	0.002	0.0004
Araneae (g/m^2)	0.007	0.0010	0.006	0.0012	0.006	0.0020	0.004	0.0012	0.005	0.0008
Vegetation metrics										
Visual obstruction (cm)	33.0	1.44	37.3	2.08	34.0	3.65	32.8	3.60	27.7	1.27
Basal area (m^2/ha)	60.3	2.66	66.7	2.55	79.0	6.46	70.3	4.81	61.6	2.87
Max vegetation height (cm)	114	2.57	122	2.96	116	6.23	114	6.17	108	2.90
Ground cover (%)	58.1	1.33	48.9	1.23	51.9	3.13	47.1	2.72	48.6	1.32
Canopy cover (%)	68.0	1.80	72.8	1.73	75.7	3.58	78.8	2.73	66.6	1.75
Grass understory (%)	30.2	1.48	17.1	0.972	23.7	3.50	16.1	2.03	20.7	1.20
Forbs understory (%)	9.80	0.655	7.73	0.522	5.84	0.822	7.40	0.883	8.24	0.589
Woody understory (%)	5.72	0.300	8.11	0.386	5.90	0.682	8.63	0.835	7.33	0.326

FIGURE 2   Density of observed ambient temperatures (°C) for day (A) and night (B) microsite locations used by and available to eastern wild turkey brooding and non-brooding females in Georgia and Louisiana, USA, May–July 2019–2020. We averaged maximum, mean, and minimum temperatures over 4 days. The dashed line at 32.2°C represents the temperature at which domestic turkeys had significant increases in body temperature (Wilson and Woodard 1955). The solid line at 47°C is the lethal body temperature for most birds (Kendeigh 1969).

Day-use selection

The top model for temperature was the mean difference model, whereas the top model for vegetation was the vegetation community model (Table S1). The top model for arthropod biomass was the large prey items (i.e., Orthoptera) model, although the total arthropod model was within 2 AIC of the large prey items model (Table S1). Thus, we compared models examining various combinations of mean temperature difference, grass understory, forb understory, woody understory, and Orthoptera biomass in the final model selection process.

The top model for the final model selection process was the global model (Table S2), which suggested that air temperature, vegetation, and arthropod biomass influenced day-use selection. Brooding females were more likely to use sites with decreasing ambient air temperature and greater Orthoptera biomass (Table 3). Brooding females were also more likely to use areas with greater grass understory, greater forb understory, and less woody understory vegetation (Table 3). Brooding females were 1.34 (1.190–1.480) times more likely to select sites with each 1°C decrease in mean temperature difference (Table 3) during the day. Brooding females were 1.37 (1.242–1.511) times more likely to select sites with each 10% increase in grass (Figure 3E; Table 3), and 1.44 (1.303–1.586) times more likely to select sites with each 10% increase in forbs (Table 3; Figure 3F) during the day. Brooding females were 1.61 (1.463–1.781) times more likely to select for sites with each 10% decrease in woody vegetation (Figure 3D; Table 3) during the day. Brooding females were 2.18 (1.088–4.372) times more likely to select sites with each 0.1-g/m^2 increase in Orthoptera biomass during the day (Figure 3C).

TABLE 3 Parameter estimates (β; logit scale) and odds ratios (OR) with 95% confidence intervals for top final models examining how differences in temperature (°C), arthropod biomass (g/m²), and vegetation (%) influence site selection by brooding female eastern wild turkeys, Georgia and Louisiana, USA, May–July 2019–2020.

| Model	Covariate	β (95% CI)	OR (95% CI)
Brood site selection: Global model			
	Total biomass	3.57 (−0.733–7.875)	35.53 (0.480–2,631.107)
	Visual obstruction	0.01 (0.002–0.018)	1.01 (1.002–1.018)
	Ground cover	0.02 (0.013–0.033)	1.02 (1.013–1.033)
	Mean temp difference	−0.22 (−0.338–−0.102)	0.80 (0.713–0.903)
Day-use site selection: Global model			
	Orthoptera biomass	7.80 (0.848–14.752)	2,446.60 (2.334–2.551e^6)
	Grass understory	0.03 (0.018–0.042)	1.03 (1.018–1.043)
	Forbs understory	0.04 (0.016–0.064)	1.04 (1.017–1.066)
	Woody understory	−0.05 (−0.091–−0.009)	0.95 (0.913–0.991)
	Mean temp difference	−0.29 (−0.435–−0.145)	0.75 (0.647–0.865)
Roost site selection: Vegetation model			
	Woody understory	−0.09 (−0.161–−0.019)	0.91 (0.852–0.981)

Roost site selection

The top model for temperature was the maximum temperature difference model, but because the null model was within 2 AIC of the top model we did not include temperature in the final model set (Table S1). The top model for vegetation was the vegetation community model (Table S1), but grass and forb covariates were not biologically significant and not included in the final model. For arthropod biomass, the top model was the null model (Table 2), so we did not include arthropod biomass in the final model list set. Therefore, we tested only woody understory vegetation against a null model in the final model selection process.

The top model for the final model selection process for roost site selection was the vegetation model (Table S2). Brooding females were more likely to use areas with decreasing woody vegetation (Table 3). Brooding females were 2.57 (95% CI = 2.328–2.832) times more likely to roost in areas with each 10% decrease in woody vegetation (Table 3).

DISCUSSION

Behavioral tradeoffs occur because resources and their respective fitness advantages are heterogeneously distributed across the landscape (Nonacs and Dill 1990, Pecor and Hazlett 2005, Zub et al. 2009). Understanding which resources affect habitat selection, assuming animals are distributing themselves in such a way to maximize potential fitness, informs vegetation management decisions. Habitat selection by wild turkeys differed based on reproductive state wherein females with broods selected day-use sites with cooler temperatures and more ground cover compared to non-brooding females. Mean ambient temperature difference and biomass of large arthropods (i.e., Orthoptera) were positively correlated, suggesting that use of thermal refuge by brooding females may necessitate a tradeoff with large arthropod prey. Selection of sites by brooding females to meet thermoregulatory needs at a broader spatial scale
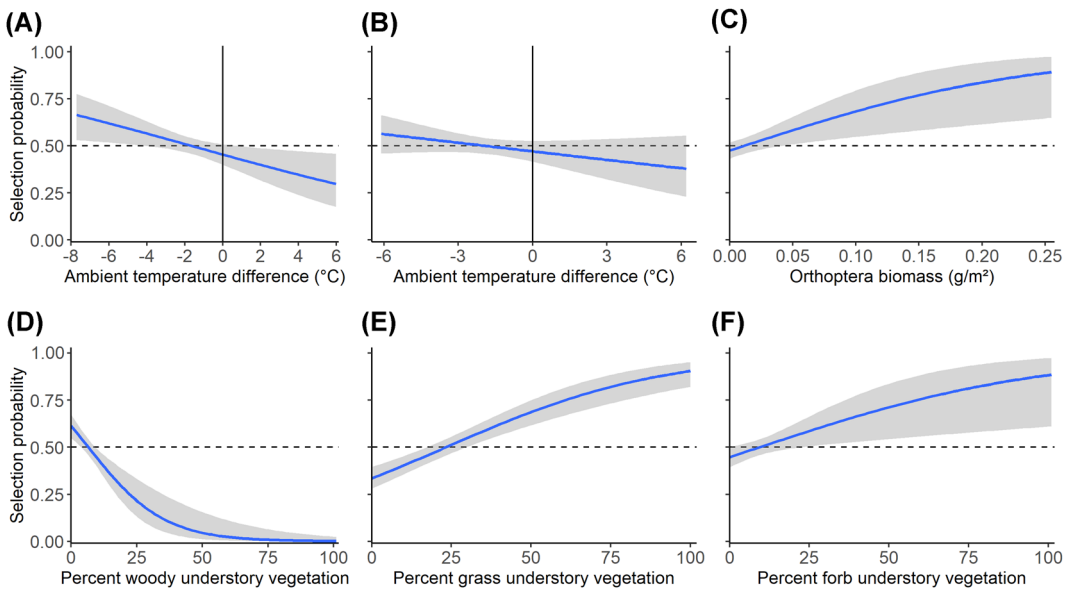
FIGURE 3 Probability of selection (and 95% CIs) for eastern wild turkeys in Georgia and Louisiana, USA, May–July 2019–2020 for brooding female site selection relative to non-brooding females for ambient temperature differences from local weather stations (A), and brooding female site selection relative to paired, random locations during the day for ambient temperature differences from local weather stations (B), Orthoptera biomass (C), percent woody understory vegetation (D), percent grass understory vegetation (E), and percent forb understory vegetation (F). The vertical line at 0°C (A, B) represents no temperature difference between ambient temperature at the microsite and local weather stations. The dashed horizontal line at 0.50 selection probability represents indifference (i.e., neither selection for or avoidance of the habitat metric). Values of other predictor variables were held constant at their mean value for predictions.

(second order) allowed them to select sites based on foraging requirements at finer spatial scales (third order). Brooding females selected for grassy and herbaceous areas that provided greater biomass of large arthropods at finer spatial scales during the day, and avoided areas with >27% woody vegetation. Our results suggest that thermal refuge is an important component of brood habitat, but within thermally suitable areas brooding females select sites with greater availability of large prey to meet the brood's energetic demands.

Females with broods selected areas with cooler temperatures compared to non-brooding females, suggesting that thermal refuge is more important to broods than non-brooding females. Turkey broods in the southeastern United States are regularly exposed to stress-inducing high temperatures, which underscores the significance in selecting habitat with favorable microclimates. For the first 4 weeks after hatch, turkeys are effectively poikilothermic and have limited ability to maintain core body temperatures with fluctuations in ambient temperatures (Dawson and Whittow 2000). Opportunity existed for hyperthermia in broods on our study areas, as daily temperatures at 29% of our sampling locations exceeded the threshold of 32.2°C, which has been shown in domestic turkeys to increase body temperature (Figure 2; Wilson and Woodard 1955). Maximum temperatures recorded at 5 sampling sites were >47°C, which is the lethal body temperature for most birds (Kendeigh 1969). During warmer periods, Galliformes broods often adjust habitat use to select for sites with cooler temperatures, which can alter space use and movements (Bell et al. 2010, Tanner et al. 2017, Carroll et al. 2018, Rakowski et al. 2019).

Investment in thermoregulatory behaviors may require individuals to devote time and energy away from other key behaviors, such as foraging (du Plessis et al. 2012, Edwards et al. 2015, Beever et al. 2017, van de Ven et al. 2019). Although there was no relationship between total arthropod biomass and ambient temperature difference,

we found little evidence that brood site selection was influenced by total arthropod biomass. Instead, brooding females selected for sites based on biomass of large prey items (i.e., Orthoptera). Orthoptera have a greater mass per individual than other arthropods, and represent a valuable food resource (Rumble and Anderson 1996). Poults grow rapidly in the first 28 days of life (Healy 1992), with males and females increasing their body weight around 658% and 510%, respectively (Healy and Nenno 1980). Turkey poults require 28% dietary protein for muscle and feather development (National Research Council 1977), and need consistent forage intake (Healy 1985), which may require behavioral trade-offs. Availability of large arthropods was less at cooler sites and arthropod activity patterns can be affected by temperature (Holm and Edney 1973, Gullan and Cranston 2000). Further, just because brooding females select sites with greater forage availability does not mean they allocate more time to feeding. Thermoregulatory behaviors are energetically expensive and may reduce time spent foraging or foraging efficiency (du Plessis et al. 2012, Edwards et al. 2015). Brooding females appear to balance the tradeoff between thermal refuge and forage availability by altering habitat selection patterns at different scales. At broader spatial scales, brooding females prioritized thermal refuge over availability of large prey by selecting cooler sites, whereas at finer scales they appeared indifferent to ambient temperature differences and focused on foraging resources.

Ground cover dominated by grasses and forbs was an important component of areas selected by brooding females, consistent with previous literature noting the importance of grasses and forbs for foraging and loafing (Sisson et al. 1991, Fettinger et al. 2002, Chitwood et al. 2017, Chamberlain et al. 2020). Importantly, however, brooding females avoided woody vegetation both during the day and when roosting at night. Brooding females were less likely to roost at sites with greater percentages of woody understory vegetation, with no observed roosts or day-use locations occurring in areas with >27% woody vegetation. Ross and Wunz (1990) noted brooding females selected areas with more herbaceous understory and less woody understory vegetation. We suggest brooding females selected areas with less woody vegetation on our sites because similar areas were dominated by hardwood saplings, which likely limited mobility and escape options when broods were threatened. Further, areas with denser woody understory are known to provide quality foraging areas for various predators of wild turkeys (Kolowski and Woolf 2002, Chamberlain et al. 2003). In addition to forage availability and thermal refuge, concealment from predators should be a central component of habitat selection by brooding females, as predation is the primary cause of brood loss (Hubbard et al. 1999). Existing literature on Galliformes has noted use of open, early successional vegetation communities by broods, which offer concealment from predators and foraging opportunities (Metzler and Speake 1985, Porter 1992, Spears et al. 2007).

Our results were likely influenced by sampling of and metrics for temperature, arthropod biomass, and vegetation characteristics. We measured relative temperature using the difference between temperature recorded on iButtons at sampling locations and temperature at nearby weather stations. Although our metric reflected whether ambient temperature was relatively cooler or warmer, we did not measure operative temperature, which combines ambient temperature, solar radiation, and convective heat transfer (Campbell and Norman 1998, Elmore et al. 2016). Therefore, our metric for temperature does not reflect actual thermal environments experienced by brooding females and is likely less variable than operative temperature (Elmore et al. 2016). Additionally, we measured environmental conditions within 14 days of when brooding females used a site. We recognize there may be slight changes in temperature, arthropod biomass, and vegetation characteristics from when a brooding female used a site to when we sampled; however, arthropod biomass and vegetation characteristics likely changed very little within 2 weeks (Montgomery et al. 2021, Nelson 2021) and we averaged temperature over 4 days to account for daily variation in ambient temperature.

A key component in determining effects of future climate conditions on animal ecology and behavior is understanding how different life-history periods may be influenced by thermal environments (Potter et al. 2013). Given declining productivity of turkeys across broad areas of the species' geographic range (Byrne et al. 2015), it is imperative to more thoroughly understand behavior of wild turkey broods to develop and tune land management activities. Wild turkey poults are poor thermoregulators (Dickson 1992) and our results suggest that sites selected

by brooding females could potentially reach detrimental temperatures. But brooding females were able to prioritize thermal refuge at the broader spatial scales, buffering their thermal environment compared to surrounding ambient temperatures. Although brooding females appear to balance tradeoffs between thermoregulatory behaviors and forage availability, fitness consequences of tradeoff behaviors are unknown.

MANAGEMENT IMPLICATIONS

The thermal environment may create unsuitable conditions in otherwise preferred vegetation communities, constraining habitat availability and forcing turkey broods to use less energetically profitable patches. Vegetation communities that provide thermal refuge like hardwood forests are critical components of brood habitat in pine-dominated landscapes. Our results suggest vegetation communities with percentages of woody understory exceeding 27% are not suitable for turkey broods. Increased woody plant stem density in pine-dominated stands is often associated with reductions in disturbance; thus, frequent (i.e., every 2–4 yr) disturbance in pine-dominated stands in the southeastern United States could create vegetation communities favored by turkey broods. Likewise, removal of woody understory from upland pine-dominated systems using methods such as herbicide application or prescribed fire may create more suitable vegetative conditions for turkey broods.

CONFLICTS OF INTEREST
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data available on request from the authors.

ETHICS STATEMENT
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, A2019 01-025-R2) and the Louisiana State University Agricultural Center (protocol A2018-13).

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