




Age-based shifts in habitat selection of wild turkey broods

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Abstract

Animals exhibit pronounced age-based shifts in habitat selection, often because of increasing body size. Body size affects how animals access resources, traverse landscapes, and perceive predation risk. While adults may be habitat generalists, offspring may be constrained by diet, predation avoidance methods, and mobility given smaller body size, and thus be more specialized. Observed declines in eastern wild turkey (*Meleagris gallopavo silvestris*) productivity and recruitment across the southeastern United States has necessitated evaluations of availability and composition of brood habitat. As poults are smaller and have more specialized resource requirements than adults, selection of vegetation likely changes as poults age. We evaluated aged-based shifts in selection relative to vegetation communities, normalized difference vegetation indices (NDVI), and distances to trails by eastern wild turkey brooding females in a pine (*Pinus* spp.)-dominated landscape in Georgia, USA, from April–July during 2017–2020. We used step-selection functions and conditional logistic regression to evaluate resource selection of 36 brooding females. Of 175 nests monitored, 36 (20.6%) successfully hatched a brood and only 12 broods had at least 1 poult survive ≥ 28 days post-hatch (i.e., 6.9% of nests produced a poult that was recruited into the population). Overall, brooding females selected for pastures ($\beta = 0.730$; 95% CI = 0.5144–0.9452), hardwoods ($\beta = 0.324$; 95% CI = 0.1608–0.4865), areas closer to trails ($\beta = -0.002$; 95%

CI = -0.0023--0.0014), and areas with greater NDVI values ($\beta = 2.714$; 95% CI = 1.7897--3.6380). Habitat selection shifted as broods aged, suggesting resource needs shift to scale allometrically with body size as broods get older. For example, selection strength waned as broods aged and broods were 2.47 times less likely to select pastures on day 28 relative to day 1 post-hatch. Pastures were selected for after broods hatched, whereas selection for young pines increased as poults aged. Despite pine-dominated cover types comprising nearly a third of the usable landscape, young pine communities were avoided by females with recently hatched broods. Managers may create better brood habitat by promoting early successional vegetation communities amidst a diversity of other land cover types to account for changing resource needs and predator avoidance capabilities as poults age.

KEYWORDS

allometric scaling, brood, Georgia, habitat selection, *Meleagris gallopavo silvestris*, ontogeny, step selection function, wild turkey

Animals respond to resource heterogeneity through selection that balances physiological needs with predation risk (Nonacs and Dill 1990, Pecor and Hazlett 2005, Zub et al. 2009) and maximizes fitness across seasons, phenological states, and allometric scales (Nagy 1987, Klassen et al. 1992, Barneche et al. 2018). Specialist species have a narrow niche compared to generalists, which can thrive in a variety of ecological settings (Devictor et al. 2008). Local specialization can occur at specific spatial or temporal scales for resource generalists (Kruuk and Parish 1981, Bolnick et al. 2003). Because resource requirements constrain habitat use, understanding habitat selection, especially when animals have specific resource needs, is necessary for effective conservation and management strategies (Root 1988, Roever et al. 2012, Gibson et al. 2016).

Resource requirements and degree of resource specialization may vary during ontogenesis and result in different patterns of resource selection between adults and juveniles (Werner and Gilliam 1984, Dahlgren and Eggleston 2000). Ontogenetic shifts in resource requirements are most dramatic in species that undergo metamorphosis and have been well documented in insects and amphibians (Werner and Gilliam 1984, Altermatt and Pearse 2011, Rudolf and Rasmussen 2013). For precocial birds, one of the greatest changes during ontogenesis is body size. The framework of allometric scaling suggests body size and its influences on morphological and physiological traits influence life-history strategies (Kleiber 1932, Schmidt-Nielsen and Knut 1984, Brown et al. 2004). Size-related effects influence animal metabolism, mobility, thermoregulation, foraging, and responses to predation risk (Van Soest 1996, Dial et al. 2008, Preisser and Orrock 2012). Allometric scaling suggests resource selection may shift within short temporal periods, especially for rapidly developing individuals (Schmidt-Nielsen and Knut 1984). Thus, ontogenetic shifts in resource requirements may alter habitat selection during growth and development (Dial et al. 2008).

Eastern wild turkeys (*Meleagris gallopavo silvestris*; turkeys) are considered generalists; however, habitat requirements of adults differ from their precocial offspring (poults; Healy 1992). The first 28 days post-hatch are important for poults because they are at their greatest mortality risk (Hubbard et al. 1999, Spears et al. 2007, Chamberlain et al. 2020), unable to fully thermoregulate, and require diets of protein-rich arthropods to support

rapid growth and feather development (Healy 1985, Lafon et al. 2001, Backs and Bledsoe 2011). Poults grow rapidly, gaining roughly 17 g/day during the first 3 months of life and flying within 2 weeks post-hatch (Barwick et al. 1970, Pelham and Dickson 1992, Coles 2009). Poults double their mass within 3 days post-hatch, and then double that mass again in less than a week (Pelham and Dickson 1992). Allometric scaling suggests that younger, smaller-bodied poults should have more specialized diets, narrower thermoregulatory tolerances, exhibit shorter movements, and use different predator avoidance strategies than adults (Hillestad and Speake 1970, Hamrick and Davis 1971, Healy et al. 1975, Matthew 1983, Chamberlain et al. 2020). Collectively, space use and resource selection of poults may be specialized when they are younger but become more generalized as they develop, even within the first 28 days post-hatch (Moscicki et al. 2022; Figure 1).

Different vegetation communities and forest age classes create conditions that affect the ability of poults to forage, thermoregulate, and move (Nelson et al. 2022), and selection of vegetation communities may shift as poults age (Chamberlain et al. 2020). For example, pine (*Pinus* spp.)-dominated stands of the southeastern United States can have different understory and mid-story vegetation communities depending on management, age, and planting density (Provencher et al. 2001, Jones et al. 2009), which affects turkey selection (Yeldell et al. 2017b, Wood et al. 2019). In managed pine stands, recently planted pines (≤ 3 years after planting) are characterized by understory vegetation dominated by herbaceous plants and hardwood shrubs with no mid-story or overstory vegetation (Kirkman et al. 2004). As pines age, however, grasses and forbs are outcompeted by woody vegetation until canopy closure occurs, and understory vegetation becomes sparse (Buckner and Landers 1979, Platt et al. 2006). If disturbed (e.g., thinning, prescribed fire), diversity of plants in the understory of pine stands increases (Harrington and Edwards 1999, Harrington 2011), and grass and herbaceous vegetation can be continually maintained with frequent disturbance (Kirkman et al. 2004). Thus, resource availability for turkeys differs among forest age classes (Nelson et al. 2022), and the optimal value of these resources to poults is likely dependent on poult size.

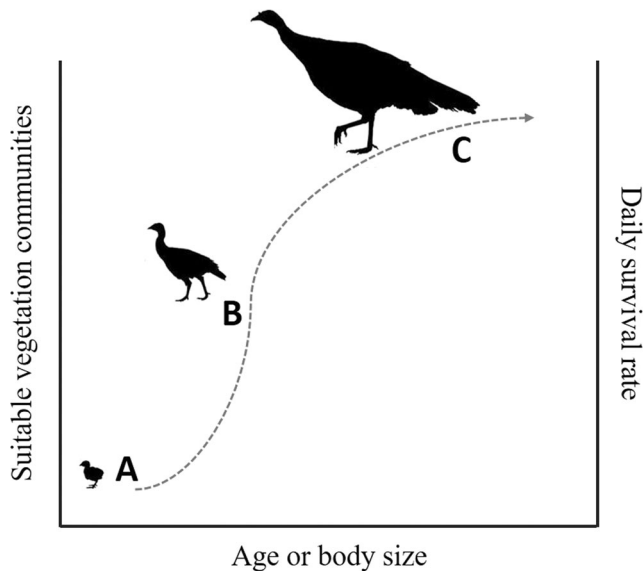


FIGURE 1 Theoretical diagram of relationship between body size as poults age and the relative quantity of suitable vegetation communities that provide wild turkey habitat. Although the least amount of lifespan is spent as poults (A), it is when they are most resource limited and survival is the lowest. Typical analyses would condense habitat selection across the poult stage (A) and the juvenile (28 days old) stage (B), which would result in under-representation of vegetation communities most selected when poults are very young. Survival and available habitat are greatest in the adult stage (C).

Observed declines in productivity of turkey populations, as indicated by declining poult to female ratios (Byrne et al. 2015), suggests brood habitat may be spatially or temporally limited across broad areas of the species' distribution. Brood survival is often linked with vegetation that reduces predation risk and increases foraging opportunity (Hubbard et al. 1999). Therefore, our objectives were to assess which vegetation communities were selected by brooding females and whether patterns of selection shifted as poults aged. We hypothesized that brooding females would alter habitat selection as poults developed and grew larger because more-developed poults with larger body sizes have wider thermoregulatory tolerances, more-diversified diets, and heightened predator avoidance capabilities (e.g., flight) than less-developed, smaller poults. We predicted trails and early successional areas would be selected by brooding females because they contain high invertebrate abundances for foraging, and we predicted hardwood communities would be selected because they had cooler air temperatures than other vegetation communities and limit thermoregulatory burdens on poults. We predicted young pine and mid-age pine stands would be avoided by brooding females throughout their first 4 weeks of life because of the high woody understory vegetation and low invertebrate abundances present in these pine communities.

STUDY AREA

We conducted our research on B. F. Grant Wildlife Management Area (WMA), Cedar Creek WMA, and surrounding private lands in the Piedmont region of Georgia, USA, during 2017–2020. The B. F. Grant WMA (4,613 ha) was in Putnam and Morgan counties, approximately 13 km northwest of Eatonton, Georgia. The B. F. Grant WMA was owned by the Warnell School of Forestry and Natural Resources at the University of Georgia and managed cooperatively with the Georgia Department of Natural Resources, Wildlife Resources Division (GADNR-WRD). The B. F. Grant WMA consisted of managed forest and was bordered by private experimental pasture grazing land for cattle. Grazing lands were mostly mixed fescue (*Festuca* spp.) fields where cattle were rotated across paddocks and maintained a high component of grass throughout the growing season. Forested areas consisted of loblolly pine (*P. taeda*) forests, mixed hardwood and pine forests, and hardwood lowlands containing white oak (*Quercus alba*), sweetgum (*Liquidambar styraciflua*), yellow poplar (*Liriodendron tulipifera*), hickory (*Carya* spp.), and other oak species (*Quercus* spp.). The understory was dominated by sweetgum, eastern redbud (*Cercis canadensis*), muscadine (*Vitis rotundifolia*), flowering dogwood (*Cornus florida*), and briars (*Smilax* spp., *Rubus* spp.), with various grass, sedge, forb, and fern species present in lesser amounts. Invasive species common on the site included privet (*Ligustrum sinense*), Japanese stilt grass (*Microstegium vimineum*), and Japanese honeysuckle (*Lonicera japonica*).

Cedar Creek WMA (16,187 ha) was 19.5 km south of B. F. Grant in Putnam, Jasper, and Jones counties on the Oconee National Forest, approximately 16 km southwest of Eatonton. Cedar Creek WMA was owned by the United States Forest Service (USFS) and managed in partnership between the USFS and GADNR-WRD. Cedar Creek WMA was bisected by Big Cedar Creek and Murder Creek, and contained portions of Glady, Cedar, and Badger creeks. Forested areas, invasive species, and understory composition were similar to that on B. F. Grant. Pasture land within Cedar Creek WMA and on adjacent private lands was nearly all managed for hay production, unlike on B. F. Grant WMA where it was nearly all managed for cattle grazing. Forest management on both sites was primarily through patch clear cuts, thinning, and prescribed fire that was applied on mature pine stands (>20 years old) on an approximately 3–5-year rotation. Young pine (3–8 years old) were not burned and mid-aged pines (8–19 years old) were infrequently burned. Surrounding private lands consisted of mixtures of planted pine forest for timber harvest, pasture used for livestock grazing and hay production, and hardwood stands.

Climate on our study sites was characterized by hot, dry summers (Jun–Sep) and cool, wet winters (Nov–Feb). Elevation ranged from 80 m to 250 m and the average elevation across our study areas was 156 m. Species known

to predate poult included coyotes (*Canis latrans*), bobcats (*Lynx rufus*), red tailed hawks (*Buteo jamaicensis*), and a wide variety of snake species (e.g., water snakes [*Nerodia* spp.], brown snakes [*Storeria* spp.], kingsnakes [*Lampropeltis* spp.], and American moccasins [*Agkistrodon* spp.]) and were available across the study regions.

METHODS

Capture and monitoring

We captured female wild turkeys using rocket nets from January–March 2017–2020. We aged captured individuals based on presence of barring on the ninth and tenth primary feathers (Pelham and Dickson 1992). We banded each individual with an aluminum rivet leg band (National Band and Tag Company, Newport, KY, USA) and 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 (23:58) and daytime locations hourly between 0500 and 2000 from capture until the battery died or the unit was recovered (Cohen et al. 2018). We immediately released all turkeys at the capture location after processing.

We located turkeys ≥ 2 times per week using handheld Yagi antennas and R4000 receivers (Advanced Telemetry Systems, Isanti, MN, USA) to monitor nesting activity. We downloaded GPS locations from each turkey ≥ 1 time per week and viewed GPS locations to determine when female locations became concentrated around a single point to indicate nest initiation (Yeldell et al. 2017a, b). Once females were known to be laying or incubating, we monitored each individual daily. After nest termination, we located 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. We located females that successfully hatched a nest every 3 days post-hatch and conducted brood surveys following methods from Chamberlain et al. (2020). For broods monitored after sunrise, we located the brooding female and approached close enough to observe the poults and verify females still had an active brood. 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, Healy 1992, Spears et al. 2007). Likewise, if we detected a brooding female roosting in a tree prior to 14 days post-hatch and could not detect poults, we assumed the brood was lost (Chamberlain et al. 2020). After females began tree roosting with poults, we approached within 30 m and observed the female leaving the roost site and we relied on visual and auditory detection of poults to confirm brood presence (Chamberlain et al. 2020). We considered a brood to be present if ≥ 1 poult was seen or heard 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 point we assumed the brood was lost (Chamberlain et al. 2020). We excluded individuals that successfully hatched a nest but were never visually confirmed to have poults.

Vegetation community classification

We developed a 30-m resolution land cover map using 2016 National Land Cover Database (NLCD; Jin et al. 2019) cover classifications. We classified 7 vegetation communities across the landscape useable to turkeys: young pine, mid-aged pine, mature pine, hardwoods, mixed-pine hardwoods, pastures, and early successional areas (Table 1). We first classified pine stands using the NLCD evergreen forest layer, which were characterized by loblolly pine plantations and occasional natural upland stands. We then delineated pine stand ages using time since last change (SCLAST) and annual land cover change (LCACHG) disturbance layers from the United States Geological Service Land Cover Map Collection 1 science products (Zhu and Woodcock 2014, Brown et al. 2020), which provide dates of most recent soil disturbances during 1 July 1983–1 July 2017. While some timber harvest occurred on our study

TABLE 1 Proportion of land cover types on study areas where eastern wild turkeys were monitored from 2017–2020, in Georgia, USA.

Vegetation community	NLCD ^a layers	% of study area
Hardwoods	Deciduous forest	22.6
	Woody wetlands	3.5
Mixed pine-hardwoods	Mixed forest layer	12.1
Young pine	Evergreen layer age 3–8 yr	8.1
Mid-aged pine	Evergreen layer age 9–19 yr	18.0
Mature pine	Evergreen layer age ≥20 yr	4.2
Early successional	Evergreen layer age 0–2 yr	0.6
	Grassy or herbaceous	5.6
Pasture	Pasture or hay	12.1
Unusable	Nine layers ^b	13.2

^aNational Land Cover Database.

^bUnusable consisted of developed layers, open water, barren land, cultivated crops, emergent herbaceous wetlands, and shrub-scrub layers.

areas during our study, we assumed that land cover designations across our study areas did not meaningfully change from 2017–2020. We defined pine stand age as the difference between SCLAST and LCACHG dates and the middle of our study period (2019). We then placed pine stands >2 years post-planting into one of 3 ages: young pine (3–8 years old), mid-aged pine (9–19 years old), and mature pine (≥20 years old) because of the marked differences in vegetation, forage, and thermal refuge conditions between these 3 seral stages (Appendix A, Table 1A). We considered pines ≥20 years old to be mature for analyses because these stands showed marked differences in vegetation community structure and were typically in pulpwood and sawtimber size classes subjected to harvest around ages 20–25 (Yeldell et al. 2017b).

We defined hardwood stands as a combination of NLCD deciduous forest and woody wetlands layers, which were characterized by lowland bottomland hardwoods, upland hardwood stands, or riparian corridors. We defined mixed pine-hardwoods as stands for which neither pine or hardwood species comprised >75% of the overstory (NLCD mixed forest layer) and that were characterized by upland systems or small transitions between upland pine stands and riparian bottomland hardwoods. We defined early successional sites as a combination of 0–2-year-old planted pine and NLCD grassy-herbaceous layer, which consisted of areas with >80% of grass or herbaceous cover. Early successional sites were similar across both WMAs and consisted of a variety of vegetation communities (i.e., old fields, wildlife openings, power lines, clear-cuts, pasture grasses, and recently planted pine) but represented areas with primarily herbaceous plants with low stature. Lastly, we defined pasture sites from the pasture-hay NLCD category. We separated pasture sites because pastures on our study area tended to have greater arthropod biomass than all other vegetation communities, including early succession fields (Appendix A, Figure A1; Nelson 2021). Hence, pastures on our study areas may provide better conditions for female turkeys to visually detect predators and allow for poults to forage on higher densities of prey (Chamberlain et al. 2020, Nelson et al. 2022).

We calculated a normalized difference vegetation index (NDVI) using 30-m resolution imagery from United States Geological Survey Landsat-8 Operational Land Imager in ArcMap 10.3 (Esri, Redlands, CA, USA) to examine vegetation density at each site (Bakner et al. 2022). We calculated NDVI for each year from the first 2 weeks of May when cloud cover was <10%. We choose NDVI values from the first 2 weeks of May because it coincided with our earliest hatched nest and acceptable cloud conditions. The NDVI is an indicator for the greenness of vegetation within each pixel, with higher values (on a scale from -1 to 1) representing greater vegetation density and

productivity. Thus, calculating NDVI allowed us to determine if vegetation density influenced habitat selection, as vegetation density is known to influence poult locomotion and foraging ability (Healy 1985).

Roads and trails within areas used by brooding females may influence selection (Miller and Conner 2007, Wood et al. 2019). Therefore, we obtained road data (i.e., roads and trails) within B. F. Grant and Cedar Creek WMAs from GADNR and used topologically integrated geographic encoding and referencing (U.S. Census Bureau 2017) data to identify roads outside the WMAs. Roads consisted of paved or gravel roads accessible to vehicles, whereas trails were paths maintained using herbicide applications and mowing or were firebreaks maintained by plowing before prescribed fire activities. Because we only expected trails to produce vegetation communities that brooding females would select (Wood et al. 2018, Chamberlain et al. 2020), we only calculated distance to trails across our study area.

Data analysis

To evaluate selection of vegetation communities and how selection changed as broods aged, we used a step-selection function (SSF) approach (Thurjfell et al. 2014) and conditional logistic regression to estimate resource selection functions (RSFs). Step-selection functions define availability conditional on the previous location and account for movement characteristics of the study animal and spatiotemporal dynamics of the available landscape. We fitted models using conditional logistic regression with strata formed by pairing observed locations with a set of random locations determined by generating random steps from the previous observed location (Compton et al. 2002, Manly et al. 2002). For each observed step at known GPS locations, we generated 5 random steps by drawing random step lengths from an exponential distribution with parameters estimated from our observed step lengths using maximum likelihood in package `fitdistrplus` (Delignette-Muller et al. 2020) in program R version 4.1.1 (R Core Team 2020). We extracted the vegetation community classification, NDVI, and distance to trails at each observed and random step, and recorded brood age as days since hatch for all locations on each day.

We calculated Pearson correlations (r) between pairs of covariates prior to building candidate models, and if covariates were highly correlated ($|r| \geq 0.6$), we retained only 1 covariate that we felt provided the simpler biological interpretation (Dormann et al. 2013). We built a suite of models representing our predictions and evaluated support for candidate models. We developed 6 candidate models (Table 2) to identify how selection of vegetation communities, NDVI, and distance to trails changed as broods aged for brooding females relative to random locations. Additionally, we included an interactive effect between brood age and vegetation communities, NDVI, and distance to trails in 3 of our candidate models. Specifically, this meant that brood age did not have a fixed effect in our analysis, so only the interaction between brood age and the aforementioned variables had an effect. Our models reflected our predictions that brooding female selection would be affected by distance to trails, vegetation communities and vegetation density, and a combination of these factors. We included a global model with all the aforementioned variables and a null model.

We performed model selection using Akaike's Information Criterion adjusted for small sample size (AIC_c) using package `AICcmodavg` (Mazerolle 2020). We considered the model with the lowest AIC_c score to be the most informative model given the data. We fitted models using conditional logistic regression for the SSF in package `survival` (Therneau and Lumley 2016), where cases were used sites (known brooding female locations) and controls were paired random steps. We provide the estimated beta coefficients and 95% confidence intervals and considered covariates to be statistically significant if 95% confidence intervals of the coefficient estimate did not contain zero.

RESULTS

We monitored 146 female turkeys between January–July 2017–2020, from which 175 nest attempts were initiated. Thirty-six of 175 (20.6%) nests produced a brood. Twenty of 36 (55.6%) broods had ≥ 1 poult survive until day 14 post-hatch, and 12 of 36 (33%) had ≥ 1 poult survive ≥ 28 days post-hatch (Figure 2). Naïve brood survival

TABLE 2 Akaike's Information Criterion with small sample bias adjustment (AIC_c), number of parameters (K), ΔAIC_c , adjusted Akaike weight of evidence (w_i) in support of the model, and log-likelihood (LL) for each final model examining brooding female eastern wild turkey habitat selection in Georgia, USA, during 2017–2020. Models used a conditional logistic regression with matched-pairs case-control sampling, where cases were known brooding female locations and controls were paired-random locations. R_j = the individual intercept estimate.

Model	K	AIC_c	ΔAIC_c	w_i	LL
Vegetation ^a + vegetation × brood age + trails ^b + trails × brood age + R_j	18	116,451.56	0.00	1.00	-58,207.77
Vegetation + vegetation × brood age + R_j	16	116,993.38	541.82	0.00	-58,480.69
Vegetation + R_j	8	117,088.09	636.53	0.00	-58,536.04
Trails + R_j	1	134,158.98	17,707.42	0.00	-67,078.49
Trails + trails × brood age + R_j	2	134,160.86	17,709.30	0.00	-67,078.43
R_j	0	134,866.90	18,415.34	0.00	-67,433.45

^aVegetation model: hardwoods + mixed pine-hardwoods + young pine + mid-age pine + mature pine + early successional + pasture + normalized difference vegetation index.

^bTrails is the distance (m) to trails.

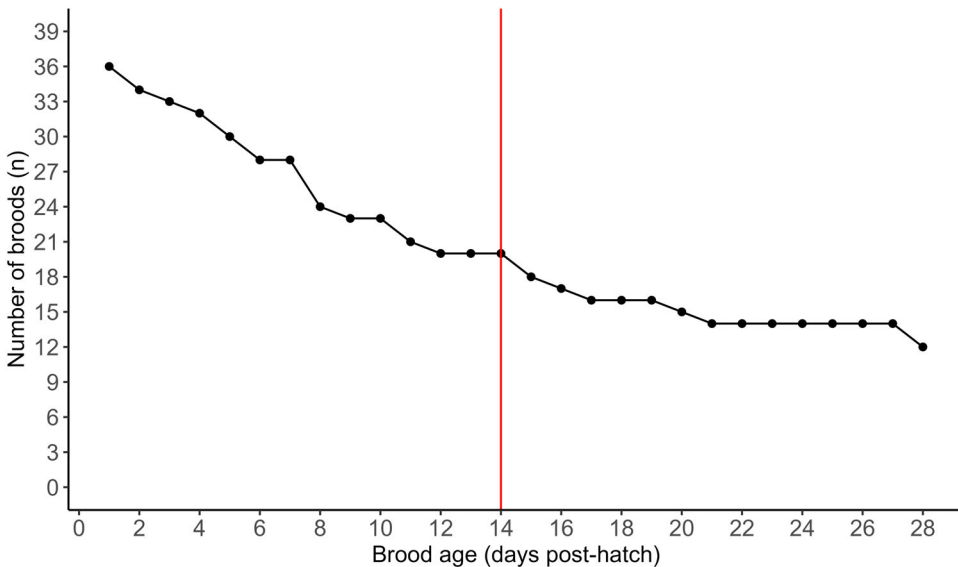


FIGURE 2 Number of female eastern wild turkeys brooding until day 28 post-hatch in Georgia, USA, 2017–2020. The red line indicates day 14 post-hatch, at which point poults can fly and their probability of daily survival increases.

was 0.60 after day 14 post-hatch, and 6.9% of nests produced a poult that lived to ≥ 28 days post-hatch. Mean distance between consecutive brood location steps (1 hour apart) was 91.9 m (range = 0.16–1,289.7 m). We did not identify correlation between any of our covariates.

Our best fitting model was the global model (Table 2). Brooding females selected hardwoods and sites closer to trails, and selection strength did not change as broods aged (Table 3). Brooding females were 1.221 (1.150–1.259; 95% CI) times more likely to select sites for every 100-m closer to trails and 22% of known brooding female locations were within 43 m from a trail. Brooding females selected for pastures and areas with increasing NDVI, but

TABLE 3 Parameter estimates (logit scale) and odds ratios for the top model examining brooding female eastern wild turkey habitat selection in Georgia, USA, during April–July 2017–2020. We provide beta estimates (β), odds ratios (OR), and scaled odds ratios (scaled) with 95% confidence intervals (CI). Scaled odds ratios represent how selection changed across the brood-rearing period from day 1 to day 28 post-hatch. Scaled odds ratios >1 indicate an increase in selection for that covariate.

Covariate	β	95% CI	OR	95% CI	Scaled	95% CI
Distance to trails ^a	-0.002	-0.0023--0.0014	0.998	0.9977-0.9986		
Hardwoods	0.324	0.1608-0.4865	1.382	1.1744-1.6267		
Mixed pine-hardwoods	0.075	-0.1122-0.2614	1.077	0.8939-1.2988		
Mid-age pine	-0.092	-0.2699-0.0853	0.912	0.7634-1.0890		
Young pine	-0.29	-0.5273-0.0535	0.748	0.5902-0.9479		
Mature pine	-0.023	-0.2699-0.2238	0.977	0.7635-1.2508		
Early successional	-0.024	-0.1818-0.1347	0.977	0.8338-1.1442		
Pasture or hay	0.730	0.5144-0.9452	2.075	1.6726-2.5733		
NDVI ^b	2.714	1.7897-3.6380	15.087	5.9874-8.0165		
Distance to trails:age	0.000	0.0000-0.0000	1.000	1.0000-1.0001	1.001	0.9996-1.0014
Hardwoods:age	-0.001	-0.0129-0.0113	0.999	0.9872-1.0114	0.978	0.6974-1.3718
Mixed pine-hardwoods:age	0.012	-0.0014-0.0254	1.012	0.9986-1.0257	1.399	0.9625-2.0343
Mid-age pine:age	0.003	-0.0095-0.0163	1.003	0.9905-1.0164	1.099	0.7662-1.5777
Young pine:age	0.022	0.0051-0.0379	1.022	1.0051-1.0387	1.826	1.1525-2.8932
Mature pine:age	-0.005	-0.0222-0.0125	0.995	0.9781-1.0126	0.873	0.5373-1.4182
Early successional:age	0.000	-0.0113-0.0122	1.000	0.9887-1.0123	1.012	0.7284-1.4072
Pasture or hay:age	-0.032	-0.0485--0.0159	0.968	0.9526-0.9842	0.405	0.2568-0.6399
NDVI:age	-0.084	-0.1492--0.0197	0.919	0.8614-0.9804	0.094	0.0153-0.5753

^aBeta estimates are reflective of probability as distance (m) from feature increases. Negative values are associated with selection.

^bNormalized difference vegetation index.

selection for these areas decreased as they aged (Table 3). Specifically, brooding females were 1.03 (95% CI = 1.016–1.050) times less likely to select pasture for each day they aged, and by day 28 post-hatch were 2.47 (95% CI = 1.561–3.888) times less likely to select pastures than day 1 post-hatch. In general, brooding females avoided young pine stands, but avoidance for young pine stands decreased as broods aged (Table 3). Brooding females were 1.02 (95% CI = 1.005–1.039) times more likely to select young pines for each day they aged as selection became more generalized for other vegetation community groups. Brooding females selected mixed pine-hardwoods, mid-aged pine, mature pine, and early successional areas in proportion to availability (neither selection nor avoidance), and selection for these communities did not change as broods aged (Table 3).

DISCUSSION

Habitat selection allows individuals to acquire resources and reduce predation risk, ultimately influencing individual fitness (Orians and Wittenberger 1991, Fontaine and Martin 2006). Because turkey poults have high mortality rates, are influenced by local environmental conditions, and have specialized diets during the first month of life

(Healy 1985, Hubbard et al. 1999, Spears et al. 2007, Backs and Bledsoe 2011), understanding habitat selection during the first weeks of life can inform managers as to what land cover types brooding females select and for how long these land cover types are uniquely preferred. Our data supported age-based shifts in habitat selection of brooding females, with brooding females becoming more generalized during the first month of brooding. Specifically, pastures and areas closer to trails were favored by brooding females initially, but as poults aged, selection for pastures declined. Our results indicate that age-based changes allow broods to exploit more land cover types, decreasing poult reliance on open areas and increasing importance of forested areas.

Pastures were initially more likely to be selected by brooding females and brooding females never selected early successional areas, which is in contrast to other work documenting strong selection of early successional areas (Hillestad and Speake 1970, Everett et al. 1985, Sisson et al. 1991). We suggest brooding females may not have selected early successional areas because this vegetation community was relatively rare across our study area (~6% of the landscape) and may have occurred too infrequently across the landscape for brooding females to rely on. Additionally, early successional areas on our study area had thicker understory vegetation and increased visual obstruction compared to pastures (Nelson et al. 2022). Pastures on our study area, which were primarily managed for hay and were cut 1–2 times during May–July, had relatively sparse understory vegetation (Table A1), potentially allowing visual detection of predators by brooding females and easier movement for younger poults; although, areas with vegetation communities dominated by forbs likely allow greater mobility than those dominated by grasses. Additionally, pastures had greater biomass of desired arthropod taxa (e.g., Orthoptera) than other vegetation communities in our study area (Table A1). Decreasing selection of pastures during ontogeny corresponds with increasing diversification of forage items such as seed, fruit, and leaf matter that poults use as they age (Healy 1992). Overall, our results indicate that in landscapes with a scarcity of early successional vegetation, communities providing open sight lines and forage like pastures may be selected during the youngest life stages of wild turkeys. This time corresponds with when broods are most vulnerable to predation and may in turn affect brood survival (Everett et al. 1980).

Sites with higher NDVI values were initially selected by brooding females, but selection of these sites decreased markedly as broods aged. Higher NDVI values represent denser vegetation that brooding females likely prioritize as both foraging and concealment cover (Nelson et al. 2022). Decreasing selection for higher NDVI values as broods age could represent broods shifting predator avoidance strategies as they develop and body size increases. Specifically, poults develop the ability to make short flights at approximately 2 weeks of age, so older poults with larger body sizes likely use flight to avoid predation risk (Peoples et al. 1995, Hubbard et al. 1999, Spears et al. 2007). Furthermore, decreasing selection for areas with higher NDVI values may be linked to poults becoming more mobile and able to exploit new prey resources as they age (Healy 1992), thus shifting the vegetation structure they select to target more diverse prey. Other authors have reported a lack of evidence for a direct relationship between NDVI and brood survival or brood habitat selection, but vegetation density is known to influence poult locomotion, foraging ability, and survival (Healy 1985, Spears et al. 2007). Features associated with vegetation density at the microsite level such as thermal refuge, presence of different arthropod taxa, and understory vegetation types, are likely more influential to poults than the overall vegetation density itself (Nelson et al. 2022).

Hardwoods were selected by brooding females, and selection for these sites did not differ as broods aged. We suggest brooding females selected hardwoods across our study area because they provided thermal refuge for poults and were the forest type with the lowest woody and highest grass understory composition (Table A1). Hardwoods in our study area had the coolest mean and maximum daytime temperatures and were the coolest sites relative to local weather stations (Table A1). Nelson et al. (2022) found that brooding females selected for cooler areas than random locations and non-brooding females. Furthermore, hardwoods on our study area had the lowest maximum visual obstruction (Table A1) and thus likely provided easier visual detection of predators by brooding females than in other vegetation communities. Additionally, Nelson et al. (2022) reported that brooding females selected areas with higher grass and lower woody understory groundcover composition. Therefore, brooding

females may have consistently selected for hardwoods because they provided the most favorable thermoregulatory and foraging conditions for poults given the limited presence of pasture and early successional sites on our study area.

Pine stands were initially avoided by brooding females despite comprising approximately a third of the landscape within our study area. Since the late 1990s, monoculture pine plantations have increased in abundance across the southeastern United States, whereas open canopy forest types have simultaneously declined (Hanberry et al. 2019, Oswalt et al. 2019), shifting space use, selection, and movement patterns of animals native to pine savanna systems (Smith et al. 1990, Demarais et al. 2017, Parish et al. 2019). Young pine stands were avoided by brooding females, although avoidance of these stands declined slightly as broods aged. Our data add to contemporary research suggesting undisturbed pine stands are not providing usable space for wild turkey broods. For example, Yeldell et al. (2017b) reported that broods were more likely to avoid pine stands ≥ 3 years post-burn, and young and mid-aged pine stands on our study area were rarely burned and contained little herbaceous understory (Appendix A, Table A1). Additionally, Smith et al. (1990) and Miller and Conner (2007) reported that brooding females were more likely to select managed pine stands with greater road densities and more frequent fire return intervals. Similarly, Wood et al. (2018) reported that pine sites burned that current year and 1-year prior were selected by brooding females during daytime. Young pine stands on our study sites were likely not selected initially by brooding females because infrequent disturbance regimes resulted in increased woody understory vegetation that brooding females avoid (Nelson et al. 2022). Although woody cover in the understory was only around 10%, Nelson et al. (2022) reported that brooding females avoided areas with $>10\%$ woody cover in the understory. Collectively, frequent disturbance (i.e., prescribed fire) may play an important role in making pine-dominated stands brood habitat (Yeldell et al. 2017b, Wood et al. 2018, Chamberlain et al. 2020), as habitat quality is strongly related to understory vegetative cover (Chance et al. 2020).

Broods became more generalized in habitat selection as they aged, and previous studies describing habitat selection by broods often reported conflicting or dichotomous results. For example, Williams et al. (1997) reported turkey broods were more likely to select hardwoods, whereas others have reported little to no selection of hardwoods (Yeldell et al. 2017a, Wood et al. 2019). In this study, 40% of broods failed by 14 days post-hatch, and only 33% of broods had ≥ 1 poult survive to ≥ 28 days post-hatch. While seemingly low, our results were similar to contemporary studies across Georgia and Louisiana, USA, that reported 24–36% of broods had ≥ 1 poult survive to ≥ 28 days post-hatch (Yeldell et al. 2017a, Wood et al. 2019, Chamberlain et al. 2020), reinforcing the important role of brood habitat when poults are younger, smaller, and unable to fly.

MANAGEMENT IMPLICATIONS

Our findings reinforce the importance of managers considering vegetation communities selected by young broods when poults have greater predation rates, have more specialized diets, and are less mobile than older age classes. Specifically, we recommend managing for vegetation communities providing open sight lines that allow brooding females to effectively detect predators. Managers interested in providing brood habitat would benefit from promoting the creation of new openings, as our data demonstrate how limited brooding cover was in the study area. Likewise, our data emphasize the importance of trails, as these were selected by brooding females during the first 2 weeks of life of broods and can facilitate locomotion and offer foraging opportunities for poults. The strong shifts in habitat selection that females exhibited during the first weeks of the brooding stage, coupled with how specialized broods were during this time, indicate vegetation conditions typically promoted by disturbance can provide quality brood habitat. Additionally, managers could consider promoting and conserving hardwood stands in pine-dominated landscapes, as brooding females selected them throughout the first month of the brood-rearing phase. Similarly, pine stands without recent disturbance are

not providing brood habitat, so managers interested in providing brood habitat would benefit by disturbing these stands using methods such as thinning or prescribed burning to create vegetative conditions selected by brooding females.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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APPENDIX A: ADDITIONAL VEGETATION INFORMATION

TABLE A1 Average site metrics for each vegetation community category where we monitored eastern wild turkeys in Georgia, USA, 2017–2020. Site metrics include percent woody, forb, grass, and total ground cover, maximum visual obstruction (VO; cm), arthropod biomass (kg/km²), orthoptera biomass (kg/km²), and mean ambient temperature difference (°C) from local weather stations. Details for data collection can be found in Nelson et al. (2022).

Vegetation community	Woody		Forbs		Ground cover		Grass		VO		Arthropod		Orthoptera		Temp	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Hardwoods	6	5.1	6	8.5	48	24.4	25	24.7	95.9	47.35	24.9	37.66	5.2	24.29	-2.8	1.34
Mature pine	8	6.2	4	3.0	46	19.2	12	10.5	130.9	51.85	11.3	18.00	1.9	8.51	-2.0	0.92
Mid-age pine	8	6.2	5	6.0	46	17.9	14	13.5	106.8	45.30	17.2	36.35	2.8	15.64	-2.2	0.92
Mixed pine-hardwoods	8	6.9	6	6.1	46	20.0	17	16.2	101.2	49.37	22.5	43.28	6.2	24.67	-2.3	1.44
Early successional	7	5.7	11	10.3	68	15.4	34	19.0	112.9	30.00	30.3	52.98	20.5	45.25	-1.2	1.88
Pasture or hay	4	5.3	8	11.6	74	26.8	57	31.2	104.1	34.05	60.2	69.89	43.4	66.57	-1.0	2.47
Young pine	10	9.0	10	9.3	56	25.8	21	17.5	102.5	40.44	11.1	23.44	3.2	16.61	-1.4	1.36

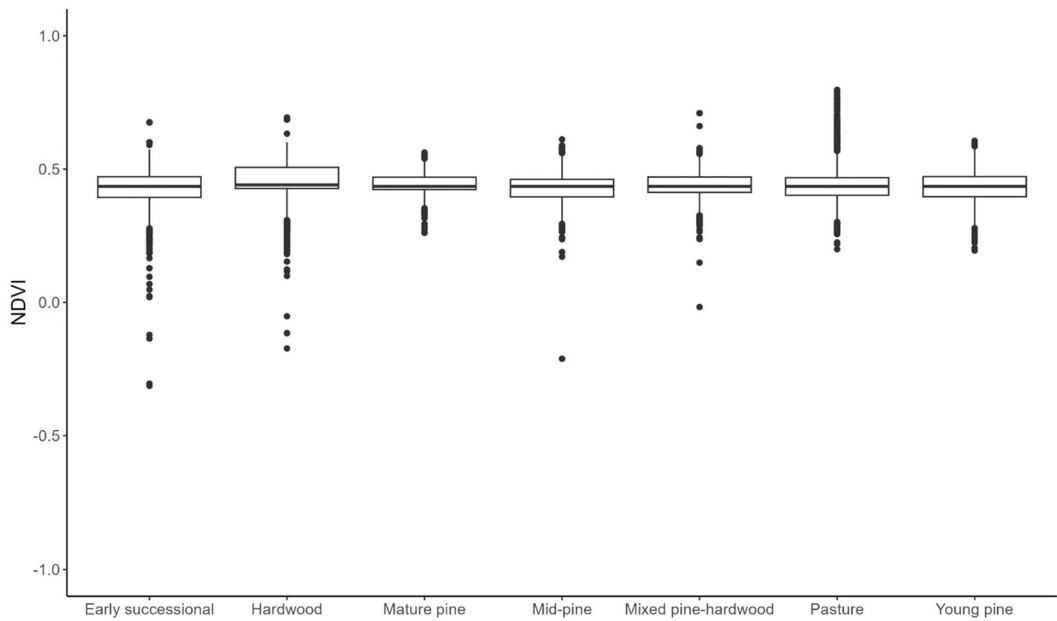


FIGURE A1 Average normalized difference vegetation index (NDVI) for each vegetation community category on study areas where we monitored eastern wild turkeys in Georgia, USA, 2017–2020.