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Research Article

Spatial Ecology and Resource Selection of Eastern Box Turtles

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ABSTRACT Eastern box turtles (*Terrapene carolina carolina*) are widely distributed throughout the eastern United States. Although once common throughout much of its distribution, the species has experienced declines in local populations. Understanding resource selection is important for the conservation of this species; however, few data exist on resource selection for eastern box turtles in the southeastern United States. We estimated home range and resource selection for 100 individual turtles in the Blue Ridge, Ridge and Valley, and Cumberland Plateau and Mountains physiographic regions in Tennessee, USA, from 2016 to 2018. We used step-selection functions to investigate eastern box turtle resource selection during May–August 2017 and May–August 2018 at 2 spatial scales. We classified vegetation type, measured vegetation composition and structure, recorded time since fire, and measured coarse woody debris abundance at 1,225 used telemetry locations and 1,225 associated available points. Home range sizes averaged 9.3 ha ± 3.0 (SE) using minimum convex polygon analysis, 8.25 ha ± 2.88 using 95% kernel density analysis, and 1.50 ha ± 0.56 using 50% kernel density analysis. Box turtles selected areas with greater visual obstruction at the 0–0.25-m level, greater amounts of 10-hour and 100-hour fuels (timelag categories used in fire-danger ratings), and greater litter depths compared to available locations. Box turtles were more likely to select areas with greater cover of brambles and coarser woody debris and were less likely to select areas with less vegetation cover. Vegetation type and time since last fire did not affect selection. Our data suggest that management activities that encourage greater understory vegetation cover, greater visual obstruction at the 0–0.25-m level, and greater bramble cover will enhance habitat quality for eastern box turtles. © 2020 The Wildlife Society.

KEY WORDS eastern box turtle, habitat selection, herpetology, radio-telemetry, resource selection, spatial ecology, step-selection function, *Terrapene carolina*.

Common box turtles (*Terrapene carolina*) and ornate box turtles (*Terrapene ornata ornata*) are widely distributed throughout the eastern, midwestern, and southwestern United States (Dodd 2001, Van Dijk 2011). Although once prevalent, concerns regarding population trends throughout portions of the common and ornate box turtle distributions have been expressed (Doroff and Keith 1990, Hall et al. 1999, Nazdrowicz et al. 2008, Van Dijk 2011, Keister and Willey 2015). Long-term monitoring has revealed >50% reductions of eastern box turtle (*Terrapene carolina carolina*; box turtle) populations in certain locales (Williams and Parker 1987, Hall et al. 1999). Moreover, fire is being used increasingly in hardwood ecosystems of the southeastern United States, and the effects of fire are poorly understood for many terrestrial reptiles, including eastern box turtles. The species is currently listed as vulnerable by the International Union for the Conservation of Nature (Van Dijk 2011). Risks include habitat loss and fragmentation, illegal collection, road mortality, and disease (Gibbons et al. 2000, Brown and Sleeman 2002, Nazdrowicz et al. 2008).

Robust resource selection data are lacking because of small sample sizes or analytical shortcomings. Box turtles are habitat generalists and are commonly associated with mature mesic hardwoods and floodplains, but patterns of habitat use for this cryptic species are not well defined (Sutton and Sutton 1985, Williams and Parker 1987, Conant and Collins 1991). Microsite characteristics could be more influential for resource selection than macrohabitat characteristics because of thermal needs, hydric requirements, and site fidelity (Dodd 2001, Rossell et al. 2006). As ectotherms, body temperature of box turtles depends on external conditions, and box turtles can reduce overall metabolic costs by selecting appropriate microclimates. Therefore, the thermal environment is an important habitat component. Body temperatures of 24–32°C allow for maximum activity (Adams et al. 1989). Box turtles behaviorally thermoregulate by selecting specific microclimates, limiting physical activity, basking, and by seeking aquatic resources

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(Adams et al. 1989, Huey 1991, Donaldson and Echternacht 2005). Additionally, box turtles create shallow depressions in a variety of substrates during unfavorable climatic conditions (Stickel 1950, Dodd 2001). These depressions (i.e., forms) can be constructed in leaf litter, herbaceous vegetation, or soil where the plastron is in contact with relatively cool soil (Dodd 2001). Box turtles may use wetlands during hot, dry periods and often make abrupt linear movements towards ephemeral ponds to soak or bury in the mud (Donaldson and Echternacht 2005). Aggregations of >30 box turtles have been recorded using ephemeral ponds for >20 consecutive days (Donaldson and Echternacht 2005).

Understanding resource selection relationships is important because box turtles exhibit site fidelity and generally have home ranges <10 ha (Stickel 1989, Donaldson and Echternacht 2005, Refsnider et al. 2012, Habeck et al. 2019). Relatively small home ranges and site fidelity can increase effects of local disturbance or habitat management (Currylow et al. 2012, 2013*a*). Understanding box turtle resource selection could allow land managers to manipulate vegetation communities to meet habitat requirements or improve existing habitat quality (e.g., food resources, nest site availability, ground cover; Dickson 2001, Morrison et al. 2006). Improving box turtle habitat to better meet ground cover and thermal conditions may reduce overall metabolic costs and affect individual survival, recruitment, and dispersal (Huey and Slatkin 1976, Huey 1991).

We estimated movement patterns and resource selection using a step-selection function of adult box turtles on 3 properties in the Blue Ridge, Ridge and Valley, and Cumberland Plateau and Mountains physiographic regions in Tennessee, USA, during 2016–2018. Our objectives were to estimate movement patterns of box turtles, including daily movement rates and home range size, assess the influence of vegetation composition and structure on resource selection at the microsite scale, and evaluate macrohabitat resource selection including vegetation type, time since fire, and effects of the thermal environment. Because box turtles behaviorally thermoregulate (Adams et al. 1989, Huey 1991, Donaldson and Echternacht 2005), we predicted that box turtles would select closed-canopy forest with deeper litter depths and select against recently burned areas at greater rates than would be expected at random.

STUDY AREA

We selected 3 study areas across 3 physiographic regions in east Tennessee during 2016–2018, to evaluate selection across a range of environmental conditions. East Tennessee experiences a temperate climate with warm summers and mild winters. Approximate annual seasons are spring (Mar–May), summer (Jun–Aug), fall (Sep–Nov), and winter (Dec–Feb). Common mammalian fauna at our study sites included white-tailed deer (*Odocoileus virginianus*), gray squirrel (*Sciurus carolinensis*), gray fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), eastern cottontail (*Syvilagus floridanus*), striped skunk (*Mephitis mephitis*), Virginia opossum (*Didelphis virginiana*), and coyote (*Canis latrans*). Each location varied in predominant vegetation types, topography, management, burn history, and burn regimes.

Study area A was a 32,374-ha wildlife management area in the Cumberland Plateau and Mountains physiographic region (Griffith et al. 1997). Elevations ranged from 425 m to 575 m and soils were mesic Dystrudepts, mesic Hapludults, and mesic Paleudults (Soil Survey Staff Natural Resources Conservation Service 2019). Annual precipitation and temperature normals were 140 cm and 13°C, respectively, from a nearby weather station (National Climatic Data Center 2019). Routine prescribed burning began in 2002 with the initiation of a 1,214-ha oak (*Quercus* spp.)-savanna restoration project, where our study efforts were concentrated. Primary vegetation types across the study area were shortleaf pine (*Pinus echinata*)-oak woodlands (61%) and shortleaf pine-oak savannas (25%). Closed-canopy deciduous forest (9%), closed-canopy mixed forest (3%), and wildlife openings (2%) were present. Managers aimed for a fire-return interval of 2–3 years to maintain woodlands and savannas.

Study area B was a 230-ha wildlife management area in the Blue Ridge physiographic region (Griffith et al. 1997). Elevations ranged from 242 m to 388 m and soils were Dystrochrepts, Dystrudepts, Eutrochrepts, Eutrudepts, Fragiudults, Hapludolls, Hapludults, and Paleudults (Soil Survey Staff Natural Resources Conservation Service 2019). Annual precipitation and temperature normals were 122 cm and 15°C, respectively, from a nearby weather station (National Climatic Data Center 2019). Study area B was dominated by early successional plant communities (61%) and closed-canopy deciduous forest (32%). Hardwood woodlands (4%) and closed-canopy eastern redcedar (*Juniperus virginiana*) stands (3%) were present. Lowland areas were flooded for waterfowl, whereas uplands were managed primarily for northern bobwhite (*Colinus virginianus*). Routine prescribed fire had been implemented on a 2–3-year fire-return interval since 1997 to maintain early successional plant communities for northern bobwhite.

Study area C was a 237-ha wildlife management area in the Ridge and Valley physiographic region (Griffith et al. 1997). Elevations ranged from 285–430 m and soils were mesic Dystrudepts, humic Hapludults, and Hapludalfs (Soil Survey Staff Natural Resources Conservation Service 2019). Annual precipitation and temperature normals were 137 cm and 13°C, respectively, from a nearby weather station (National Climatic Data Center 2019). Study area C was dominated by closed-canopy deciduous forest (43%) and closed-canopy eastern redcedar stands (29%). Closed-canopy mixed forests (21%), oak woodlands (3%), wildlife food plots (3%), and old-fields (1%) were present. All vegetation types at study area C had been burned periodically since 2004 to enhance habitat for eastern wild turkey (*Meleagris gallopavo silvestris*) and white-tailed deer.

METHODS

Turtle Capture

We captured adult box turtles using opportunistic finds, active searches, and wildlife detector dogs (Refsnider et al. 2011, Kapfer et al. 2012). We classified box turtles as adults if carapace length was >95 mm and mass was >170 g (Dolbeer 1969, Donaldson and Echternacht 2005). We did not capture turtles if carapace length was <95 mm and mass was <170 g. Opportunistic finds were incidental captures made while researchers were not actively searching for box turtles (e.g., turtles found crossing roads). Active searches were visual searches along meandering transects in all vegetation types on study areas (Currylow et al. 2012). Lastly, we used 5 wildlife detector dogs (Boykin spaniels) to find turtles through olfaction (Kapfer et al. 2012). Wildlife detector dogs were not leashed but responded to auditory commands. We walked directional paths with the wildlife detector dogs across study areas. All procedures were approved by the University of Tennessee Institutional Animal Care and Use Committee (UT-IACUC 2473-0616).

We recorded the initial capture location of each box turtle using a handheld global positioning system (GPS; Garmin GPSMAP 64st, Garmin International, Olathe, KS, USA). We measured body mass with a Pesola Medio-Line spring scale (Pesola, Feusisberg, Switzerland) to the nearest 10 g. We recorded the sex of each turtle using external physical characteristics including eye color, plastron shape, rear claw length, and position of the cloaca (Dodd 2001). We measured carapace length with a 20-cm digital caliper to the nearest millimeter.

Radio-Telemetry and Spatial Ecology

We affixed a very high frequency (VHF) radio-transmitter (model R2020, Advanced Telemetry Systems, Isanti, MN, USA) to the second pleural scute on the left side of each turtle using 5-minute epoxy. We affixed transmitters to the center of one scute to avoid inhibiting scute development. Transmitters and epoxy weighed 15 g (about 4% of average mass of an adult box turtle). We monitored box turtle movement using the homing method and direct observation with a folding 3-element Yagi antenna and an Advanced Telemetry Systems R-1000 telemetry receiver (Communications Specialist, Orange, CA, USA). We recorded box turtle locations 1–3 times/week from July to November 2016, May to November 2017, and from March to August in 2018. We recorded ≥1 location/turtle for each month during the inactive season (Dec–Mar) of 2016 and 2017. We recorded GPS locations at each telemetry location. We removed all transmitters at the end of the study using a jeweler's saw.

We used movement data from turtles with >40 locations during the active season (Apr–Nov) to estimate home ranges (Seaman et al. 1999). We calculated 100% minimum convex polygon (MCP) home ranges in ArcMap 10.5 (Esri, Redlands, CA, USA). We used Geospatial Modelling Environment (GME; Beyer 2012) and the plugin bandwidth to calculate 95% and 50% kernel density home range estimates (Gitzen et al. 2006, Rittenhouse et al. 2007, Bauder et al. 2015). We used the movement.pathmetrics tool in GME to calculate the straight-line distance between successive locations and estimated daily movement rate by dividing the total straight-line distance by the number of days between locations. We excluded inactive months (Dec–Mar) from average daily movement analysis.

Resource Selection

We used step-selection function (SSF) models to estimate resource selection from May to August of 2017 and 2018. Step-selection functions were developed to accommodate changing resource availability over time or as an animal moves across the landscape (Fortin et al. 2005). Step-selection functions break down the movement paths of animals collected with radio-telemetry into steps, which are defined as the straight-line segments between successive locations. These observed steps are then paired with a user-defined number of random steps of varying lengths and turning angles (based on empirical data or probability distributions of the observed steps) that are unique for each animal and step. The method then uses conditional logistic regression to evaluate various environmental predictors to discriminate between the used and available steps (Fortin et al. 2005, Duchesne et al. 2010, Thurfjell et al. 2014). Like all resource selection models, SSF models assume an animal will choose resources with maximum utility within a given set of available resources (Cooper and Millspaugh 1999, Hoffman et al. 2010).

We defined our choice set using movement.ssfsamples in GME. This tool was designed to facilitate the implementation of SSF models and generates sampled steps along a movement path (Fortin et al. 2005). We used empirical distributions of observed step lengths and turning angles to generate 1 available point for each telemetry point. We grouped those data into 18 20-degree bins and 26 equal step-length category bins within each telemetry interval. We conducted resource measurements at 1 used telemetry location and 1 associated available point (Table 1). We used only 1 location for each telemetry point because data for many variables had to be collected on site. We randomly selected locations using the random number generator function in Microsoft Excel. We excluded 18 box turtles from our step-selection analysis that experienced transmitter loss or failure.

We used a 4-m modified point-intercept transect to measure vegetation cover (Goodall 1952, Bonham 2013) at used and available locations. Point-intercept transects consisted of 4 transects, each 1 m in length, centered at the turtle telemetry or available location and oriented in each cardinal direction. We systematically placed a 1.37-m tall, narrow-diameter sampling pin at 20-cm intervals along transects. We recorded any plant species that touched the pin, along with the substrate (i.e., litter, bare ground, coarse woody debris, rock, other). We used percent cover of brambles, forbs, grasses, shrubs, trees, ferns, and vines as plant composition variables. We calculated percent cover by dividing the number of occurrences by the number of points ($n = 21$) along transects for each used and available location.

We recorded litter depths at the used and available turtle locations and at 60 cm from the center locations in each cardinal direction. We recorded any downed woody debris that intersected transects. Downed woody debris included any dead twig, branch, stem, or trunk on the ground

Table 1. Variables used to assess resource selection for eastern box turtles in 3 study areas between May and August, Tennessee, USA, 2017–2018.

Variable	Description	Units
Litter	$\bar{x}$ litter depth	cm
N1–n5	Visual obstruction estimate, (1 for each stratum)	0–5
Fuel 1	$\bar{x}$ count of 1-hour fuels	count/2-m transect
Fuel 10	$\bar{x}$ count of 10-hour fuels	count/2-m transect
Fuel 100	$\bar{x}$ count of 100-hour fuels	count/2-m transect
Fuel 1k	$\bar{x}$ count of 1,000-hour fuels	count/2-m transect
Fuel 10k	$\bar{x}$ count of 10,000-hour fuels	count/2-m transect
Species rich	Plant species richness	count/2-m transect
Brambles	Absolute cover of brambles	%
Fern	Absolute cover of ferns	%
Grass	Absolute cover of grass	%
Forb	Absolute cover of forbs	%
Shrub	Absolute cover of shrubs	%
Tree	Absolute cover of trees	%
Vine	Absolute cover of vines	%
No veg	Absolute cover of no vegetation	%
Litter	Absolute cover of litter	%
Bg	Absolute cover of bare ground	%
Rock	Absolute cover of rock	%
CWD	Absolute cover of coarse woody debris	%
Macro	Vegetation type[a]	1–8
Burn	Elapsed time since fire[b]	1–3

[a] 1 = deciduous, 2 = early succession, 3 = coniferous 4 = mowed, 5 = mixed forest, 6 = no vegetation, 7 = food plot, 8 = woodland.

[b] 1 = no fire since study initiation, 2 = 1 growing season since fire (1–12 months), 3 = 2 growing seasons since fire (13–24 months).

(Brown 1974). We classified downed woody debris as 1-hour, 10-hour, 100-hour, 1,000-hour, and 10,000-hour fuels with the following diameter classes: 1 hour = 0–0.5 cm, 10 hour = 0.6–2.5 cm, 100 hour = 2.6–7.5 cm, 1,000 hour = 7.6–20.0 cm, and 10,000 hour >20.0 cm. These classes were equivalent to timelag categories used in fire-danger ratings (U.S. Forest Service 1956, Fahnestock 1970). We measured vertical structure using a modified Nudds board divided into 5 strata, with stratum 1 being the uppermost stratum and stratum 5 being closest to the ground (Nudds 1977). The top 3 strata each measured 0.5 m × 0.18 m, whereas the bottom 2 strata each measured 0.25 m × 0.18 m. We used 0.25-m dimensions for the bottom 2 strata to determine structural differences at a finer scale relevant to box turtle height, as opposed to the original Nudds stratification. We measured vertical structure 5 m east and 5 m west of the used and available locations. One researcher kneeled and estimated the percent cover of each stratum, assigning a value of 0 to 5 for each stratum, whereby 0 = no vegetation, 1 = 1–20% obstruction, 2 = 21–40% obstruction, 3 = 41–60% obstruction, 4 = 61–80% obstruction, 5 = 81–100% obstruction. We averaged litter depth, downed woody debris classes, and each Nudds stratum for each sample point, resulting in 1 value for each measurement.

We delineated vegetation types using aerial imagery from the National Agricultural Inventory Program (U.S. Department of Agriculture, Farm Service Agency) and Google Earth (Google, Mountain View, CA, USA) in ArcMap 10.5. We validated vegetation types by ground-truthing areas during the summer of 2016 and adjusted accordingly. We categorized vegetation types into the following 8 categories: deciduous (areas dominated by deciduous forest with ≥80% canopy closure), early succession (areas maintained in early successional vegetation by periodic prescribed burning, mowing, or disking), coniferous (areas dominated by closed-canopy pine or eastern red-cedar), mowed (areas mowed for aesthetics), mixed forest (areas dominated by a mix of closed-canopy deciduous forest and closed-canopy coniferous forest), no vegetation (areas lacking any vegetation cover), food plot (areas planted as a supplementary food source for wildlife), and woodland (areas with 30–80% canopy closure with an understory dominated by grasses, forbs, and shrubs).

We used the Extract by Points tool in ArcMap 10.5 to extract the vegetation type associated with each telemetry and available point. Similarly, we extracted the time since fire of each telemetry and available point using a geospatial database of burned units at each site. We classified telemetry and available points into 3 categories to represent the number of growing seasons elapsed since fire: no fire since study initiation, 1 growing season since fire (1–12 months), and 2 growing seasons since fire (13–24 months).

We measured and compared thermal variation within each vegetation type at each site using a handheld infrared thermometer (Omegascope, model OS530 series, Norwalk, CT, USA) to ascertain the influence of thermal variation in habitat selection. We randomly placed 15 transects in each vegetation type at each site using the Create Random Points tool in ArcMap 10.5. We recorded surface temperatures at 1-m increments along a 10-m transect under maximum solar radiation (1100–1400) between 20 July and 14 August 2018.

We measured daily temperature fluctuations in relation to ambient temperatures among vegetation types by randomly placing 10 thermal stations in each vegetation type at each site. We generated random thermal-station locations using the Create Random Points tool in ArcMap 10.5. Thermal stations were temperature data loggers (iButton model DS1921G-F5, Maxim Integrated, San Jose, CA, USA) attached to a wooden stake with a small-diameter string. We attached iButtons to the string and to the ground using clear double-sided tape. We programmed each iButton to record temperatures at 1-hour intervals for ≥48 hours. We recorded ambient temperatures from weather stations within 9.5 km of the respective study sites.

Statistical Analysis

We performed a 2-way analysis of covariance (ANCOVA) using Program R 3.3.1 (R Core Team 2016) to compare mass between male and female box turtles and among study sites. We used carapace length as a covariate for mass because carapace length is positively correlated with body mass (Dodd 2001, Howey and Roosenburg 2013). We checked normality and equality of variances using the Shapiro-Wilk test and the Levene's test, respectively, for mass, movement, and thermal analyses. We used the Tukey's honestly significant difference test to compare means at $\alpha = 0.05$ for mass analyses (Welkowitz et al. 2012). We used 2-way analysis of variance (ANOVA) to compare 100% MCP, kernel density estimates, and average daily movement between male and female box turtles and among study sites. We used a log transformation prior to conducting ANOVAs on home range and movement data to meet normality assumptions. We used a 1-way ANOVA and least-squares mean to compare thermal variation within and among vegetation types. We performed Kruskal–Wallis tests and used least-squares means to compare fuel loads and litter depths among major vegetation types and time since fire classifications.

We used COXPH and COXME packages in Program R 3.3.1 to fit a Cox proportional hazards regression model to perform our SSF (Therneau 2013, Brooke et al. 2015). We did not detect differences in resource selection of any variable among years or study sites so we pooled the data (Table S1, available online in Supporting Information). We performed a correlation analysis and removed 1 variable of any pair of correlated variables (i.e., Pearson's $|r| > 0.75$) based on their perceived biological significance. We fit univariate models with and without random effects to determine resource selection of box turtles. We developed the best main effects model, main effect + quadratic terms, main effect + interaction terms, and main effect + quadratic terms + interaction terms. Finally, we fit additional models with site and turtle identifiers as random terms to determine if variation among box turtles or study sites needed to be included to improve the models (Duchesne et al. 2010).

We used the purposeful model-building strategy to determine candidate SSF models (Fortin et al. 2005, Hosmer et al. 2013, Brooke et al. 2015). We first developed univariate models to analyze each variable independently to determine its influence on resource selection (Brooke et al. 2015). We used variables with $P < 0.25$ to create a global model (Brooke et al. 2015). We removed nonsignificant variables ($P > 0.05$) individually from the global model, based on the magnitude of their P-value, until our model only contained significant ($P < 0.05$) variables (Brooke et al. 2015). We added variables that were eliminated in the first step, 1 by 1, into the reduced global model to determine if the inclusion of previously eliminated variables changed model or variable significance (Brooke et al. 2015). Once we created the best main-effects model, we incorporated quadratic and interaction terms and included those if $P < 0.05$ (McCracken et al. 1998, Brooke et al. 2015).

We used Akaike's Information Criterion (AIC) and P-values to compare models and considered models with $\Delta\text{AIC} < 2$ to be competing models. We considered the most parsimonious model as the most-supported model when $\Delta\text{AIC} < 2$ (Burnham and Anderson 2002). We used the most-supported model to predict the odds of selection given the significant variables. We created selection ratios through slope estimate (β_i) exponentiations, and only considered variables as significant influences on resource selection when their confidence limits did not overlap zero (McDonald et al. 2006). We used a variable adequacy analysis to estimate the importance of variables within the top model (Harrell 2001, Brooke et al. 2015).

RESULTS

Spatial Ecology

We captured, radio-marked, and radio-tracked 118 adult box turtles (61 males, 57 females) from July 2016 to July 2018. We captured 69 turtles via opportunistic finds, 15 during active searches, and 34 with the use of wildlife detector dogs. Box turtle mass did not differ among sites ($P = 0.134$) but did differ with sex ($P < 0.001$). The average mass of male turtles was 389 ± 8.1 g (SE), whereas the average mass of females was 417 ± 8.6 g. We collected ≥40 locations for 100 box turtles ($\bar{x} = 77.3 \pm 1.8$, range = 41–104) from which we calculated home range and analyzed movements. Of the 7,705 locations, 1,024 locations were recorded in 2016 ($\bar{x} = 17.4 \pm 2.3$ locations/individual), 3,817 in 2017 ($\bar{x} = 38.1 \pm 3.8$ locations/individual), and 2,864 in 2018 ($\bar{x} = 28.9 \pm 2.9$ locations/individual).

Movement rates and home ranges did not differ among male and female box turtles (Table S2, available online in Supporting Information). Kernel density estimates and average daily movement differed by site (Table A1). The average MCP home range was 9.30 ± 3.00 ha. The average 95% and 50% kernel density estimates were 8.25 ± 2.88 ha and 1.50 ± 0.56 ha, respectively. The average daily movement rate during the active season was 11 ± 0.21 m/day (Fig. 1). We documented 22 of the 118 turtles changing hibernacula locations ≥1 time during inactive periods with an average relocation distance of 7.4 ± 0.9 m.

Resource Selection

We used 1,225 telemetry locations and 1,225 associated available locations from 100 box turtles ($n = 32$, 34, and 34 at study area A, B, and C, respectively) to develop step-selection models. Of the 1,225 locations, 616 locations were recorded in 2017 (May = 41 locations, Jun = 263, Jul = 303, Aug = 9), and 609 locations were collected in 2018 (May = 93 locations, Jun = 251, Jul = 244, Aug = 21). We removed the following variables from our models as a result of correlation analysis: visual obstruction at the 0.25–0.50 level, visual obstruction at the 1.0–1.5 level, and leaf litter cover. We fit 109 models, including 27 univariate models without random effects and 9 with random effects. Our top model contained 7 variables and 1 quadratic term (Table 2): box turtles selected areas with greater cover of brambles, more coarse woody debris, greater litter depth, greater visual obstruction at the 0–0.25-m level, and greater 10-hour and 100-hour fuel abundance compared with available points and were less likely to select areas with reduced vegetation cover (Table 3).

Selection ratios indicated the odds of a turtle selecting a location decreased 3.9% with every 1% increase in percent cover with no vegetation (Table 3). The model was improved with the addition of a quadratic no vegetation cover term ($\Delta\text{AIC} = 8.27$). We calculated a selection ratio of 1.00 for the no vegetation cover quadratic term, indicating odds of selection for percent cover with no vegetation stabilized at 73%. The odds of a box turtle selecting a location increased 1.4% with every 1% increase in bramble cover, whereas selection increased 0.8% with every 1% increase in visual obstruction at the 0–0.25-m level. Probability of selection was 100% once bramble cover and visual obstruction

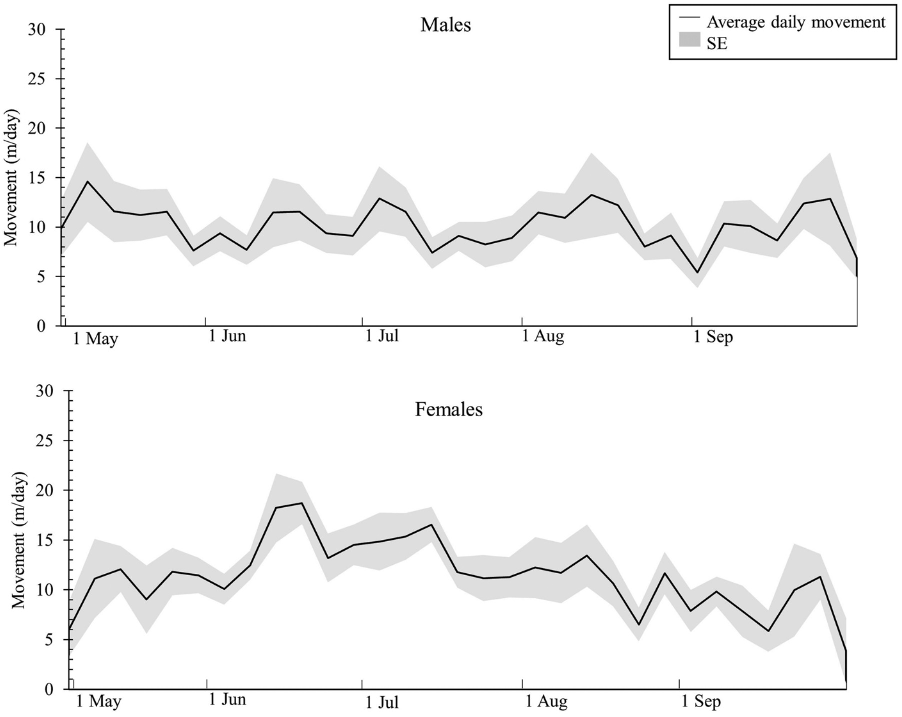

Figure 1. Average daily movements for eastern box turtles at study area A ($n = 32$ turtles), B ($n = 34$), and C ($n = 34$) combined, Tennessee, USA, 2016–2018.

at the 0–0.25-m level were ≥22% and ≥31%, respectively. Odds of selection increased 43.8% with every 1-cm increase in litter depth. Probability of selection was 100% when litter depths were ≥4 cm. Odds of selection increased 2.3% with every 10% increase in coarse woody debris. Odds of selection increased 4.4% and 12.9% with each additional piece of 10-hour and 100-hour fuel per 2-m transect, respectively. Probability of selection was 100% when the average number of 10-hour and 100-hour fuels were ≥13 and ≥8 per 2-m transect, respectively. Probability of selection was 100% once coarse woody debris cover was ≥18%. Litter depths and fuel loads differed between time-since-fire classification and vegetation type (Tables S3 and S4, available online in Supporting Information). Box turtles did not exhibit selection or avoidance for any major vegetation type ($P = 0.248$) or any elapsed time-since-fire classification ($P = 0.391$).

Mowed areas, early successional vegetation, and woodlands had higher temperatures under the same ambient conditions compared to other vegetation types (Fig. 2). We recorded lower temperatures for mixed forest, deciduous forest, and coniferous forests compared with woodlands and early successional vegetation under the same ambient conditions at each study site (Fig. 2). During peak solar radiation (1100–1400), we recorded the greatest surface temperatures in mowed areas at study area A and study area C, and in woodlands at study area B (Fig. 3). We recorded the greatest variability in surface temperatures during peak solar radiation in mowed areas at study area A compared with all other available vegetation types, and in woodlands at study area B and study area C. During peak solar radiation, we recorded the lowest surface temperatures, with the least variability, in deciduous forests at all sites.

DISCUSSION

Microsite factors were more influential on box turtle habitat use than macrohabitat factors, such as vegetation type and time since fire, partially refuting our hypotheses. Lack of

Table 2. Models explaining resource selection of eastern box turtles between May and August, Tennessee, USA, 2017–2018. Support for each model is indicated by the Akaike's Information Criterion values (AIC) and log likelihood (log[L]).

Model[a]	df	log(L)	AIC	ΔAIC	Model weight	Model likelihood
Litter + VO + fuel 10 + fuel 100 + brambles + no veg + CWD + no veg^2 + (litter|site) + (VO | site) + (fuel 10|site) + (fuel 100|site) + (CWD | site) + (no veg^2 | site) + (brambles | site) + (no veg|site)	10	−676.90	1,374.23	0.00	0.58	1.00
Litter + VO + fuel 10 + fuel 100 + brambles + no veg + CWD + no veg^2	8	−679.47	1,374.94	0.71	0.48	0.70
Null	0	−839.40	1,678.80	304.57	0.00	0.00

[a] litter = average litter depth, VO = visual obstruction at the 0–0.25-m level, fuel 10 = count of 10-hour fuels per 2-m transect, fuel 100 = count of 100-hour fuels per 2-m transect, brambles = percent cover of brambles, no veg = percent cover of no vegetation, CWD = percent cover of coarse woody debris, no veg^2 = percent cover of no vegetation quadratic term, |site = random effect of study site.

Table 3. Model coefficients, standard errors, confidence intervals, and selection ratios for the top model for eastern box turtle resource selection between May and August, Tennessee, USA, 2017–2018. Variables are ranked based on variable adequacy analysis by importance (positive or negative, highest importance = 1).

Variable[a]	Estimate	SE	95% CI		Selection ratio	Rank
No veg	−0.039	0.007	−0.052	−0.026	0.961	1
Brambles	0.014	0.003	0.009	0.019	1.014	2
VO	0.008	0.003	0.002	0.012	1.008	3
Litter	0.364	0.044	0.276	0.45	1.438	4
No veg^2	<0.001	<0.001	0.0001	0.0004	1.000	5
Fuel 10	0.043	0.018	0.008	0.078	1.044	6
Fuel 100	0.121	0.057	0.009	0.234	1.129	7
CWD	0.023	0.004	0.014	0.031	1.023	8

[a] no veg = percent cover of no vegetation, brambles = percent cover of brambles, VO = visual obstruction at the 0–0.25-m level, litter = average litter depth, no veg^2 = percent cover of no vegetation quadratic term, fuel 10 = count of 10-hour fuels per 2-m transect, fuel 100 = count of 100-hour fuels per 2-m transect, CWD = percent cover of coarse woody debris.

selection for cooler macrovegetation types indicates that suitable microclimates for box turtles exist in many vegetation types across the landscape. Various species and subspecies of box turtles (e.g., eastern box turtle, three-toed box turtle [*T. c. triunguis*], Gulf Coast box turtle [*T. c. major*], ornate box turtle) are often associated with particular vegetation types; however, habitat management efforts that focus on creating appropriate microsite conditions likely are

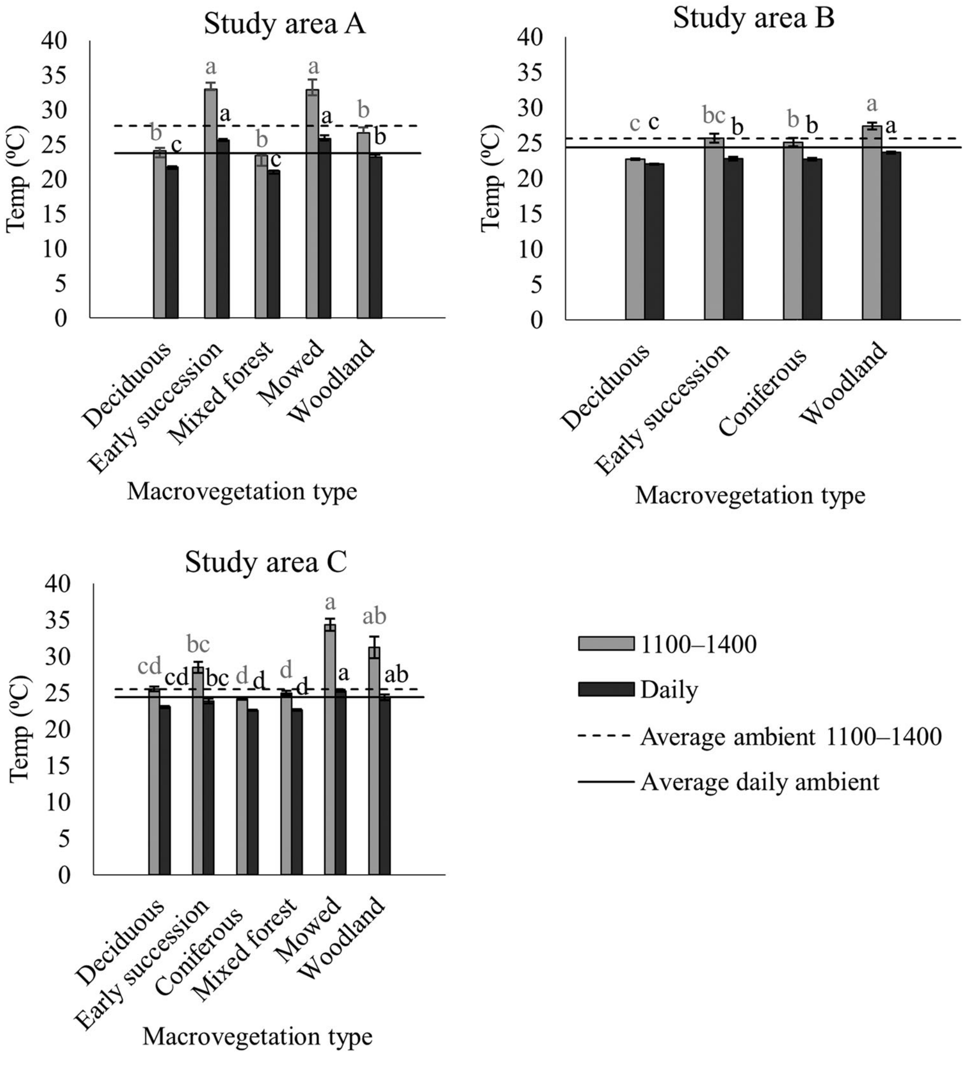

Figure 2. Average daily temperature and average temperatures during maximum solar radiation (1100–1400) for vegetation types at study area A, B, and C, Tennessee, USA, August 2018. Mixed forest and mowed vegetation were absent from study area B. Gray letters represent results of Tukey test comparisons of average temperatures during maximum solar radiation, whereas black letters represent comparisons of average daily temperatures. Averages with the same letters do not differ. The dashed line represents ambient temperature at the weather station collected under maximum solar radiation. The solid line represents average daily ambient temperature at the weather station. Weather stations were within 9.5 km of study sites. We measured daily temperature fluctuations between vegetation types using thermal stations placed within each vegetation type.

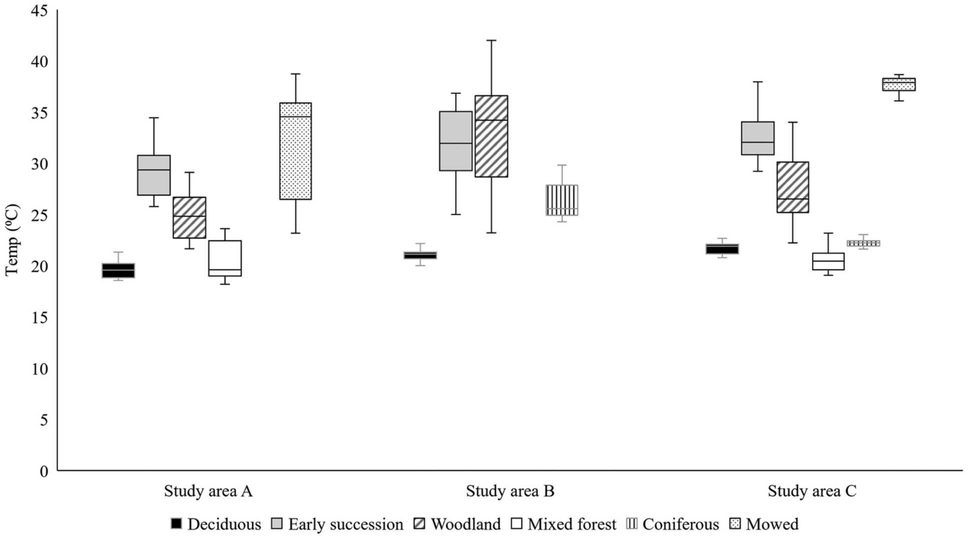

Figure 3. Average surface temperatures during peak solar radiation (1100–1400) within available vegetation types, Tennessee, USA, August 2018. Mixed forest and mowed vegetation were absent from study area B. We measured thermal variation of surface temperatures within each vegetation type using a handheld infrared thermometer.

more effective than managing for particular vegetation types. Specifically, total ground cover, litter depth, bramble cover, coarse woody debris, and vegetation structure influenced resource selection in our study. A lack of understory vegetation was the most important predictor of selection, followed by bramble cover and visual obstruction at the 0–0.25-m level. Vegetation growth habits (e.g., forb, grass, shrub, tree, vine) were not important variables of resource selection, except for bramble cover, which was the second-most influential variable affecting resource selection.

Although litter depth and fuel loading were important indicators of resource selection, increased litter depths and fuel abundance were less important if vegetation cover was ≥35% and visual obstruction at the 0–0.25-m level was ≥31%. Increased litter depths and fuel abundance became important if vegetation cover was limited, likely resulting from selection of appropriate microclimates.

Microsite temperature variation is determined largely by vegetation composition and structure (Rossell et al. 2006, Fredericksen 2014, Elmore et al. 2017, Parlin et al. 2017). Box turtles may reduce overall metabolic costs by selecting appropriate microclimates within vegetation types, by selecting areas with increased vegetation cover, or by burrowing into litter (Stickel 1950, Dodd 2001, Donaldson and Echternacht 2005, Rossell et al. 2006). We observed that box turtles selected areas with greater leaf litter depths than would be expected at random. Concealment in leaf litter or understory vegetation lessens the risk of evaporative water loss and can aid in maintaining a thermal optimum (Stickel 1950, Dodd 2001). Deeper litter layers, however, may lead to increased risk of mortality if prescribed fire is used to manage the vegetation type (Harris et al. 2020). Box turtles are physiologically incapable of sustaining high body temperatures with temperatures of 24–32°C allowing for maximum activity (Adams et al. 1989). Box turtles were commonly found burrowed alongside coarse woody debris in areas with reduced vegetation cover and when ambient temperatures exceeded 27°C.

Turtles did not exhibit selection for or avoidance of major vegetation types, despite differences in litter depth, fuel loads, and temperature among types. Although certain vegetation types were consistently warmer than others during peak solar radiation, the thermal variability that was present within those vegetation types indicates that thermal refuges were present (e.g., areas with increased vegetation cover, visual obstruction, and leaf litter depths). For example, deciduous forest floors were 2.5°C cooler than ambient temperatures under maximum solar radiation, and 11.1°C and 5.9°C cooler than mowed areas and early succession areas, respectively, during the same ambient conditions. Temperatures in early successional plant communities at study area B were similar to ambient conditions under maximum solar radiation, whereas temperatures in early successional plant communities at study area A and study area C were warmer than ambient temperatures under maximum solar radiation. Temperatures in early successional plant communities at study area B were similar to ambient conditions because of increased vegetation cover and vertical structure compared with other sites. We recorded consistently warmer surface temperatures in woodlands under maximum solar radiation compared with deciduous forests at each site. Temperatures in woodlands at study area A were cooler than ambient temperatures under maximum solar radiation because of increased canopy cover and a well-developed herbaceous layer. Despite cooler temperatures during summer months, turtles did not exhibit selection towards cooler vegetation types at our latitude. Furthermore, variation in surface temperatures in early successional plant communities was 4 times greater than that in deciduous forests under maximum solar radiation, suggesting that though certain vegetation types were consistently warmer, relatively cool areas of refuge were present.

Temperatures in woodlands were consistently more variable than temperatures in coniferous forests.

Lack of selection for major vegetation types and time since fire likely are a result of site fidelity, in addition to presence of microsites with adequate thermal conditions. Box turtles typically do not abandon home ranges despite disturbance (Stickel 1950, Dodd 2001). Size of box turtle home ranges varied considerably among individuals but 90% of MCP home ranges were <10 ha. Average daily movements were short (11 m), but turtles (especially females) occasionally made long-distance movements up to 1.26 km, presumably for nesting. Our reported average MCP home range (9.3 ha) was 4.5 times larger than the 1.9 ha reported by Donaldson and Echternacht (2005) based on 13 thread-trailed turtles in east Tennessee. Our MCP home range estimates were more similar to average home ranges (10.3 ha) of box turtles in fire-maintained longleaf pine (*Pinus palustris*) stands in Georgia, USA (Greenspan et al. 2015). We documented a long-distance movement of 1 adult male, which inflated the average home range estimate by 2.74 ha. The male turtle made a linear movement of 3.46 km from its core home range. The actual distance would have been longer, but we removed the transmitter while the turtle was continuing to move away from the core home range and onto properties where we could no longer monitor the turtle. Long-range movements of up to 1.9 km have been documented previously (Williams and Parker 1987, Currylow et al. 2013*b*, Greenspan et al. 2015), but to our knowledge, this is the longest reported linear movement of a tracked eastern box turtle that was not translocated. Our average MCP estimate with the exclusion of the 1 male outlier was 6.6 ha and was similar to the overall mean of 50 studies (7.54 ha) reported by Habeck et al. (2019).

We recorded 6 females making abrupt, linear excursions to nest. It is not known why box turtles travel long distances to nest, though it may be that females return to their own natal region or that nesting sites are uncommon on the landscape (Dodd 2001, Kipp 2003). Nesting locations were commonly associated with management activities, especially soil disturbance. Of the 6 recorded nesting females, 2 excavated nests along disked firebreaks, whereas others excavated nests in a disked field, a recently burned pine stand, a recently thinned hardwood stand, and along a roadside. Similarly, we documented annual movements up to 1.26 km from core home ranges for an additional 12 females. The purpose of these movements is unknown but were likely related to unobserved nesting activity because box turtles can deposit eggs and cover nests in <2 hours (Congello 1978). These long-distance movements occurred annually during the nesting season for each of the 12 females and followed the same travel path during successive years. Similar behavior has been documented previously and may suggest some level of nesting-site fidelity (Stickel 1950, Wilson and Ernst 2008). Exploratory excursions, feeding forays, and trips to overwintering or nesting sites up to 900 m from the core home range have been reported (Stickel 1950, Dodd 2001, Greenspan et al. 2015). Our findings of average daily movement of 11 m/day was lower than previously documented reports of 26–40 m/day (Strang 1983, Donaldson and Echternacht 2005, Iglay et al. 2007), but Strang (1983) and Donaldson and Echternacht (2005) used thread trailers that provide more fine-scale movement data than VHF telemetry data.

Although box turtles have been associated with mature, mesic hardwoods, little research has measured selection of vegetation types or microsites. We determined that microsite resources, including vegetation composition and structure, were more important than large-scale vegetation types when determining resource selection for box turtles. Box turtles did not select for or against major vegetation types or time-since-fire classifications; instead, box turtles more frequently selected areas with increased understory vegetation, greater bramble cover, and increased visual obstruction at the 0–0.25-m level. Small home ranges and limited movements increase the need to focus habitat management efforts towards improving vegetation conditions and creating appropriate thermal conditions.

MANAGEMENT IMPLICATIONS

Our results suggest managers can positively influence box turtle habitat by increasing vegetation coverage, with emphasis on visual obstruction at the 0–0.25-m level. At our study sites, vegetation cover, structure, and thermal heterogeneity were increased in stands that allowed ≥20% sunlight to reach the forest floor following thinning or cutting. Managers used prescribed fire during the dormant season or late in the growing season to maintain increased understory vegetation and bramble cover at our study sites. Our study indicates low-intensity fire in closed-canopy forests should be used with caution where box turtles are of concern because fire in stands allowing <20% sunlight to the forest floor consumes leaf litter and often does not stimulate additional groundcover; increased litter depth and groundcover were associated with increased selection in our study.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

APPENDIX A. HOME RANGE AND MOVEMENT DATA

Table A1. Comparison of eastern box turtle average daily movement and home range estimates among study areas using 2-way analysis of variance for pooled male and female data for the active season (Apr–Nov), Tennessee, USA, 2016–2018. Values with the same letters are not different.

		Tukey letter	Min.	$\bar{x}$	SE	Max.
Daily movement ($\bar{x}$)[a]	Study area A	A	5.2	13	1.0	25.8
	Study area B	B	4.9	9	0.6	20.5
	Study area C	AB	4.6	10	0.6	19.8
	Overall		4.6	11	1.5	25.6
Minimum convex polygon[b]	Study area A	A	0.6	19.8	9.1	282.2
	Study area B	A	0.4	4.5	1.1	38.5
	Study area C	A	0.5	4.3	0.6	15.5
	Overall		0.4	9.3	3.0	282.2
50% kernel density[c]	Study area A	A	0.1	3.5	1.7	54.1
	Study area B	B	0.1	0.6	0.1	1.8
	Study area C	B	0.2	0.5	0.1	2.2
	Overall		0.1	1.5	0.6	54.1
95% kernel density[d]	Study area A	A	0.7	18.9	8.8	270.8
	Study area B	B	0.6	3.3	0.5	13.6
	Study area C	B	0.7	3.1	0.5	11.6
	Overall		0.6	8.3	2.9	270.8

[a] Unit = m/day, $P = 0.001$, $F = 7.16$.
[b] Unit = ha, $P = 0.869$, $F = 0.14$.
[c] Unit = ha, $P = 0.002$, $F = 6.58$.
[d] Unit = ha, $P = 0.003$, $F = 6.13$.