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Research Article

Direct and Indirect Effects of Fire on Eastern Box Turtles

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ABSTRACT Prescribed fire is an increasingly important management tool for eastern deciduous forests, but relativity little is known about the direct effects of fire on the eastern box turtle (*Terrapene carolina carolina*). We used very high frequency (VHF) transmitters to monitor mortality, movement, and spatial ecology of 118 box turtles in response to 17 prescribed fires across 4 seasons and 3 sites in east Tennessee, USA, during 2016–2018. Annual survival of box turtles that experienced a prescribed fire event was lower (0.87 ± 0.04 [SE]) than turtles that did not (0.98 ± 0.01) and was negatively correlated with fire intensity, fire temperature the turtle experienced, and litter depth. All prescribed fire-related mortalities occurred during the early (Apr–May, $n = 5$) or late growing season (Sep–Oct, $n = 1$). Fourteen percent of box turtles we captured exhibited damage to their carapace from previous fire events. Box turtles that survived prescribed fires were in microsites that did not burn, moved to unburned areas during the fire, or burrowed following ignition. Home range size was similar before and after burns and sinuosity of movements did not differ in burned or unburned areas. Our results indicate that though box turtles are susceptible to prescribed fire during their active season, they have behavioral and physical traits that reduce the direct effects of prescribed fire. Prescribed fire practitioners should be aware of the risks of fire, particularly during the active season. We suggest managers consider altering prescribed fire intensity, seasonality, and firing pattern to minimize risk of direct effects where box turtles are of concern.

KEY WORDS direct effects, eastern box turtle, habitat management, indirect effects, prescribed fire, radio-telemetry, survival, *Terrapene carolina carolina*.

Land managers use prescribed fire to influence vegetation composition and structure for various wildlife species and for ecosystem maintenance and restoration (McShea and Healy 2002, Van Lear and Harlow 2002, McCord et al. 2014). Effects of fire on vegetation and wildlife are well described for some ecosystems, such as the longleaf pine (*Pinus palustris*) or tallgrass prairie ecosystems but less understood for others (Conner et al. 2001, Van Lear et al. 2005, Knapp et al. 2009, Stambaugh et al. 2015). Fire is being used increasingly in hardwood ecosystems of the southeastern United States, and the effects of fire on various plant and animal species continue to be investigated (Russell et al. 1999, Harper et al. 2016). Fire effects are poorly understood for terrestrial reptiles, including eastern box turtle (*Terrapene carolina carolina*; box turtle). The need for this information is increasing given the concerns regarding declining population trends throughout portions of the box turtle distribution (Hall et al. 1999, Nazdrowicz et al. 2008, Van Dijk 2011, Keister and Willey 2015).

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Late reproductive age, slow somatic growth, and low to variable recruitment make box turtle populations vulnerable to disturbance events (Budischak et al. 2006, Nazdrowicz et al. 2008, Laarman et al. 2018). Disturbance effects have the potential to be exacerbated because box turtles have limited mobility, use small home ranges, and often do not abandon home ranges despite environmental perturbations (Stickel 1950, Dodd 2001). Prescribed fire is a disturbance that can have direct negative effects on box turtles, including mortality, physical injury, and decreased body condition (Babbitt and Babbitt 1951, Rose 1986, Platt et al. 2010, Howey and Roosenburg 2013, Roe et al. 2019). Only 1 study has investigated direct effects of fire on adult box turtles using radio-telemetry, but burn regime parameters were not reported (Roe et al. 2019).

The most frequent effects of fire on wildlife are indirect (Harper et al. 2016). Fire modifies vegetation composition and structure, which alters the distribution and availability of food and cover, and reptile presence is closely associated with vegetation composition (Lindenmayer et al. 2008, Moorman et al. 2011). Prescribed fire has been suggested as an important contributor to improved habitat for some reptiles (Russell 1999, Keyser et al. 2004, Greenberg and

Waldrop 2008). Habitat quality influences the presence, movements, and home range size of individuals (Bowne et al. 2006, Kapfer et al. 2010, Fortin et al. 2012, Row et al. 2012, Fouts et al. 2017). From a population standpoint, density, survival, and reproductive potential within a given area can be altered by changes in habitat quality (Greenberg et al. 1994, Seebacher and Franklin 2012). Specifically, a reduction in basal area with increased forb cover following fire events may favor reptile occurrence because of improved conditions for foraging, nesting, and thermoregulation (Kilpatrick et al. 2010, Laarman et al. 2018, Roe et al. 2020). But such indirect effects are greatly influenced by fire intensity, seasonality, and frequency (Knapp et al. 2009, Waldrop and Goodrick 2012, Holcomb et al. 2014, Lashley et al. 2015).

The lack of detailed information on direct and indirect effects of prescribed fire on box turtles is concerning because an increasing number of agencies and landowners are using prescribed fire (Ryan et al. 2013, Kobziar et al. 2015). Although box turtles occurring in fire-adapted ecosystems are physically or behaviorally adapted at some level to fire (Babbitt and Babbitt 1951, Rose 1986, Russell et al. 1999, Perry et al. 2012), recent population stressors (i.e., habitat fragmentation, habitat loss, pet collection) may have reduced population stability in some localities (Stickel 1978, Williams and Parker 1987, Hall et al. 1999, Nazdrowicz et al. 2008). Increased population stressors, in combination with slow maturation rates, are concerning from a conservation perspective and it is important to identify mortality potential in areas maintained with prescribed fire.

Our objectives were to evaluate direct (i.e., mortality and injury via shell condition) and indirect effects (i.e., changes in movements and space use) of prescribed fire on box turtles in eastern deciduous forest landscapes. We evaluated box turtles before, during, and after fire events in a control-treatment experimental design. We predicted that survival would be lower for turtles that experienced a prescribed burn compared with those that did not, survival would be affected by burn season because turtle activity varies among seasons, and survival would be inversely related to fire intensity. Furthermore, we predicted that turtles would move out of recently burned areas because of limited resources and that body mass and condition would be negatively affected (e.g., decreased mass, scute loss, shell damage) by fire events.

STUDY AREA

We implemented field experiments on 3 study sites in east Tennessee, USA from 2016–2018. East Tennessee is characterized by 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). Each location varied in predominant vegetation types, topography, management, burn history, and burn regimes.

Catoosa Wildlife Management Area (WMA; 36.063°N, 84.882°W) encompassed 32,374 ha in the Cumberland Plateau and Mountains physiographic region of Cumberland, Morgan, and Fentress counties, and was managed by the Tennessee Wildlife Resources Agency (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 the nearby Crossville Memorial Airport weather station (National Climatic Data Center 2019). Routine prescribed burning began in 2002 with the initiation of an oak (*Quercus* spp.)-savanna restoration project (Vander Yacht et al. 2017). 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%) also were present. Managers aimed for a fire-return interval of 2–3 years to maintain woodlands and savannas.

Kyker Bottoms Waterfowl Refuge and WMA (35.605°N, 84.115°W) encompassed 230 ha in the Blue Ridge physiographic region of southern Blount County and was managed by the Tennessee Wildlife Resource Agency (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 the nearby Knoxville Airport weather station (National Climatic Data Center 2019). Kyker Bottoms 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%) also were present. Lowland areas were flooded for waterfowl, whereas uplands were managed primarily for northern bobwhite (*Colinus virginianus*). Prescribed fire had been implemented regularly since 1997 with early successional areas and woodlands burned on a 2–3-year fire-return interval.

Tanasi Girl Scout Camp (36.246°N, 83.966°W) encompassed 237 ha in the Ridge and Valley physiographic region of Tennessee and was privately owned and managed (Griffith et al. 1997). Elevations ranged from 285 m to 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 the nearby Norris weather station (National Climatic Data Center 2019). Tanasi bordered Norris Lake and was dominated by closed-canopy deciduous forest (43%) and closed-canopy eastern redcedar stands (29%). Closed-canopy mixed forests (21%), oak woodlands (3%), wildlife openings (3%), and early successional areas (1%) also were present. All vegetation types at Tanasi were burned regularly since 2004 on a 2–8-year fire-return interval, depending on vegetation type, to enhance habitat for

eastern wild turkey (*Meleagris gallopavo*) and white-tailed deer (*Odocoileus virginianus*).

METHODS

We captured adult box turtles using opportunistic finds, active searches, and wildlife detector dogs from July 2016 to July 2018 (Refsnider et al. 2011, Kapfer et al. 2012). We considered box turtles to be adults if carapace length was >115 mm and mass was >170 g (Dolbeer 1969, Donaldson and Echternacht 2005, Keister and Willey 2015). Opportunistic finds were incidental captures while researchers were not actively searching for box turtles (e.g., turtles found crossing roads). Active searches were visual searches along meandering transects throughout search 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 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 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 at initial capture and following mortality or at the conclusion of the study. 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 straight carapace length with a 20-cm Pittsburgh digital caliper (Pittsburgh, Camarillo, CA, USA) to the nearest millimeter. We noted any injuries or defects to the plastron, carapace, eyes, digits, limbs, or skin.

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 1 scute to avoid inhibiting scute development. Transmitters weighed 15 g (about 4% of average mass of an adult box turtle). We replaced transmitters with new transmitters when transmitters were reaching the end of their battery capacity (535 days). We monitored box turtle movement 1–3 times/week from July to November 2016, May to August 2017, and March to November 2018 using the homing method (Mech 1983) and direct observation with a folding 3-element Yagi antenna and an R-1000 telemetry receiver (Communications Specialist, Orange, CA, USA). We recorded ≥1 location/month from December to April 2017 and 2018 because of winter inactivity. We measured the depth at which turtles were brumating below the soil surface to the nearest centimeter by removing a minimal amount soil until the carapace could be seen. We defined spring emergence as the time when turtles fully emerged and came to the soil surface. We removed all transmitters at the end of the study using a jeweler's saw.

We radio-located all box turtles in burn units within 4 hours prior to each prescribed fire and considered turtles to have experienced a fire if they occurred in a prescribed fire unit during this period. We defined box turtles that experienced a prescribed fire at any time during the study as the treatment group for the duration of the study, whereas box turtles that did not experience a prescribed fire during the study were the control group.

We used an equal number of observers to walk and observe firebreaks during fire events to estimate number of marked and unmarked turtles leaving burn units. We captured unmarked turtles leaving burn units and subsequently radio-tagged them but did not considered them in treatment group estimates. We located each turtle within prescribed burn units within 2 hours after the completion of the burn and recorded injuries and mortality status. We measured weather parameters during each prescribed fire, including ambient temperature, relative humidity, and wind speed using a Kestrel© 3500 fire weather meter (Nielsen-Kellerman, Boothwyn, PA, USA).

We performed a 1-way analysis of covariance (ANCOVA; Program R 3.3.1, R Core Team 2016) to determine if turtle mass differed for control and treatment groups. We used carapace length as a covariate because carapace length is positively correlated with body mass (Dodd 2001, Howey and Roosenburg 2013). We used Tukey's honestly significant difference test to compare means between treatments (Welkowitz et al. 2012).

Survival Analysis

We estimated survival rates using a staggered-entry known-fate model in Program Mark using weekly encounter histories (version 8.2; Pollock et al. 1989, White and Burnham 1999). We first developed models to compare survival of turtles exposed to burning treatments (treatment group) to those that were not (control group). We used study area (Catoosa, Kyker, Tanasi) as covariates for the 3 control sites. We defined burning seasons as early growing season (Apr–May), summer (Jun–Aug), late growing season (Sep–Oct), and dormant season (Nov–Mar). We used combinations of treatment (control, treatment), study area (Catoosa, Kyker Bottoms, Tanasi), and burn season to create the following groups: control (at each site), early growing-season prescribed fire (at each site), late growing-season prescribed fire (at each site), Catoosa dormant prescribed fire, Kyker Bottoms summer and late growing-season prescribed fire, and Kyker Bottoms late growing-season and early growing season prescribed fire. A wildfire occurred on the Catoosa study site, but because this was not a prescribed activity, we treated any mortalities as natural and not related to the treatment.

We also compared survival by breaking the weekly mortality observations by year (3 yrs). Not all site and treatment combinations were represented each year. To compare differences in survival on the treatment sites, we separated control sites as a covariate and compared survival rates by burn season for the treatment turtles by combining the various groups described above using the design matrix

in Program Mark. Similarly, we compared survival by burning season, site, and year by modifying the design matrix as appropriate. We defined all non-treatment mortality causes (e.g., road kill, wildfire mortality, senescence) as natural mortalities and included those in our overall estimates of survival. Other than potential year effects, we assumed constant survival over time. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to rank candidate models, and we considered models with AIC_c values <2 as having support (Burnham and Anderson 2002).

We also tested the effects of the following covariates for treatment turtles: distance to nearest firebreak, fire intensity, temperature experienced by the turtle, litter depth, burn size, and burn coverage. We calculated the distances of turtles to the nearest firebreaks prior to fire events using the Point Distance tool in ArcMap 10.5 (Esri, Redlands, CA, USA) because turtles may use firebreaks as refuge from fire or could cross firebreaks to escape fire treatments. We evaluated fire intensity using Tempilaq® heat-sensitive indicator paint (Tempil, Elk Grove Village, IL, USA) applied to ceramic tiles (Vander Yacht et al. 2017). Twelve temperatures were represented, ranging from 79° to 427°C in roughly 14°-increments. We wrapped tiles in aluminum foil to avoid charring. We placed 3 tiles 3 m away from each turtle prior to the fire event at random azimuths. We attached an iButton temperature data logger (Model DS1922L, Maxim Integrated, San Jose, CA, USA) with 5-minute epoxy to the center of the second pleural scute of the carapace of each box turtle in the burn unit during the 4-hour period prior to ignition to evaluate the temperature experienced by the turtle. The iButtons were programmed to record carapace temperatures at 1-second intervals. We removed the iButtons within 2 hours following the completion of the burn. We measured litter depth before each fire event at 1-m intervals along 4 5-m transects in each cardinal direction from a point centered at each turtle location because sites with heavy forest litter might burn hotter. We delineated burn coverage by walking the perimeter and interior of burned areas with a handheld GPS unit. We calculated the area of burn units using ArcMap 10.5 and evaluated whether survival was related to the percent of the site burned or size of the area burned.

Spatial Ecology

We used a step-selection function (SSF) model to determine changes in space use from prescribed fire. We measured selection to determine if turtles were selecting for or against recently burned areas. Step-selection functions were developed to accommodate changing resource availability over time or as an animal moves across the landscape (Manly et al. 2002, Fortin et al. 2005, Avgar et al. 2016). 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 then are 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. Conditional logistic regression then is used 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). We used the Extract by Points tool in ArcMap 10.5 and detailed shapefiles of burn units to determine whether observed and random points were in burned or unburned areas.

We used the COXPH and COXME package in Program R 3.3.1 to conduct our SSF model analysis for space use analysis (Therneau 2013, Brooke et al. 2015). We did not detect differences in selection between years; therefore, we pooled locations from 2017 and 2018. We tested for selection differences between years by creating a subset of data for each year and comparing model beta values and confidence intervals. We considered statistical significance for our selection model if beta-value confidence limits did not overlap zero and if the burned area variable was significant ($P < 0.05$; Brooke et al. 2015).

We calculated 100% minimum convex polygon, 50% kernel density, and 95% kernel density home ranges for turtles with >40 locations (Seaman et al. 1999). We used Pearson's chi-squared test to determine if sex ratios differed between control and treatment groups. We estimated minimum convex polygon home ranges in ArcMap 10.5 using the Minimum Bounding Geometry tool. We estimated fixed kernel density home ranges in Geospatial Modelling Environment (GME; Beyer 2012) using the Isopleth and Kde tool. We used the plugin bandwidth for a smoothing parameter algorithm in combination with a 20 × 20-m cell size (Gitzen et al. 2006, Rittenhouse et al. 2007, Bauder et al. 2015, Fill et al. 2015).

We used a 2-sample *t*-test to evaluate whether home range sizes differed between control and treatment groups. We performed a linear mixed effects analysis using the lme4 package in Program R to test whether home range sizes were different prior to and following burn events for turtles with >40 locations prior to and following burn events (Bates et al. 2015). We used home range size and burn status (i.e., pre-fire, post-fire) as fixed effects and turtle identification number as a random intercept for random effects. We log-transformed home range estimates to meet normality and equal variance assumptions.

We also evaluated turtle movements before and after fires in treatment and control units with a linear mixed effects analysis. Our expectation was that turtle movements immediately following a fire would be more directed (less sinuous) compared with those before fire or in control units. We estimated sinuosity (length of the movement path divided by the straight-line distance between the beginning and end points of the path) with the Calculate Sinuosity tool in ArcMap 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) for turtles with ≥40 locations and ≥10 consecutive locations in a single management unit. We used the lme4 package in Program R to perform a linear mixed effect analysis of sinuosity and burn treatment (Bates et al. 2015). We used burn status (i.e., burned area,

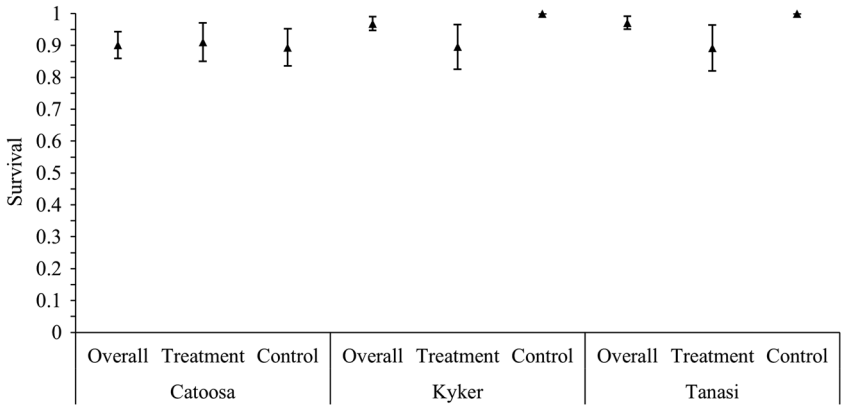

Figure 1. Average annual known-fate survival rates for control and treatment (prescribed burn) eastern box turtles at Catoosa Wildlife Management Area, Kyker Bottoms Wildlife Management Area, and Tanasi Girl Scout Camp, Tennessee, USA, 2016–2018. Error bars represent standard error.

unburned area) and sinuosity as fixed effects and turtle identification number as a random intercept.

RESULTS

Survival

We captured, radio-marked, and recorded locations for 118 adult box turtles from July 2016 to October 2018 (61 males:57 females). The sex ratio of turtles in control (41 males:38 females) and treatment (20 males:19 females) did not differ ($P = 0.950$, $\chi^2 = 0.004$). We documented 17 prescribed fires and 1 wildfire event and recorded 11 mortalities of radio-marked-turtles during our study, 6 (3 males:3 females) of which resulted from prescribed fire (Appendix A). The remaining mortalities were the result of wildfire ($n = 3$), vehicle strike ($n = 1$), and unknown causes ($n = 1$). Average annual survival rate across all 3 sites was 0.94 ± 0.02 (SE). Survival rates did not differ between the 3 sites ($AIC_c = 172.34$ compared with 172.19 for null model) or by year ($AIC_c = 175.85$ compared with 172.19 for null; Fig. 1). Known-fate models with treatment effects were supported and the annual survival rate from the base treatment model (Table 1) was 0.98 (95% CI = 0.93–0.99) for control and 0.87 (95% CI = 0.76–0.93) for treatment turtles ($\beta = 1.73$, 95% CI = 0.41–3.06). Turtle mass averaged 391 ± 9 g for turtles that experienced a burn and 409 ± 7 g for those that did not, and did not differ ($P = 0.208$, $F_{1, 107} = 1.603$). Only 1 turtle that experienced a fire experienced scute loss (Fig. 2A). We recorded preexisting carapace damage that was presumed a result of fire events prior to the start of our research in 14% of radio-marked turtles ($n = 17$; Fig. 2B).

Resource managers conducted 11 early growing-season prescribed fires from 11 April to 17 May during 2017 and 2018. Mean emergence date for box turtles was 23 April (Fig. 3). We documented 5 mortalities of 25 turtles in units subjected to early growing-season prescribed fires, resulting in an average annual survival rate of 0.84 ± 0.06. Burn coverage for the 11 early growing-season fires averaged

Table 1. Model comparisons of survival rates of eastern box turtles, depending on treatment, prescribed fire seasonality, and prescribed fire variables, Tennessee, USA, 2016–2018. Model support is indicated by corrected Akaike's Information Criterion values (AIC_c) and the difference in AIC_c (ΔAIC_c).

Model[a]	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	K[b]	Deviance
Fire treatment + tile	161.411	0.000	0.488	1.000	3	155.409
Fire treatment + litter	163.920	2.509	0.139	0.285	3	157.918
Fire treatment + iButton	164.614	3.202	0.098	0.202	3	158.611
Fire treatment	166.529	5.118	0.038	0.077	2	162.527
Fire treatment + size	166.679	5.267	0.035	0.072	3	160.676
Fire treatment + DRM	167.336	5.925	0.025	0.052	3	161.333
Fire treatment + EGS	167.868	6.456	0.019	0.040	3	161.865
Fire treatment + SUM	167.868	6.457	0.019	0.040	3	161.866
Fire treatment + site	168.193	6.782	0.016	0.034	4	160.189
Fire treatment + LGS	168.372	6.960	0.015	0.031	3	162.369
Fire treatment + coverage	168.468	7.057	0.014	0.029	3	162.466
Fire treatment + firebreak	168.509	7.099	0.015	0.029	3	162.525
Fire treatment + EGS + LGS	169.044	7.633	0.011	0.022	4	161.040
Fire treatment + LGS + firebreak	169.148	7.737	0.010	0.021	4	161.144
Null	172.194	10.782	0.002	0.005	1	170.193
Site	172.341	10.930	0.002	0.004	3	166.339
Year	175.854	14.443	0.000	0.001	3	169.852

[a] Fire seasonality variables: LGS = late growing season, EGS = early growing season, DRM = dormant, and SUM = summer. Null = no treatment, site, or other covariates. Prescribed fire variables: iButton = external carapace temperature, coverage = percent of management area burned, litter = average litter depth, tile = fire intensity, size = burn area size, and firebreak = distance of box turtle to a firebreak before ignition.

[b] Number of parameters.

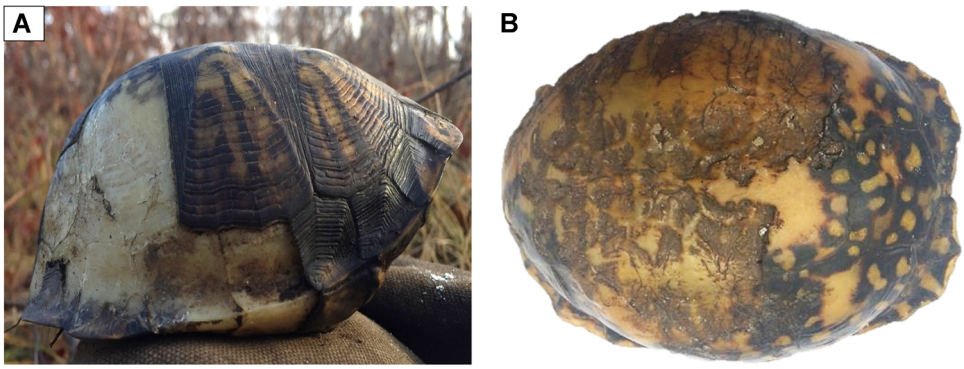

Figure 2. Eastern box turtles with A) scute loss following prescribed burns and B) preexisting carapace damage presumed to be a result of fire prior to transmitter attachment, Tennessee, USA, 2016–2018. Turtles were alive and continued to live with scute damage.

57 ± 11%. Of the 20 turtles that survived an early growing-season burn, 5 were brumating below ground, 7 occurred in microsites that did not burn, and 7 moved to unburned areas following ignition. Of the 7 turtles that moved to unburned areas following ignition, 1 moved to an adjacent unburned unit, 1 burrowed, and 5 moved to unburned areas within the burn unit (e.g., stump holes, overhanging rocks, coarse woody debris). An additional turtle survived and remained in the burn unit; however, its survival strategy is unknown. The average maximum iButton temperature of turtles that encountered flames during early growing-season burns was 73.2 ± 5.1°C ($n = 8$ turtles). Mean pyrometer tile temperatures for surviving turtles in areas that burned was 110.4 ± 52.5°C ($n = 10$), whereas mean pyrometer tile temperatures of turtles that died during early growing-season burns was 184.6 ± 61.8°C ($n = 5$). Average litter depth for surviving and deceased turtles was 1.9 ± 1.9 cm and 4.0 ± 1.5 cm, respectively. We recorded 2 turtles leaving burn units during early growing-season burns (1 radio-marked, 1 unmarked).

Resource managers conducted 1 summer prescribed fire on 6 June 2018. Burn coverage was 32%. One turtle was present in the burn unit but moved to a portion of the unit that did not burn and survived. The mean pyrometer tile temperature for that turtle was 62°C.

Resource managers conducted 4 late growing-season prescribed fires from 8 September to 5 October during 2016 and 2017. Burn coverage averaged 99 ± 2% for the 4 burns. We documented only 1 mortality of 13 turtles that experienced a late growing-season prescribed fire, with an average annual survival rate of 0.89 ± 0.07. Of the 13 turtles that survived a late growing-season burn, 3 occurred in microsites that did not burn, 8 moved to unburned areas following ignition, and 1 survived and remained in the burn unit though its survival strategy is unknown. Of the 8 turtles that moved to unburned areas following ignition, 7 moved to areas of refuge within the burn unit (e.g., creek beds, stump holes, unburned vegetation), and 1 moved to an adjacent unburned unit. The turtle that experienced mortality survived the prescribed fire by burrowing under a fallen tree; however, the tree continued to burn into the following day resulting in mortality. The average maximum iButton temperature of turtles that encountered flames during late growing-season burns, excluding the 1 turtle mortality because of iButton failure, was 84.2 ± 11.2°C ($n = 5$ turtles). The average pyrometer tile measurement of the turtle that experienced mortality was 135°C, whereas the average pyrometer tile measurement of surviving turtles in areas that burned ($n = 9$ turtles) was 151.9 ± 63.5°C. We recorded 22 turtles leaving burn units during late growing-season burns (1 radio-marked, 21 unmarked).

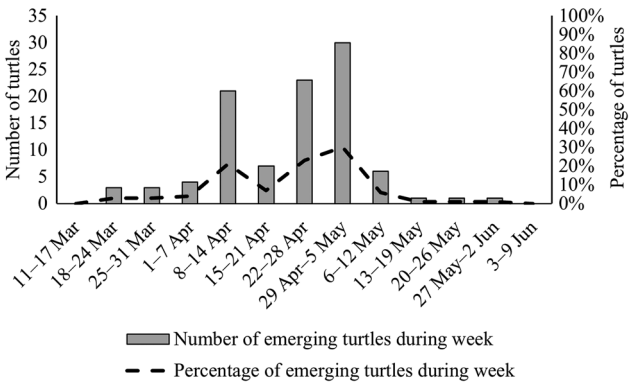

Figure 3. Emergence dates of eastern box turtles, Tennessee, USA, 2018.

Resource managers conducted 1 dormant-season prescribed fire on 4 March 2018. The dormant-season burn included 3 radio-marked turtles, all of which were brumating underground. Dormant-season prescribed fire did not result in any box turtle mortalities and box turtles did not exhibit abnormal behavior following the fire event.

A series of wildfires, totaling approximately 600 ha, occurred in treatment and control units at Catoosa WMA in October 2016. Drought conditions preceded and followed these fire events. Eight turtles survived the wildfire event, whereas 3 turtles died, and 2 transmitter failures occurred during the fires. The 3 turtles that died during wildfire had survived a prescribed fire 10 days prior by moving to an unburned unit.

Among the treatments, models that indicated survival differed by burning in early growing season, late growing season, summer, or dormant season were not supported compared with the model that grouped all burn seasons

Table 2. Model comparisons of survival rates from *post hoc* analysis of eastern box turtles whereby we censored animals that died of natural causes. Burn season models were not supported compared with the model that grouped burn seasons. We modeled treatment, prescribed fire seasonality, and prescribed fire variables for turtles in Tennessee, USA, 2016–2018. Model support is indicated by corrected Akaike's Information Criterion values (AIC_c) and the difference in AIC_c (ΔAIC_c).

Model[a]	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	K[b]	Deviance
Fire treatment + tile	82.324	0.000	0.632	1.000	3	76.322
Fire treatment + iButton	85.190	2.866	0.151	0.239	3	79.187
Fire treatment + litter	87.571	5.248	0.046	0.073	3	81.569
Fire treatment	90.420	8.096	0.011	0.018	2	86.418
Fire treatment + size	90.660	8.335	0.01	0.016	3	84.657
Fire treatment + EGS	91.048	8.724	0.008	0.013	3	85.045
Fire treatment + DRM	91.525	9.201	0.006	0.010	3	85.522
Fire treatment + LGS	91.742	9.419	0.006	0.009	3	85.74
Fire treatment + coverage	92.220	9.897	0.004	0.007	3	86.218
Fire treatment + firebreak	92.420	10.096	0.004	0.006	3	86.417
Fire treatment + site	94.378	12.054	0.002	0.002	4	86.374
Null	102.105	19.781	0.000	0.000	1	100.104
Year	103.336	21.012	0.000	0.000	3	97.333
Site	105.980	23.655	0.000	0.000	3	99.977

[a] Fire seasonality variables: LGS = late growing season, EGS = early growing season, and DRM = dormant. NULL = no treatment, site, or other covariates. Prescribed fire variables: iButton = external carapace temperature, coverage = percent of management area burned, litter = average litter depth, tile = fire intensity, size = burn area size, and firebreak = distance of box turtle to a firebreak before ignition.
[b] Number of parameters.

(Table 1). Because there were relatively few mortalities across burn seasons, the mortalities from non-treatment causes (e.g., roadkill, wildfire mortality) could have compromised our ability to detect differences, so we performed a *post hoc* analysis by censoring animals that died from non-treatment causes. We found similar results and burn season models were not supported compared with the model that grouped burn seasons (Table 2).

Within the treatment group, we detected negative relationships between survival and pyrometer tile temperature ($\beta = -0.012$, 95% CI = −0.020 to −0.003) and litter depth ($\beta = -0.384$, 95% CI = −0.720 to −0.049). Burn unit size, iButton temperature, burn coverage, and distance to firebreak were not supported as covariates for survival (Table 1).

Spatial Ecology

We collected 1,225 telemetry locations and 1,225 associated available locations from 100 turtles from May to August 2017 and 2018 to develop a step-selection model to measure space use related to prescribed burning. We excluded 18 turtles from the step-selection analysis because they moved to private property or experienced transmitter loss or failure. Box turtles did not exhibit selection for or against burned areas when they were available ($P = 0.253$, $\beta = -0.0256$, 95% CI = −0.247–0.196).

Home ranges did not differ between control ($n = 66$) and treatment ($n = 34$) turtles (Table 3). We recorded >40 locations before and after fire events for 19 individuals that experienced prescribed fire. Minimum convex polygon home ranges did not differ before and after fire events with home ranges measuring 2.2 ± 1.7 ha prior to and 5.6 ± 4.7 ha following fire events ($\beta = 3.429$, 95% CI = −1.028–7.866). Likewise, 95% kernel density estimates did not differ before and after fire events averaging 5.1 ± 2.0 ha before and 4.4 ± 1.7 ha following fire events ($\beta = 0.685$, 95% CI = −2.546–4.880). Lastly, 50% kernel density estimate home ranges did not differ and were 0.9 ± 0.4 ha prior to fire events and 1.0 ± 0.4 ha following fire events ($\beta = -0.140$, 95% CI = −0.434–1.338).

Mean sinuosity in burned and unburned units (0.15 ± 0.02 and 0.19 ± 0.02, respectively) did not differ ($\beta = -0.004$, 95% CI = −0.572–0.564). Of the 33 turtles that survived a prescribed fire, 31 remained in the burn units during and following fire events. Two turtles left the burn unit during the fire events, with 1 returning to the burn unit after 13 days, whereas the other remained in the unburned unit for 10 days when it was killed by a wildfire. Of the 22 untagged turtles that were observed crossing firebreaks during a prescribed burn, 16 were subsequently radio-tagged. All of the subsequently radio-tagged turtles returned to the burn unit (6 returned within 1 week, 1 returned within 2 weeks,

Table 3. Average home range estimates (ha) of eastern box turtles ($n = 100$) and tests for differences between control and treatment (prescribed burn) groups, Tennessee, USA, 2016–2018.

	Control group		Treatment group			
	Estimate (ha)	SE	Estimate (ha)	SE	P	t
Minimum convex polygon	9.8	4.4	8.3	2.6	0.824	−0.223
95% kernel density	8.9	4.2	7.1	2.2	0.444	0.769
50% kernel density	1.6	0.8	1.3	0.3	0.971	−0.036

2 returned within 3 weeks, 1 returned within 7 weeks, 2 returned after brumation).

DISCUSSION

Prescribed fire negatively influenced box turtle survival in our study and all prescribed fire mortalities occurred during growing-season fires. Box turtles avoided mortality from prescribed fires by occurring in microsites that did not burn, burrowing after ignition, or by moving to areas that did not burn. We documented 24 (2 radio-marked, 22 unmarked) turtles crossing firebreaks during fire events, including 1 hatchling, presumably to avoid fire. Box turtles were less susceptible to mortality during the dormant season because they were brumating in underground hibernacula. Turtles that experienced a prescribed fire remained in the burn unit or returned to the burn unit within a relatively short period of time. Sinuosity of movements and home range estimates did not differ between burned and unburned areas, suggesting space use and movement patterns were similar among treatment groups. Our results indicate that though box turtles are vulnerable to prescribed fire mortality during their active season, they possess behavioral and physical traits that may reduce direct effects of prescribed fire.

In addition to behavior, box turtles have physical traits that can lessen the direct effects of prescribed fire, such as the ability to withdraw limbs and completely close the shell (Rose 1986, Howey and Roosenburg 2013). We documented surviving box turtles experiencing carapace temperatures up to 90.1°C. Prescribed fires adversely affected shell condition of only 1 radio-tagged turtle that experienced a fire event. We documented fewer preexisting burn injuries (14%) than Howey and Roosenburg (2013) who documented 20% of turtles in burned areas with burn injuries. We documented preexisting burn injuries that ranged from mild scute discoloration to severe carapace damage that led to carapace regeneration (Fig. 2). Researchers should exercise caution when determining post-burn mortality because mortality can be delayed for several weeks. We documented delayed mortality up to 4 weeks in our study.

Our sample size of fire treatments during the midsummer and dormant season was low because resource managers on our study sites rarely burned during those seasons. Summer burns likely are a reduced threat to box turtle survival because vegetation moisture and relative humidity are often high, and few burns are conducted during midsummer in the Central Hardwoods and Appalachian region. If conditions allow a summer burn, fire spread is relatively slow and unburned patches are common (Knapp et al. 2009, Platt et al. 2010, Harper et al. 2016), allowing box turtles opportunities to escape to fire refuge. We did not document any box turtle mortality during the dormant season because box turtles were brumating below ground at depths ranging from 0–20 cm. Although only 1 dormant season fire was conducted, mortality potential from dormant season fire is low because box turtles typically brumate at depths that provide insulation from fire events. Scute loss following dormant-season burns can occur for turtles with shallow hibernacula that expose portions of the carapace (Fig. 2A). Additionally, box turtles may surface and briefly emerge during warm periods when soil temperatures approach 8°C and may be susceptible to fire-related mortality, but such behavior during the dormant season is uncommon (Dodd 2001, Woodley 2013).

Altering the season in which fire is implemented has been suggested to influence the direct effects of prescribed fire on reptiles (Platt et al. 2010, Beaupre and Douglas 2012, Cross et al. 2015). Although we did not detect statistical differences in survival by burn season, we detected differential behavior between seasons. Box turtles were less likely to move in response to fire during the early growing season compared to late growing-season burns. We observed 5.5 ± 2.7 turtles/burn crossing firebreaks during late growing-season burns to avoid prescribed fire, whereas we only observed 0.18 ± 0.60 turtles/burn crossing firebreaks during early growing-season burns. We did not estimate population density on our study sites, but we assume the seasonal variation in movements we documented is an accurate representation of behavioral responses to fire events as opposed to variation in local population size because vegetation types and topography were similar among burn units at each site. Limited movements resulting from temperature constraints and recent hibernacula emergence make box turtles more susceptible to mortality from prescribed fire during the early growing season. The probability of mortality during our study was 2.5 times less likely during the late growing-season burns than the early growing-season burns (1 mortality of 13 during late growing season compared to 5 mortalities of 25 during early growing season) despite 41% greater burn coverages during the late growing season. These data suggest that even when burn coverages were high, many box turtles were able to move to unburned units or unburned microsites within burned units, likely as a result of increased movement ability.

Recently emerged box turtles remain lethargic for 1–2 weeks following emergence, which increases vulnerability to prescribed fire (Woodley 2013); however, turtles emerge over a 1–3-month period and emergence may vary by latitude (Woodley 2013, DeGregorio et al. 2016). We recorded emergence from 22 March until 31 May. If turtles are of concern, managers should consider avoiding prescribed fire during the early growing season (Apr–May).

Fire intensity (i.e., pyrometer tile temperature and litter depth) was the dominant predictor of box turtle survival, which suggests fire regimes could be altered to lessen risk of box turtle mortality. For example, frequent burning in forests and woodlands could decrease mortality probability from each fire event because frequent burning can reduce fuel loads and result in less-intense fires. Low-intensity fires likely increase opportunities for box turtles to seek refuge, and may be less likely to consume coarse woody debris, which is an important refuge for turtles and other reptiles during prescribed fires and is often selected for in fire-maintained areas (Roe et al. 2018, Harris et al. 2020). Neither burn unit size nor turtle distance to firebreak were predictors of survival likely because unburned areas were common within prescribed fire units. Percentage of burn

units that actually burned was not a predictor of survival despite low burn coverages during the early growing season. We suspect this was because turtles were lethargic during this period and rarely made movements to unburned areas of refuge.

Like Roe et al. (2020), we did not detect differences in MCP home range sizes before and after fire events. Although Roe et al. (2020) documented larger kernel density estimate home ranges for turtles in unburned areas, we did not. Home range differences documented by Roe et al. (2020) may have been the result of differences in overall habitat quality, food availability, or some other factor that was not evaluated. Inherent site differences were not a factor in our study because we included treatment and control units at each of our study sites. We did not document selection for or against burned or unburned areas. This lack of selection may be a result of high site fidelity. Roe et al. (2020) reported high site fidelity in burned and unburned areas. Unlike Howey and Roosenburg (2013), mass between control and treatment turtles in our study did not differ. Howey and Roosenburg (2013) hypothesized reduced mass of turtles in burned areas resulted from water loss from warmer ground temperatures and greater total radiation in burned areas, but they did not measure vegetation or thermal parameters. Our study sites included areas with reduced canopy cover, increased herbaceous cover, and increased vertical structure. Abundant vegetation cover may have reduced water loss and increased food availability. A lack of selection between burned and unburned areas and similar body mass suggest burned areas at our study sites provided habitat for box turtles at least equal to unburned areas. Unchanged movements and favorable responses following prescribed fires have been documented for other turtle species (Yager et al. 2007, Lovich et al. 2011, Sanz-Aguilar et al. 2011, Dziadzio et al. 2016).

Although we recorded 6 mortalities from growing-season prescribed fire, local population-level effects of prescribed burning on box turtles remain unclear. Whether increased mortality rates result in local population declines would depend on recruitment or immigration levels. Dodd et al. (2016) reported greater population-level effects when mortalities occurred prior to egg deposition when using a 3-state deterministic matrix population model. Therefore, relatively frequent burning during the early growing season may be problematic for long-term population viability, especially if mortalities include gravid females (Dodd et al. 2016). We suggest that land managers can meet vegetation-management goals and reduce mortality of slow-moving reptiles by burning prior to spring emergence or during the latter portion of the growing season when reptiles are not lethargic from temperature constraints.

Prescribed fire was not novel to any of our study sites, having been routinely implemented for >12 years prior to our study. Our average annual survival estimates, with or without fire treatments (0.87, 95% CI = 0.76–0.93 and 0.98, 95% CI = 0.93–0.99, respectively), were similar to those of previously documented stable populations (Dodd 2006, Roe et al. 2019). Roe (2019) reported box turtle populations can be resilient to some forms of mortality from disturbance if the population growth rate is increasing or stable, the population is initially relatively large, and if habitat quality is high. But intensively managed sites that rely on early growing-season burning may function as reproductive sinks if mortality routinely includes gravid females (Congdon et al. 1993, Heppell 1998, Dodd 2016). Mortality from prescribed fires may be offset if recruitment increases from improved habitat quality and nest site availability (Laarman et al. 2018). Although we noted evidence of recruitment in burned areas, our study lacks information on reproductive output, juvenile survival, and immigration. Future research that includes recruitment following prescribed fires is needed to offer a more comprehensive view of population-level effects.

MANAGEMENT IMPLICATIONS

Fire intensity was the dominant predictor of box turtle survival, which suggests fire regimes could be altered to lessen risk of box turtle mortality, and likely other reptiles. Burning when fuel moisture is relatively high (but still allows for adequate combustion) and using less-intense firing patterns can create areas of reduced fuel or unburned microsites, which are important refuges for box turtles. Slow-moving fires with relatively low flame lengths increase the probability that slow-moving reptiles can move to an area of refuge. Small-scale fires or fires that result in a mosaic of burned patches can increase opportunities for turtles to escape to unburned refuge. We suggest prescribed fire practitioners avoid using early growing-season prescribed fire if reptiles are a concern or management objective. Dendrochronological evidence suggests growing-season fire was historically less common than dormant-season fire in our region, and early growing-season burns elicit vegetation effects similar to dormant-season burns. Therefore, other than increased burn opportunities, there is little ecological or historical justification to burn during the early portion of the growing season in our region. Although fire in our region historically occurred more frequently during the dormant season, land managers sometimes rely on growing-season burns to control woody encroachment and increase vegetation heterogeneity. Burning during the latter portion of the growing season may be used to elicit differential vegetation effects and lessen negative effects on box turtles.

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LITERATURE CITED

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Babbitt, L. H., and C. H. Babbitt. 1951. A herpetological study of burned-over areas in Dade County, Florida. Copeia 1951:79.

Bates, D. M., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bauder, J. M., D. R. Breininger, M. R. Bolt, M. L. Legare, C. L. Jenkins, and K. McGarigal. 2015. The role of the bandwidth matrix in influencing kernel home range estimates for snakes using VHF telemetry data. Wildlife Research 42:437–453.

Beaupre, S. J., and L. E. Douglas. 2012. Responses of timber rattlesnakes to fire: lessons from two prescribed burns. Pages 192–204 *in* Proceedings of the 4th Fire in Eastern Oak Forests Conference. D. C. Dey, M. C. Stambaugh, S. L. Clark, and C. J. Schweitzer, editors. U. S. Forest Service General Technical Report NRS-P-102, Newtown Square, Pennsylvania, USA.

Beyer, H. L. 2012. Geospatial Modelling Environment (version 0.7.2.1). Software. http://www.spatialecology.com/gme. Accessed 9 Oct 2016.

Bowne, D. R., M. A. Bowers, and J. E. Hines. 2006. Connectivity in an agricultural landscape as reflected by interpond movements of a freshwater turtle. Conservation Biology 20:780–791.

Brooke, J. M., D. C. Peters, A. M. Unger, E. P. Tanner, C. A. Harper, P. D. Keyser, J. D. Clark, and J. J. Morgan. 2015. Habitat manipulation influences northern bobwhite resource selection on a reclaimed surface mine. Journal of Wildlife Management 79:1264–1276.

Budischak, S. A., J. M. Hester, S. J. Price, and M. E. Dorcas. 2006. Natural history of *Terrapene carolina* (box turtles) in an urbanized landscape. Southeastern Naturalist 5:191–204.

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

Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7:826–833.

Conner, R., D. C. Rudolph, and J. R. Walters. 2001. The red-cockaded woodpecker: surviving in a fire-maintained ecosystem. University of Texas Press, Austin, Texas, USA.

Cross, M. D., K. V. Root, C. J. Mehne, J. McGowan-Stinski, D. Pearsall, and J. C. Gillingham. 2015. Multi-scale responses of eastern massasauga rattlesnakes (*Sistrurus catenatus*) to prescribed fire. American Midland Naturalist 173:346–362.

Currylow, A. F., B. J. MacGowan, and R. N. Williams. 2012. Short-term forest management effects on a long-lived ectotherm. PLoS One 7:e40473.

DeGregorio, B. A., T. D. Tuberville, R. A. Kennamer, B. B. Harris, and I. L. Brisbin, Jr. 2016. Spring emergence of eastern box turtles (*Terrapene carolina*): influences of individual variation and scale of temperature correlates. Canadian Journal of Zoology 95:23–30.

Dodd, C. K., Jr. 2001. North American box turtles: a natural history. University of Oklahoma, Norman, USA.

Dodd, C. K., Jr. 2006. Remembering common species during restoration: lessons form Egmont Key (Florida). Restoration Ecology 24:211–212.

Dodd, C. K., Jr., V. Rolland, and M. K. Oli. 2016. Consequences of indiviudal removal on persistence of a protected population of long-lived turtles. Animal Converstation 19:369–379.

Dolbeer, R. A. 1969. A study of population density, seasonal movements and weight changes, and winter behavior of the eastern box turtle, *Terrapene c. carolina* L., in eastern Tennessee. Thesis, University of Tennessee, Knoxville, USA.

Donaldson, B. M., and A. C. Echternacht. 2005. Aquatic habitat use relative to home range and seasonal movement of eastern box turtles (*Terrapene carolina carolina*: Emydidae) in eastern Tennessee. Journal of Herpetology 39:278–284.

Duchesne, T., D. Fortin, and N. Courbin. 2010. Mixed conditional logistic regression for habitat selection studies. Journal of Animal Ecology 79:548–555.

Dziadzio, M. C., L. L. Smith, R. B. Chandler, and S. B. Castleberry. 2016. Effect of nest location on gopher tortoise nest survival. Journal of Wildlife Management 80:1314–1322.

Fill, J. M., J. L. Waldron, S. M. Welch, J. M. Gibbons, S. H. Bennett, and T. A. Mousseau. 2015. Using multiscale spatial models to assess potential surrogate habitat for an imperiled reptile. PloS One 10:e0123307.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a tropic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Fortin, G., G. Blouin-Demers, and Y. Dubois. 2012. Landscape composition weakly affects home range size in Blanding's turtles (*Emydoidea blandingii*). Ecoscience 19:191–197.

Fouts, K. L., C. T. Moore, K. D. Johnson, and J. C. Maerz. 2017. Lizard activity and abundance greater in burned habitat of a xeric montane forest. Journal of Fish and Wildlife Management 8:181–192.

Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. Journal of Wildlife Management 70:1334–1344.

Greenberg, C. H., D. G. Neary, and L. D. Harris. 1994. Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. Conservation Biology 8:1047–1057.

Greenberg, C. H., and T. A. Waldrop. 2008. Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. Forest Ecology and Management 255:2883–2893.

Griffith, G. E., J. M. Omernik, and S. H. Azevedo. 1997. Ecoregions of Tennessee. EPA/600R-97/022. United States Environmental Protection Agency, Corvallis, Oregon, USA.

Hall, R. J., P. F. Henry, and C. M. Bunck. 1999. Fifty-year trends in a box turtle population in Maryland. Biological Conservation 88:165–172.

Harper, C. A., W. M. Ford, M. A. Lashley, C. E. Moorman, and M. C. Stambaugh. 2016. Fire effects on wildlife in the Central Hardwoods and Appalachian regions, USA. Fire Ecology 12:127–159.

Harris, K. A., J. D. Clark, R. D. Elmore, and C. A. Harper. 2020. Spatial ecology and resource selection of eastern box turtles. Journal of Wildlife Management 84:in press.

Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia. 367–375.

Holcomb, E. D., P. D. Keyser, and C. A. Harper. 2014. Responses of planted native warm-season grasses and associated vegetation to seasonality of fire in the southeastern US. Southeastern Naturalist 13:221–236.

Howey, C. F., and W. M. Roosenburg. 2013. Effects of prescribed fire on the eastern box turtle (*Terrapene carolina carolina*). Northeastern Naturalist 20:493–497.

Kapfer, J. M., D. J. Munoz, and T. Tomasek. 2012. Use of wildlife detector dogs to study eastern box turtle (*Terrapene carolina carolina*) populations. Herpetological Conservation and Biology 7:169–175.

Kapfer, J. M., C. W. Pekar, D. M. Reineke, J. R. Coggins, and R. Hay. 2010. Modeling the relationship between habitat preferences and home-range size: a case study on a large mobile colubrid snake from North America. Journal of Zoology 282:13–20.

Keister, A. R., and L. L. Willey. 2015. *Terrapene carolina* (Linnaeus 1758)—eastern box turtle, common box turtle. Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC tortoise and freshwater turtle specialist group. Chelonian Research Monographs 5:085.1–085.25.

Keyser, P. D., D. J. Sausville, W. M. Ford, D. J. Schwab, and P. H. Brose. 2004. Prescribed fire impacts to amphibians and reptiles in shelterwood-harvested oak-dominated forests. Virginia Journal of Science 55:159–168.

Kilpatrick, E. S., T. A. Waldrop, J. D. Lanham, C. H. Greenberg, and T. H. Contreras. 2010. Short-term effects of fuel reduction treatments on herpetofauna from the southeastern United States. Forest Science 56:122–130.

Knapp, E. E., B. L. Estes, and C. N. Skinner. 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. U.S. Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Kobziar, L. N., D. Godwin, L. Taylor, and A. C. Watts. 2015. Perspectives on trends, effectiveness, and impediments to prescribed burning in the southern U.S. Forests 6:561–580.

Laarman, P. B., P. W. Keenlance, J. T. Altobelli, C. M. Schumacher, P. Huber, J. J. Jacquot, and J. A. Moore. 2018. Ecology of neonate eastern box turtles with prescribed fire implications. Journal of Wildlife Management 82:1385–1395.

Lashley, M. A., M. C. Chitwood, C. A. Harper, C. E. Moorman, and C. S. DePerno. 2015. Variability in fire prescriptions to promote wildlife foods in the longleaf pine ecosystem. Fire Ecology 11:62–79.

Lindenmayer, D. B., J. T. Wood, C. MacGregor, D. R. Michael, R. B. Cunningham, M. Crane, R. Montague-Drake, D. Brown, R. Muntz, and D. A. Driscoll. 2008. How predictable are reptile responses to wildfire? Oikos 117:1086–1097.

Lovich, J. E., J. R. Ennen, S. V. Madrak, C. L. Loughran, K. P. Meyer, T. R. Arundel, and C. D. Bjurlin. 2011. Long-term post-fire effects on spatial ecology and reproductive output of female Agassiz's desert tortoises (*Gopherus agassizii*) at a wind energy facility near Palm Springs, California, USA. Fire Ecology 7:75–87.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

McCord, J. M., C. A. Harper, and C. H. Greenberg. 2014. Brood cover and food resources for wild turkeys following silvicultural treatments in mature upland hardwoods. Wildlife Society Bulletin 38:265–272.

McShea, W. J., and W. M. Healy. 2002. Oak forest ecosystems: ecology and management for wildlife. Johns Hopkins University Press, Baltimore, Maryland, USA.

Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, USA.

Moorman, C. E., K. R. Russell, and C. H. Greenberg. 2011. Reptile and amphibian response to hardwood forest management and early successional habitats. Sustaining young forest communities: ecology and management of early successional habitats in the Central Hardwood region, USA. Managing Forest Ecosystems 2011:191–208.

National Climatic Data Center. 2019. 1981–2010 climate normals. <http://www.ncdc.noaa.gov/land-based-station-data/climate-normals/1981-2010-normals-data>. Accessed 23 Sep 2019.

Nazdrowicz, N. H., J. L. Bowman, and R. R. Roth. 2008. Population ecology of the eastern box turtle in a fragmented landscape. Journal of Wildlife Management 72:745–753.

Perry, R. W., D. C. Rudolph, and R. E. Thill. 2012. Effects of short-rotation controlled burning on amphibians and reptiles in pine woodlands. Forest Ecology and Management 271:124–131.

Platt, S. G., H. Liu, and C. K. Borg. 2010. Fire ecology of the Florida box turtle (*Terrapene carolina bau*ri Taylor) in pine rockland forests of the lower Florida Keys. Natural Areas Journal 30:254–260.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Refsnider, J. M., T. S. Mitchell, H. M. Streby, J. T. Strickland, D. A. Warner, and F. J. Janzen. 2011. A generalized method to determine detectability of rare and cryptic species using the ornate box turtle as a model. Wildlife Society Bulletin 35:93–100.

Rittenhouse, C. D., J. J. Millspaugh, M. W. Hubbard, and S. L. Sheriff. 2007. Movements of translocated and resident three-toed box turtles. Journal of Herpetology 41:115–122.

Roe, J. H., A. L. Kish, and J. P. Nacy. 2020. Variation and repeatability of home range in a forest-dwelling terrestrial turtle: implications for prescribed fire in forest management. Journal of Zoology 310:71–82.

Roe, J. H., K. H. Wild, and M. S. Chavez. 2019. Reponses of a forest-dwelling terrestrial turtle, *Terrapene carolina*, to precribed fire in a longleaf pine ecosystem. Forest Ecoloy and Management 432:949–956.

Roe, J. H., K. H. Wild, and Z. R. Lunn. 2018. Inter- and intra-population variation in habitat selection for a forest-dwelling terrestrial turtle, *Terrapene carolina*. Herpetological Conservation and Biology 13:711–725.

Rose, F. L. 1986. Carapace regeneration in *Terrapene* (Chelonia: Testudinidae). Southwestern Naturalist 31:131–134.

Row, J. R., G. Blouin-Demers, and S. C. Lougheed. 2012. Movements and habitat use of eastern foxsnakes (*Pantherophis gloydi*) in two areas varying in size and fragmentation. Journal of Herpetology 46:94–99.

Russell, K. R., D. H. Van Lear, and D. C. Guynn. 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildlife Society Bulletin 27:374–384.

Ryan, K. C., E. E. Knapp, and J. M. Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Frontiers in Ecology and the Environment 11:e15–e24.

Sanz-Aguilar, A., J. D. Anadon, A. Gimenez, R. Ballestar, E. Gracia, and D. Oro. 2011. Coexisting with fire: the case of the terrestrial tortoise *Testudo graeca* in Mediterranean shrublands. Biological Conservation 144:1040–1049.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Seebacher, F., and C. E. Franklin. 2012. Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. Philosophical Transactions of the Royal Society B Biological Sciences 367:1607–1614.

Soil Survey Staff Natural Resources Conservation Service. 2019. United States Department of Agriculture, Web Soil Survey. <http://websoilsurvey.nrcs.usda.gov/>. Accessed 23 Sep 2019.

Stambaugh, M. C., J. M. Varner, R. F. Noss, D. C. Dey, N. L. Christensen, R. F. Baldwin, R. P. Guyette, B. B. Hanberry, C. A. Harper, S. G. Lindblom, et al. 2015. Clarifying the role of fire in the deciduous forests of eastern North America: reply to Matlack. Conservation Biology 29:942–946.

Stickel, L. F. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). Ecological Monographs 20:351378.

Stickel, L. F. 1978. Changes in a box turtle population during three decades. Copeia 1978:221–225.

Therneau, T. 2013. A package for survival analysis in S. R package version 2.37-4. <https://CRAN.R-project.org/package=survival>. Accessed 15 Nov 2016.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology 2:4.

Van Dijk, P. P. 2011. *Terrapene carolina*. Version 2015–4. The IUCN Red List of Threatened Species 2011:e.T21641A97428179. <https://www.iucnredlist.org/species/21641/97428179>. Accessed 23 Jun 2016.

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. Forest Ecology and Management 211:150–165.

Van Lear, D. H., and R. F. Harlow. 2002. Fire in the eastern United States: influence on wildlife habitat. Pages 2–10 *in* W. M. Ford, K. R. Russell, and C. E. Moorman, editors. The role of fire in nongame wildlife management and community restoration: traditional uses and new directions. Proceedings of a special workshop. U.S. Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania, USA.

Vander Yacht, A. L., S. A. Barrioz, P. D. Keyser, C. A. Harper, D. S. Buckley, D. A. Buehler, and R. D. Applegate. 2017. Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. Forest Ecology and Management 390:187–202.

Waldrop, T. A., and S. L. Goodrick. 2012. Introduction to prescribed fires in southern ecosystems. Science Update SRS-054. U.S. Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Welkowitz, J., B. H. Cohen, and R. B. Lea. 2012. Introductory statistics for the behavioral sciences. John Wiley and Sons, Hoboken, New Jersey, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Williams, E. C., and W. S. Parker. 1987. A long-term study of a box turtle (*Terrapene carolina*) population at Allee Memorial Woods, Indiana, with emphasis on survivorship. Herpetologica 43:328–335.

Woodley, C. L. 2013. Predicting spring emergence in a northern population of the eastern box turtle (*Terrapene c. carolina*). Thesis, Indiana University-Purdue University, Fort Wayne, Indiana, USA.

Yager, L. Y., C. D. Heise, D. M. Epperson, and M. G. Hinderliter. 2007. Gopher tortoise response to habitat management by prescribed burning. Journal of Wildlife Management 71:428–434.

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APPENDIX A. PRESCRIBED BURN INFORMATION

Table A1. Average weather statistics occurring between 1130–1500 during fire events experienced by eastern box turtles, Tennessee, USA, 2016–2018.

Date	Site	Season of burn[a]	Temperature (°C)	Dew point (°C)	Relative humidity (%)	Wind speed (km/hr)
8 Sep 2016	Kyker	LGS	33	16	35	13
5 Oct 2016	Catoosa	LGS	26	12	42	8
5 Oct 2016	Catoosa	LGS	26	12	42	8
15 Oct 2016	Catoosa	WILD	23	13	52	16
26 Apr 2017	Tanasi	EGS	24	13	42	6
17 May 2017	Kyker	EGS	31	12	31	21
17 May 2017	Kyker	EGS	31	12	31	21
4 Oct 2017	Kyker	LGS	27	12	40	7
4 Mar 2018	Catoosa	DRM	14	−9	20	5
11 Apr 2018	Tanasi	EGS	26	10	36	10
20 Apr 2018	Kyker	EGS	16	0	36	19
20 Apr 2018	Kyker	EGS	16	0	36	19
30 Apr 2018	Catoosa	EGS	21	−1	24	10
30 Apr 2018	Catoosa	EGS	21	−1	24	10
1 May 2018	Tanasi	EGS	25	8	34	5
1 May 2018	Tanasi	EGS	25	8	34	5
1 May 2018	Tanasi	EGS	25	8	34	5
20 Jun 2018	Kyker	SUM	31	19	54	14

[a] LGS = late growing season, WILD = wildfire, EGS = early growing season, SUM = summer, DRM = dormant.

Table A2. Synopsis of early growing-season prescribed fires experienced by eastern box turtles, Tennessee, USA, 2017–2018.

Date	Site	Unit size (ha)	Ignition pattern	Number of marked box turtles in burn unit	Number of marked box turtle mortalities	Burn coverage (%)
11 Apr 2017	Tanasi	2.3	backing, flanking	3	1	30
26 Apr 2017	Tanasi	5.8	heading	4	0	50
17 May 2017	Kyker	0.5	strip-heading	2	0	10
17 May 2017	Kyker	1.0	strip-heading	2	0	6
20 Apr 2018	Kyker	1.0	backing, flanking	3	1	100
20 Apr 2018	Kyker	0.7	heading	1	0	100
30 Apr 2018	Catoosa	38.3	ring	2	1	100
30 Apr 2018	Catoosa	6.3	flanking	4	1	100
1 May 2018	Tanasi	35.0	heading	2	0	26
1 May 2018	Tanasi	0.6	heading	1	0	85
1 May 2018	Tanasi	2.4	heading	1	1	25

Table A3. Synopsis of dormant-season prescribed fire, summer prescribed fire, and a wildfire event experienced by eastern box turtles, Tennessee, USA, 2016–2018.

Date	Site	Season	Unit size (ha)	Ignition pattern	Number of marked box turtles in burn unit	Number of marked box turtle mortalities	Burn coverage (%)
4 Mar 2018	Catoosa	dormant	97.7	ring	3	0	88
20 Jun 2018	Kyker	summer	1.8	flanking	1	0	32
15 Oct 2016	Catoosa	wild	~600		13	3[a]	100

[a] Two transmitter failures occurred in addition to the 3 mortalities of radio-marked turtles.

Table A4. Synopsis of late growing-season prescribed fires experienced by eastern box turtles, Tennessee, USA, 2016–2018.

Date	Site	Unit size (ha)	Ignition pattern	Number of marked box turtles in burn unit	Number of marked box turtle mortalities	Burn coverage (%)
8 Sep 2016	Kyker	6.2	flanking	1	0	94
5 Oct 2016	Catoosa	223	ring	6	0	100
5 Oct 2016	Catoosa	43.9	flanking	3	0	100
4 Oct 2017	Kyker	3.2	flanking	3	1	100