



Thermal biology of eastern box turtles in a longleaf pine system managed with prescribed fire



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ABSTRACT

Fire can influence the microclimate of forest habitats by removing understory vegetation and surface debris. Temperature is often higher in recently burned forests owing to increased light penetration through the open understory. Because physiological processes are sensitive to temperature in ectotherms, we expected fire-maintained forests to improve the suitability of the thermal environment for turtles, and for turtles to seasonally associate with the most thermally-optimal habitats. Using a laboratory thermal gradient, we determined the thermal preference range (T_{set}) of eastern box turtles, *Terrapene carolina*, to be 27–31 °C. Physical models simulating the body temperatures experienced by turtles in the field revealed that surface environments in a fire-maintained longleaf pine forest were 3 °C warmer than adjacent unburned mixed hardwood/pine forests, but the fire-maintained forest was never of superior thermal quality owing to wider T_e fluctuations above T_{set} and exposure to extreme and potentially lethal temperatures. Radiotracked turtles using fire-managed longleaf pine forests maintained shell temperatures (T_s) approximately 2 °C above those at a nearby unburned forest, but we observed only moderate seasonal changes in habitat use which were inconsistent with thermoregulatory behavior. We conclude that turtles were not responding strongly to the thermal heterogeneity generated by fire in our system, and that other aspects of the environment are likely more important in shaping habitat associations.

1. Introduction

Fire disturbance plays a critical role in the maintenance of structure and function in many habitats worldwide (Wright and Bailey, 1982; Nowacki and Abrams, 2008), with strong implications for the ecology and evolution of biota (Keeley and Rundel, 2005; Beerling and Osborne, 2006; Pausas and Keeley, 2009). Fire can directly kill, injure, or damage biota by exposure to extreme temperatures, but among the most important impacts of fire are indirect changes to the microclimate. For instance, while most prescribed fires do not remove overstory trees, the removal of ground litter, debris, and vegetation can open the forest understory resulting in higher light levels and altered hydric and temperature conditions (Iverson and Hutchinson, 2002; Greenburg and Waldrop, 2008; Hossack et al., 2009). The magnitude and duration of such effects and animal responses to them varies depending on habitat, fire frequency, intensity, and whether the fire was naturally ignited or intentionally set for management purposes (i.e., prescribed fire; Pastro et al., 2011; Elzer et al., 2013).

Environmental temperature directly influences the body temperature (T_b) of ectotherms, which in turn strongly affects their physiology, behavior, and performance (Huey, 1982). In environments where

temperature varies spatially or temporally, ectothermic vertebrates such as reptiles often behaviorally regulate T_b to maximize time at or near temperatures where performance is optimized (Angilletta et al., 2002). The links between thermoregulatory behavior and temperature-sensitive performance should be strong owing to the influence of temperature on fitness-related activities and processes such as movement, energy and water balance, and reproduction (Huey and Slatkin, 1976; Huey and Bennett, 1987; Congdon, 1989). Canopy openings and understory removal in fire-maintained habitats could thus offer more opportunities to maintain T_b in the optimal performance range (Elzer et al., 2013). Indeed, many ectotherms respond positively to fire disturbance (Mushinsky, 1985; Ashton et al., 2008; Hossack et al., 2009; Matthews et al., 2010; Steen et al., 2013).

The eastern box turtle, *Terrapene carolina*, provides a useful model to study the effects of post-fire habitat alteration on T_b and habitat use. *T. carolina* populations are typically found in a variety of forest types, often associating with canopy openings, habitat edges, and early successional or grassland habitat on a seasonal basis (Keister and Willey, 2015). As T_b is strongly associated with environmental temperature in *T. carolina* (Adams et al., 1989), which in turn influences their performance and energy balance (Adams et al., 1989; Penick et al., 2002), the

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increased light penetration following fire could offer thermoregulatory opportunities for this small-bodied terrestrial turtle. Alternatively, the increased temperature under open canopies could at times expose them to lethal extremes, requiring movement out of openings and into more shaded forest environments. For instance, in a study on turtle responses to silvicultural management, *T. carolina* experienced considerably higher T_b in areas where the canopy was opened by timber harvesting, with associated modifications to their fine-scale movements and activity (Currylow et al., 2012). However, the limited mobility and small home range size of *T. carolina* may prohibit behavioral modifications over broad spatial scales, though individuals and populations differ in their vagility (Dodd, 2001; Currylow et al., 2012; Greenspan et al., 2015).

A large part of the range of *T. carolina* is in historically fire-prone habitats, such as the southeastern Coastal Plain and Sandhills ecoregions, which historically burned at a frequency of 1–3 and 4–6 years, respectively (Frost, 1998). Natural wildfires have been replaced increasingly by prescribed burning in an attempt to mimic this fire return interval for silvicultural, hazard reduction, pest control, grazing, wildlife management, and biodiversity conservation purposes (Haines et al., 2001). However, we have little knowledge of the direct or indirect effects of fire on *T. carolina*. Here, we investigate the potential for fire to impact the thermal environments of *T. carolina*, and whether turtles behaviorally respond by seasonal changes in habitat use. We expect the open canopy maintained by fire to increase both environmental temperature and turtle T_b , and that turtles will seasonally associate with the most thermally-optimal habitats.

2. Material and methods

2.1. Study site

The study was conducted at the Weymouth Woods Sandhills Nature Preserve (hereafter WEWO), a 202-ha state park in the sandhills physiographic region of south-central North Carolina. The habitat is a mosaic of longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), and hardwood trees in relatively equal proportion (40% longleaf, 33% hardwood, and 27% loblolly; J. Roe, unpubl. data). Longleaf occurs primarily in the xeric uplands, except where fire has been excluded or where loblolly were replanted in remnant forestry plantations. Hardwood forests, including mixed oak (*Quercus* spp.), hickory (*Carya* spp.), red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), American holly (*Ilex opacum*), sassafras (*Sassafras albidum*), and tulip poplar (*Liriodendron tulipifera*) trees are patchily distributed in upland habitats, but are primarily restricted to stream margins, bottomland habitats, and park units that have not been part of the prescribed fire program. In the upland areas where fire has been intentionally excluded, a few large living remnant longleaf pine trees and stumps indicate that these habitats were once more populated with longleaf. Prescribed fire has been used in the park since 1974, with 76% of the area being managed using controlled burns. Management units are 12.9 ± 7.8 ha (mean \pm standard deviation; 0.9–23.9 ha range) in size, with a target burn frequency of 3–5 years.

2.2. Temperature preference trials

Fourteen *Terrapene carolina* adults (11 male, 3 female, carapace length 120.3–148.2 mm, mass 340–500 g) were captured from 21 August to 16 September 2014 for temperature preference trials. All turtles appeared healthy, were uninjured, and females were unlikely to be gravid at this time of year (typical nesting season is from May–July at this location, J. Roe pers. obs.). Turtles were housed at the University of North Carolina at Pembroke for three to seven days before trials. Individuals were kept in separate rubber bins with constant access to water, but were not fed while in captivity.

T_b was measured along a thermal gradient constructed from

plywood (170 cm \times 50 cm \times 25 cm) with a bottom of aluminum flashing covered by sand 2 cm deep. A temperature gradient was created using an overhead ceramic heat lamp and heat pads (Reptitherm U.T.H., Zoo Med Laboratories, Inc., San Luis Obispo, CA) placed under the aluminum and maintained at constant temperatures by a Herpstat thermostat (Spyder Robotics LLC, Chana, IL). The heat lamp was placed 30 cm over one end of the gradient, with a heat pad maintained at 38 °C approximately 40 cm from the same end. Another heat pad, maintained at 27 °C, was placed halfway down the gradient. The room was constantly maintained at 15 °C, creating a relatively cold end opposite the heat lamp. Overhead lights were set on natural light cycles of 12L:12D (photophase starting at 0700 h and scotophase at 1900 h). Temperatures were spot checked at the beginning and end of each trial with an infra-red thermometer. In addition, five temperature data loggers (Thermocron iButton, Dallas Semiconductor, Dallas, TX) were placed in the sand along the thermal gradient and recorded temperatures every 5 min.

Turtles were fitted with a hermetically sealed tip insulated thermocouple (Omega Engineering, Inc., Norwalk, CT) inserted 2 cm into the cloaca. Temperature was monitored with an EasyLog data logger (Lascar Electronics, Erie, PA) that recorded temperature every 5 min. Turtles were placed individually in the gradient and remained undisturbed for 24 h. The initial three hours of recordings were discarded before analysis to allow turtles to become acclimated to the gradient. We determined the preferred body temperature, or set-point range (T_{set}) for each turtle from the bounds of the central 50% (i.e., the 25th and 75th quartiles) of selected T_b (Hertz et al., 1993). Given the highly skewed sex ratios, males and females were grouped together in all analyses. Turtles had no access to food or water during the temperature preference trials, and were released at their point of capture following completion of trials.

2.3. Operative environmental temperatures

We estimated the operative environmental temperature (T_e), the T_b available to a non-thermoregulating ectotherm (Bakken, 1992), using physical models placed in various habitats in the field. Models were water filled Snapware® plastic bins painted in a flat black and tan mottled pattern of the approximate size, dimensions (135 cm \times 85 cm \times 58 cm), and color of adult *T. carolina* in our study system. Internal temperatures were recorded every hour using iButtons sealed in a black rubber coating (Plasti Dip International, Blaine, MN). Models were calibrated alongside two fresh turtle carcasses with iButton dataloggers recording internal T_b and external shell temperature (T_s). One model and carcass pair was placed on the surface in the open for 24 h, while the other model and carcass pair was buried in the nearby litter. Day-time conditions were mostly sunny (0–50% cloud cover) during model calibrations.

From May to November 2013, models were placed in five randomly selected locations each in a fire-maintained longleaf forest unit and an adjacent mixed hardwood/non-longleaf pine unburned forest unit where fire has been intentionally excluded at least since the park began the prescribed fire program in 1974. The most recent fire was in May 2012 in the longleaf habitat. Locations were selected using the “create random points” tool in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA, USA). Each forest unit was of similar topography (2–15% slopes), elevation (364–416 m), and soils (combinations of sand, loamy sand, sand clay loam, sandy loam profiles; USDA Natural Resources Conservation Service). Models were placed 50–500 m from their counterparts in the adjacent forest units. At each location, one model was placed on the surface, while another was placed under the nearest cover object (leaf litter, logs, grasses, or shrubs) under which we commonly observed *T. carolina* to seek refuge. Models were rotated to new random locations each week over a period of several weeks during a spring (8 May to 18 June 2013), summer (16 July to 27 Aug 2013), and fall (22 Oct to 12 Nov 2013) sampling period. The rotations

resulted in 25 unique locations for each surface-refuge model pair in each habitat type per season in spring and summer, and 15 unique locations in fall. The thermal quality (d_e) of each habitat type (longleaf or mixed hardwood/non-longleaf pine), position (surface or refuge), and season (spring, summer, fall) combination was calculated as the mean of absolute values of deviations of T_e from T_{set} (Hertz et al., 1993). For surface models, we also calculated the percentage of T_e above the lower bound of T_{set} ($\% \geq T_{set}$) as an index of the degree to which T_{set} could be maintained in a given habitat by behavioral adjustments (i.e., movement between surface and refuge positions). This final index assumes that suitable refuge microhabitats (litter, shrubs, woody debris) that did not exceed T_{set} were available for retreat when T_e exceeds T_{set} on the surface.

2.4. Free-ranging turtle temperatures and habitat use

We captured turtles opportunistically and equipped them with radiotransmitters (RI-2B, 10–15 g, Holohil Systems Ltd., Carp, ON, Canada) using 5 min epoxy gel (Devcon, Solon, OH) in the field. We tracked 27 turtles (14 male and 13 female) from WEWO and recorded T_s for a subset of individuals (5 male and 7 female). Hourly T_s was recorded using iButton temperature dataloggers coated in black Plasti Dip and attached to the rear of the carapace. For comparison, we include data from 23 turtles (12 male and 11 female; five of each sex equipped with iButtons) radiotracked at a site 24 km to the south on the border of the Sandhills and Upper Coastal Plain physiographic regions, the Lumber River State Park (LRSP). This park is comprised of mixed pine (39% loblolly, 0.5% longleaf) and hardwood (60%) forests where prescribed fire has not been employed at least since 2001 when the park took over management of the property (J. Roe unpubl. data).

We located telemetered turtles once per week using a receiver (R-1000, Communication Specialists, Orange, CA) and a Yagi antenna. At each location, we assessed the relative composition of tree types in the immediate surrounding area using a CRUZ-ALL angle gauge (Forestry Suppliers, Inc., Jackson, MS, USA). This method involved rotating 360° while holding the angle gauge at head height at a standard length (~64 cm) from the observer's eye, and counting the number of tree trunks that completely filled (or more than filled) the 10-factor gauge opening. Trees were grouped into three categories which included 1) longleaf pine, 2) other non-longleaf pine species, and 3) hardwood species. The number of trees in each category was counted, and the relative proportion of each category was calculated and used as an index of forest microhabitat composition. We assessed canopy openness at a subset of locations ($n = 518$), which were the first 23 ± 1 locations for the first 23 turtles we studied (ten from LRSP and 13 from WEWO), excluding any locations where the turtle was moving. Canopy openness was assessed with a spherical densiometer facing the four cardinal directions and scores averaged for a single estimate at each location.

2.5. Data analyses

We performed statistical analyses with SPSS 23.0 (SPSS, 2015). Males and females were pooled in all analyses. Where appropriate, we examined the assumptions of homogeneity of variances and normality; when data failed to meet assumptions, they were transformed to approximate normal distributions or equal variances. Statistical significance was accepted at the $\alpha \leq 0.05$ level.

We used linear regression to examine the relationships between the temperature of physical models, carcass temperature, and shell temperature. We used paired t -tests to examine the degree to which models and T_s underestimated or overestimated carcass temperature. We examined variation in the estimates derived from physical models using analysis of variance (ANOVA) with mean T_e , d_e , and $\% \geq T_{set}$ as the dependent variables, and habitat type, season, and habitat \times season as the independent variables. In the above analyses, both T_e and d_e were \log_{10} -transformed, and $\% \geq T_{set}$ was arcsine square root transformed.

Data from physical models was not separated based on variation in environmental conditions (e.g., cloud cover, precipitation, and wind) that could influence heating and cooling rates.

We used ANOVA to examine differences in mean monthly T_s between sites (WEWO and LRSP) for each month separately. We also calculated mean canopy openness and mean proportion representation of each tree class (longleaf pine, non-longleaf pines, and hardwood) for each turtle. We used regression analyses to assess the relationships between canopy openness (dependent variable) and the proportional representation of each tree habitat class (independent variables). Both canopy openness and proportion representation values were arcsine square root transformed prior to analyses.

To examine seasonal variation in forest microhabitat use, we used repeated measures ANOVAs with month as the repeated variable and mean proportion of non-longleaf pine and hardwood trees as the dependent variables. We used Friedman tests to examine monthly variation in use of longleaf pine, with month as the repeated variable and mean proportion of longleaf pine as the dependent variable. All proportional values were arcsine square root transformed. We restricted our analysis of seasonal use of forest microhabitats to the active season, between May–October.

3. Results

3.1. Temperature preference

We obtained 3182 measurements of T_b from turtles in the thermal gradient. T_b ranged from 17.5 to 34.5 °C, with a mean (\pm SE) of 28.8 ± 0.6 °C. The 25% and 75% quartiles (T_{set}) averaged across individuals was 27.0–31.0 °C (Fig. 1). Available temperatures along the gradient measured by dataloggers under the sand ranged from 18.5 to 37.0 °C, while surface temperature directly under the heat lamp was as high as 45 °C.

3.2. Operative environmental temperatures

Temperature of physical models was correlated with T_b of turtle carcasses ($R^2 = 0.963$, $F_{1,158} = 4115.2$, $P < 0.001$), but temperatures of physical models deviated by as much as 6 °C above and 3 °C below T_b . Because models slightly underestimated T_b by 0.41 ± 0.11 °C (paired $t = 3.85$, $P < 0.001$), we adjusted temperatures of models using the equation:

$$\text{body temperature} = 1.0215(\text{model temperature}) - 0.1033$$

We recorded 19,600, 18,270, and 2012 measures of T_e in the spring, summer, and fall seasons respectively. For surface positions, T_e , d_e , and $\% \geq T_{set}$ varied by habitat, season, and the interaction of these two variables (Table 1). Surface T_e ranged from 0 to 62 °C across habitats and seasons and was highest in summer, intermediate in spring, and lowest in fall (Table 2, Fig. 2). Surface T_e was approximately 3 °C higher in burned longleaf forests than in adjacent unburned mixed hardwood/

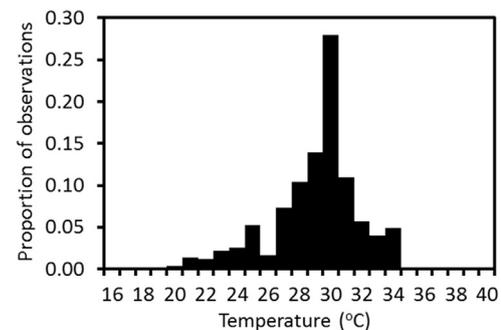


Fig. 1. Body temperatures (T_b) of eastern box turtles (*Terrapene carolina*) on a laboratory thermal gradient.

Table 1

Summary results of ANOVA for the effects of habitat type (longleaf forest or mixed hardwood and pine forest), season (spring, summer, or fall), and their interaction on operative temperature (T_e), thermal quality (d_e), and percentage of T_e within or above T_{set} ($\% \geq T_{set}$) in surface and refuge positions.

Position	Effect	Metric	num df	den df	F	p	
Surface	Habitat	T_e	1	24	57.6	< 0.001	
		d_e	1	24	30.2	< 0.001	
		$\% \geq T_{set}$	1	24	99.4	< 0.001	
	Season	T_e	2	24	2364.1	< 0.001	
		d_e	2	24	2010.4	< 0.001	
		$\% \geq T_{set}$	2	24	376.3	< 0.001	
		Habitat × season	T_e	2	24	36.7	< 0.001
			d_e	2	24	21.6	< 0.001
			$\% \geq T_{set}$	2	24	11.4	< 0.001
Refuge	Habitat	T_e	1	21	4.0	0.059	
		d_e	1	21	10.3	0.004	
	Season	T_e	2	21	643.3	< 0.001	
		d_e	2	21	266.3	< 0.001	
	Habitat × season	T_e	2	21	5.2	0.014	
		d_e	2	21	4.9	0.018	

non-longleaf pine forests in both spring and summer, but did not differ between habitats in fall (Table 2). Surface d_e was lowest (i.e., of higher thermal quality) in summer, intermediate in spring, and highest in fall in all habitats (Table 2). Surface d_e was lower in unburned mixed hardwood/non-longleaf pine forests than adjacent burned longleaf forests in the summer, but did not differ between habitats in spring or fall (Table 2). The amount of time T_e was within or above T_{set} ($\% \geq T_{set}$) was 17–20% higher in burned longleaf forests than in unburned mixed hardwood/non-longleaf pine forests in spring and summer, but differences between habitats were minimal in fall (Table 2).

For refuge positions, T_e and d_e varied by habitat, season, and their interaction, though the effect of habitat was only marginally significant for T_e (Table 1). Refuge T_e ranged from 1 to 37 °C across habitats and seasons and was higher in burned longleaf forests than unburned mixed hardwood/non-longleaf pine forests in spring and summer, but did not differ between habitats in fall (Table 2, Fig. 3). Refuge d_e was lowest (i.e., of higher thermal quality) in summer, intermediate in spring, and highest in fall in both habitats, and lower in burned longleaf forests than unburned mixed hardwood/non-longleaf pine forests in all seasons (Table 2).

In spring, hourly average T_e remained above the minimum T_{set} threshold (27 °C) from 1100 to 1900 h on the surface in burned longleaf habitat, but neither refuge longleaf nor mixed hardwood/non-longleaf pine (surface or refuge) habitats reached the minimum T_{set} threshold (Fig. 4). In summer, hourly average T_e in burned longleaf habitats reached the minimum T_{set} threshold from 1000 to 2000 h on the surface, and from 1300 to 2000 h in refuge habitats (Fig. 4). Summer

Table 2

Summary of seasonal habitat variation in operative environmental temperatures (T_e), thermal quality (d_e), and percentage of time T_e was within or above T_{set} ($\% \geq T_{set}$). The burned forest was predominately longleaf pine, while the unburned forest was a mixture of hardwood and non-longleaf pine species.

Position	Season	Habitat	T_e °C (se)	d_e (se)	$\% \geq T_{set}$ (se)	T_e °C range
Surface	Spring	Burned	24.7 (0.2)	5.3 (0.1)	31.4 (1.3)	7–62
		Unburned	21.8 (0.1)	5.4 (0.1)	11.0 (1.5)	8–37
	Summer	Burned	27.4 (0.2)	4.0 (0.1)	41.1 (1.7)	14–55
		Unburned	24.5 (0.1)	3.0 (0.1)	24.3 (1.9)	11–47
	Fall	Burned	13.0 (0.1)	14.0 (0.0)	1.2 (0.3)	0–32
		Unburned	13.4 (0.3)	13.5 (0.3)	0.2 (0.2)	1–31
Refuge	Spring	Burned	21.5 (0.2)	5.6 (0.2)	–	10–37
		Unburned	20.3 (0.2)	6.7 (0.2)	–	10–27
	Summer	Burned	25.2 (0.5)	2.4 (0.3)	–	15–35
		Unburned	23.6 (0.2)	3.4 (0.2)	–	16–32
	Fall	Burned	12.9 (0.2)	14.3 (0.2)	–	4–25
		Unburned	13.4 (0.5)	13.7 (0.4)	–	1–22

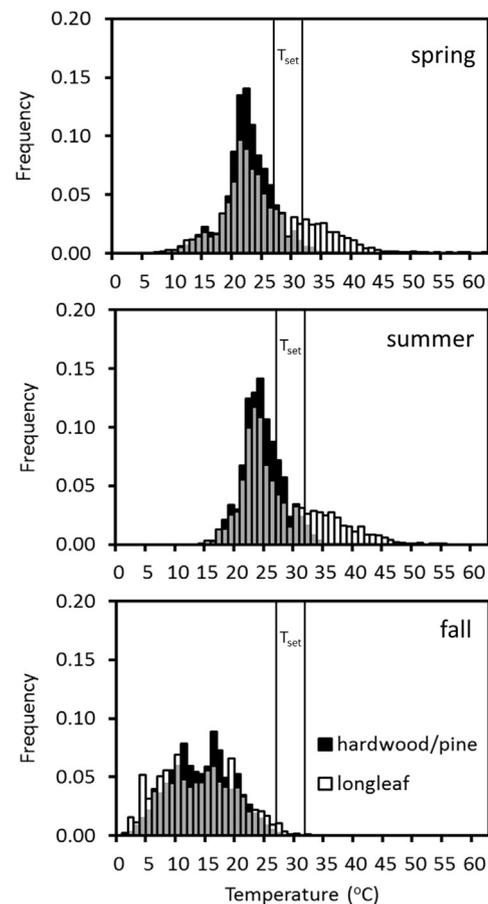


Fig. 2. Frequency distribution of seasonal operative environmental temperatures for surface habitats in fire-maintained longleaf pine forests and unburned mixed hardwood/non-longleaf pine forests. Note that the grey color represents areas where the two habitats' distributions overlap. The preferred body temperature, or set-point range (T_{set}) for eastern box turtles (*Terrapene carolina*) is 27–31 °C.

hourly average T_e in unburned mixed hardwood/non-longleaf pine habitats reached the minimum T_{set} threshold from 1300 to 1900 h on the surface, but never reached T_{set} in refuge habitats (Fig. 4). Fall hourly average T_e did not reach T_{set} in either habitat (Fig. 4).

3.3. Free-ranging turtle temperatures

T_s was correlated with T_b of carcasses ($R^2 = 0.912$, $F_{1,92} = 948.3$, $P < 0.001$), with T_s overestimating T_b by 0.70 ± 0.34 °C (paired $t = 2.06$, $P = 0.04$). However, some measures of T_s deviated by as much as

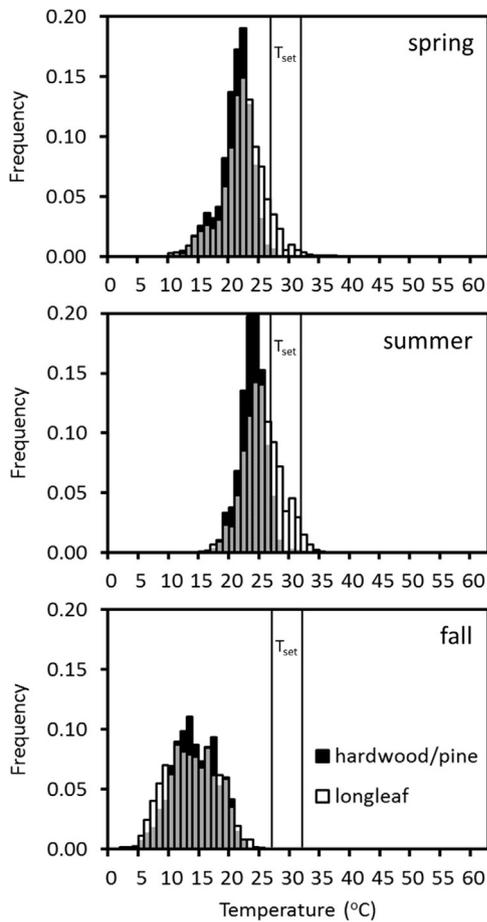


Fig. 3. Frequency distribution of seasonal operative environmental temperatures for refuge habitats in fire-maintained longleaf pine forests and unburned mixed hardwood/non-longleaf pine forests. Note that the grey color represents areas where the two habitats' distributions overlap. The preferred body temperature, or set-point range (T_{set}) for eastern box turtles (*Terrapene carolina*) is 27–31 °C.

15 °C above and 3 °C below T_b when on the surface.

From 1 May–31 October, we obtained 28,896 and 29,640 measures of T_s at WEWO and LRSP, respectively. T_s ranged from 1.5 to 43.5 °C at WEWO and from 1.0 to 42.0 °C at LRSP. Monthly mean T_s was 0.4–1.8 °C higher at WEWO than LRSP (Fig. 5), but differed significantly only during August ($F_{1,13} = 12.40, P = 0.004$) and October ($F_{1,13} = 8.08, P = 0.014$). However, comparisons between sites for most other months approached significance (May: $F_{1,14} = 3.95, P = 0.067$, June: $F_{1,15} = 3.87, P = 0.068$, July: $F_{1,17} = 4.09, P = 0.059$, August: $F_{1,13} = 1.86, P = 0.196$). The most pronounced differences in T_s between sites occurred during the day between 1100–1700 h, while overnight T_s was similar (Fig. 6).

3.4. Habitat use

Turtles used habitats with predominantly hardwood trees in all months at both sites, but the relative amounts of each tree class in the nearby habitat varied moderately over the course of the active season (Fig. 7). Turtles at WEWO used forests with increasing percentages of non-longleaf pine from May–October ($F_{5,130} = 2.4, P = 0.042$), while using forests with a decreasing percentage of hardwoods over the same time period ($F_{5,130} = 6.1, P < 0.001$; Fig. 7). At LRSP, turtles also used forests with increasing percentage of non-longleaf pine from May–October ($F_{5,110} = 2.7, P = 0.046$), but the percentage of hardwood trees in used forests did not vary over this time period ($F_{5,130} = 1.8, P = 0.147$; Fig. 7). There was no seasonality of use for longleaf habitat at either site ($P > 0.334$; Fig. 7).

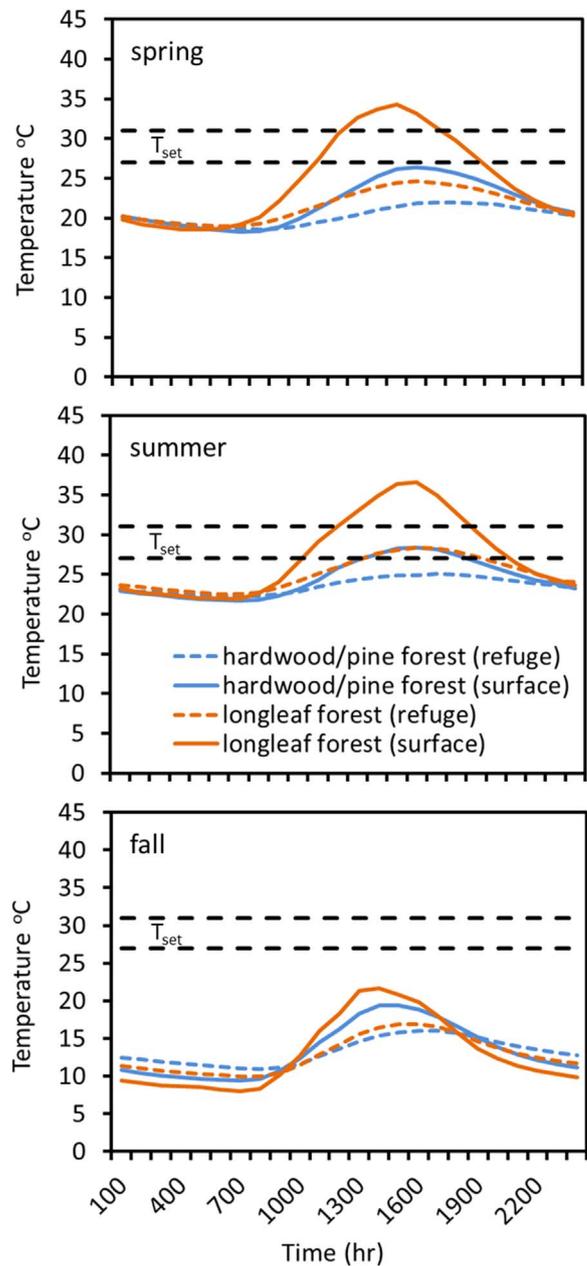


Fig. 4. Seasonal mean hourly operative environmental temperatures for surface and refuge models in fire-maintained longleaf pine forests and unburned mixed hardwood/non-longleaf pine forests. The preferred body temperature, or set-point range (T_{set}) for eastern box turtles (*Terrapene carolina*) is 27–31 °C.

Variation in canopy openness depended on tree types in the immediate surrounding area. Canopy openness increased logarithmically with increasing percent longleaf ($F_{1,11} = 25.4, R^2 = 0.70, P < 0.001$), but decreased linearly with increasing percent hardwood trees ($F_{1,9} = 85.6, R^2 = 0.91, P < 0.001$; Fig. 8). Canopy openness was not correlated with percent non-longleaf pine species ($F_{1,9} = 1.6, P = 0.233$).

4. Discussion

The use of prescribed fire in forest habitat management affects the thermal characteristics of the environment, and thus has the potential to indirectly influence the physiology and behavior of ectothermic vertebrates such as turtles. Our results indicate that the burned longleaf habitat experienced considerably higher temperatures than the adjacent unburned mixed hardwood/non-longleaf pine forest, but surface

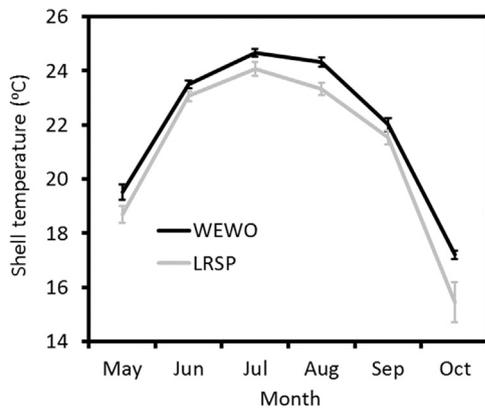


Fig. 5. Monthly shell temperatures (mean ± SE) for field-active eastern box turtles (*Terrapene carolina*) at a site managed using prescribed fire (WEWO) compared to turtles at an unburned site (LRSP).

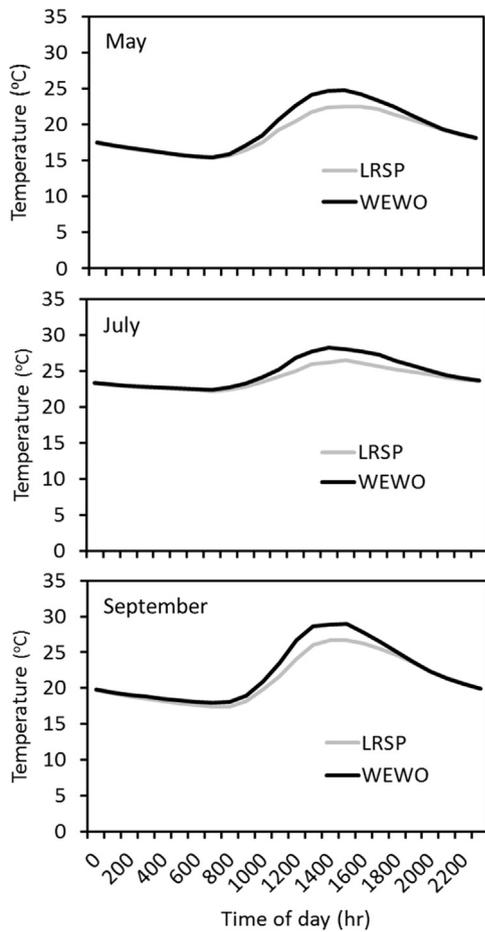


Fig. 6. Hourly mean shell temperatures for field-active eastern box turtles (*Terrapene carolina*) at a site managed using prescribed fire (WEWO) compared to turtles at an unburned site (LRSP) during May, July, and September.

environments in the fire-managed longleaf forest were not of superior thermal quality in any part of the active season. The longleaf forest also had a more variable thermal environment, where surface-active turtles would be regularly exposed to temperatures above their thermal preference range and sometimes exceeding lethal limits. Turtles using fire-managed longleaf forests experienced seasonally higher T_s , but despite the potential thermal costs and benefits associated with the different habitats and seasons, there was little evidence to suggest habitat use behaviors were linked to variation in the habitats' thermal

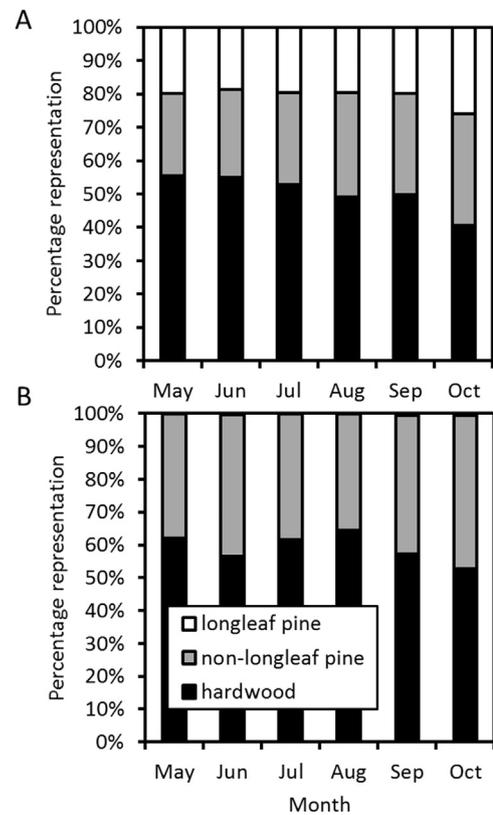


Fig. 7. Seasonal forest habitat use for eastern box turtles (*Terrapene carolina*) at A) a site managed using prescribed fire (WEWO) compared to B) turtles at an unburned site (LRSP).

characteristics.

This is the first quantification of T_{set} for any subspecies of *T. carolina*. Our estimates of T_{set} (27.0–31.0 °C) and mean preferred T_b (28.8 °C) are higher than the preferred T_b reported for *T. carolina* elsewhere (20–25 °C; Erskine and Hutchison, 1981; do Amaral et al., 2002a, 2002b). Compared more broadly to other species, our estimates of preferred T_b are within the upper range reported for turtles from temperate regions; 20.7–22.4 °C for *Sternotherus odoratus* (Graham and Hutchison, 1979); 21.1–24.9 °C for *Clemmys guttata* (Graham and Hutchison, 1979); 22.0–27.0 °C for *Glyptemys insculpta* (Dubois et al., 2008); 22.0–27.2 °C for *Chrysemys picta* (Graham and Hutchison, 1979; Edwards and Blouin-Demers, 2007); 24.6–29.1 °C for *Trachemys scripta* (Gatten, 1974); 28.1 °C for *Chelydra serpentina* (Schuett and Gatten, 1980); 28.3–29.8 °C for *Terrapene ornata* (Gatten, 1974), and 28.7–32.5 °C for *Graptemys geographica* (Bulté and Blouin-Demers, 2010). Temperature preferences in turtles can vary among populations over latitudinal gradients, including in *Terrapene* spp. (Ellner and Karasov, 1993), and can even differ among individuals within a population exposed to different local thermal environments (Curtin, 1998). Our study populations were from lower latitude and elevation (and thus a warmer climate) compared to most other species for which preferred T_b has been assessed, and the higher preferred T_b in our study is consistent with observations of ectotherms from warmer climates (Ellner and Karasov, 1993). Turtles may also vary in thermal preference due to nutritional status (Gatten, 1974), infection (Monagas and Gatten, 1983; do Amaral et al., 2002b), and perhaps other intrinsic factors. Our sample was limited to apparently healthy and postabsorptive adult turtles in the late active season when potentially confounding variation due to reproductive status would also be minimized. Our estimates of preferred T_b were within the range of temperatures for optimized performance in turtles for feeding (29–30 °C, Gatten, 1974; 26–29 °C, Parmenter, 1980; 30 °C, Dubois et al., 2008) and locomotion (24–32 °C,

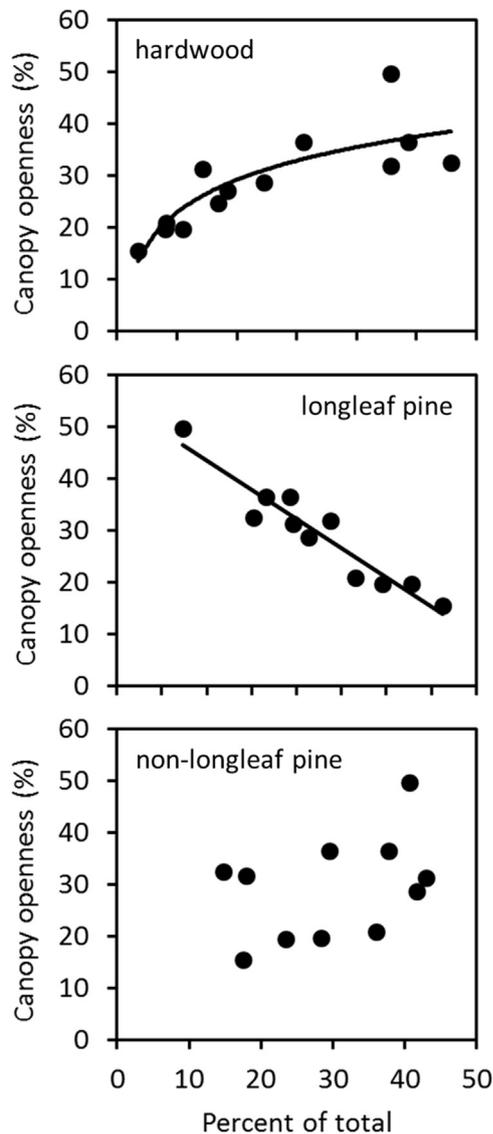


Fig. 8. Relationships between canopy openness and relative forest composition of hardwood, longleaf pine, and non-longleaf pine trees at a site managed using prescribed fire.

Adams et al., 1989), further justifying our use of T_{set} estimates in assessing the suitability of the thermal environment for various important processes in *T. carolina*.

The long-term use of prescribed fire in the longleaf pine system was likely a strong contributor to the altered thermal environments available to turtles at our site, resulting in part through changes in vegetative structure. Fire reduces vegetative and ground cover, and opens the canopy allowing more direct solar radiation to the forest floor (Mushinsky, 1992; Greenberg and Waldrop, 2008; Matthews et al., 2010), resulting in increased temperature for several years after fire (Hossack et al., 2009). Indeed, in areas where prescribed fire has been regularly employed at our study site, where longleaf pines predominate, canopy openness was higher than in predominantly hardwood forest habitats that are not managed with fire. That the higher mean surface T_e in fire-maintained longleaf habitats was closer to T_{set} at first suggests this would be the most thermally-optimal habitat for *T. carolina*, yet this habitat was never of superior thermal quality, likely due to its wider T_e fluctuations. Minimum T_e was similar among habitats, but surface T_e exceeded T_{set} for 20–25% of recordings in burned longleaf forests in spring and summer compared to just 1–3% in unburned mixed hardwood/non-longleaf pine habitats. Moreover, surface T_e in fire-maintained longleaf forests exceeded temperatures presumed to be lethal, or

the critical thermal maximum (CT_{max}), in turtles. While we did not measure CT_{max} in our study population, based on measures from other studies, we presume it unlikely that *T. carolina* would tolerate extended exposure to temperatures above 40 °C (Sturbaum, 1981; Plummer et al., 2003; Lagarde et al., 2012). Consistent with this explanation, the only time when thermal quality differed between surface environments was during the hot summer period, when the unburned mixed hardwood/non-longleaf pine forest was of higher thermal quality due to the cooler temperatures. During this period, the more open fire-maintained longleaf forest exceeded CT_{max} 7% of the time.

It is important to recognize that comparisons of thermal quality only reflect the relative availability of thermally favorable environments without taking into consideration thermoregulatory behaviors. Many reptiles maximize thermal benefits by shuttling among microhabitats or altering position in thermally heterogeneous environments to remain within or closer to T_{set} for more extended periods (Christian and Weavers, 1996; Edwards and Blouin-Demers, 2007; Dubois et al., 2009; Besson and Cree, 2010). Assuming turtles in our study were behaviorally thermoregulating, fire-maintained longleaf forest could offer more opportunities to maintain T_b closer to or within T_{set} . For instance, surface T_e exceeded the lower bound of T_{set} for 17% and 20% more of the time than in unburned mixed hardwood/non-longleaf pine forests in summer and spring seasons, respectively, while refuge environments always offered T_e below the upper bound of T_{set} in both forest types at these times. To exploit these opportunities in the fire-maintained longleaf habitat, suitable thermal refuge microsites would need to be readily available, and turtles would need to move between surface and nearby refuge environments. We were not able to assess how carefully turtles thermoregulated in the different habitats because we did not measure T_b in field-active animals. Instead, we measured T_s as an approximation of T_b , as these two measures can be tightly linked in small-bodied turtles (Grayson and Dorcas, 2004). However, the degree to which T_s accurately reflects T_b may differ among species due to shape and size variation and their effects on heating and cooling rates (Polo-Cavia et al., 2009; Bulté and Blouin-Demers, 2010). While our measures of T_s were correlated with T_b , the magnitude of deviations was at times high, so we were cautious in using T_s as an accurate proxy of T_b for all scenarios in field-active turtles. Nevertheless, the higher T_s of turtles at the fire-maintained site (WEWO) suggest they would have also experienced relatively higher T_b than turtles at a nearby site where fire is not used in management (LRSP). However, T_s differences between sites were only moderate (< 2 °C), and whether this difference was a result of habitat alterations from fire, or whether this resulted in measurably different vital rates or performance measures is not yet known. We are currently monitoring growth rates, body condition, survivorship, and other endpoints that could elucidate any temperature effects with fitness consequences.

Turtles often respond to thermally heterogeneous environments by behavioral thermoregulation, including habitat selection to maximize heat gain (Dubois et al., 2009; Picard et al., 2011), alterations to activity timing and use of refuges in times of temperature extremes (Nieuwolt, 1996; Lagarde et al., 2012), and seasonal migration between areas differing in temperature (Swingland and Lessells, 1979). Given the variation in thermal characteristics of habitats at the fire-maintained site, we expected to observe strong links between seasonal habitat use and thermoregulatory behavior in *T. carolina*. As the fire-maintained and unburned forests occur in close proximity to one another at WEWO, turtles could hypothetically move between the different habitats to maximize thermal benefits (maintain T_b closer to T_{set}) or minimize costs (avoid overheating) on a temporal basis. Indeed, individual turtles did regularly move between burned and unburned habitats and among different forest types. However, while we did observe some seasonality in habitat use, the magnitude of changes was only moderate, and the directions of change were not consistent with behavioral thermoregulation. For instance, use of the unburned, predominantly hardwood forests should have peaked in summer when this

habitat offered superior thermal quality, but associations with such environments decreased moderately (minus 14% from May to October) throughout the active season at WEWO and did not vary seasonally at LRSP. Likewise, if turtles were behaving in ways to minimize risks of exposure to temperature extremes, use of the fire-maintained longleaf forests should have decreased in summer, but we observed no seasonality in use of this habitat. We did observe moderately increased use of forests with more non-longleaf pine species at both sites over the active season (plus 6–8% from May to October), but because canopy openness did not vary according to this tree class, it is unlikely that this shift in habitat use was driven by thermoregulation.

Habitat use is shaped by multiple requirements in including hydration, feeding, reproduction, and predator avoidance. While all of these processes are dependent on temperature in ectotherms (Huey, 1982; Angilletta et al., 2002), perhaps the relatively low variation in thermal characteristics among habitats and overall benign thermal environment of our system minimizes the influence of temperature in habitat use “decisions”. Ectotherms must invest more effort into thermoregulation in extreme climates with low thermal quality, such as at higher latitudes and elevations (Blouin-Demers and Nadeau, 2005); as a result, we typically see stronger thermoregulatory behaviors, such as habitat selection and activity timing, in thermally challenging environments (Blouin-Demers and Weatherhead, 2001; Edwards and Blouin-Demers, 2007; Besson and Cree, 2010). In our study, the largest difference in thermal quality (d_c) between habitats in any season (for comparable positions) was 1.1, and all habitats were of relatively high thermal quality during most of the active season compared to measures from terrestrial habitats in colder climates (Blouin-Demers and Weatherhead, 2001; Blouin-Demers and Nadeau, 2005; Row and Blouin-Demers, 2006). *T. carolina* may thus be able to more easily maintain T_b close to T_{set} in both fire-maintained and unburned forests without employing potentially costly thermoregulatory behaviors.

In the only other study of *T. carolina* in a longleaf system, turtles selected predominantly hardwood and mixed pine-hardwood forests and used predominantly pine forests (including longleaf) less often than expected based upon availability (Greenspan et al., 2015), which is consistent with high use of hardwood forests in all seasons at our sites. However, longleaf pines accounted for approximately 21% of the trees in the microhabitats used by turtles at the fire-maintained site (WEWO), while accounting for less than 1% of forest composition at turtle locations at the unburned site (LRSP). It should be noted that we did not assess habitat selection here, as this would require comparing habitat use with availability. Our approach was simply to examine whether seasonal shifts in the forest composition of the habitats used by turtles could be linked to temporal variation in habitat thermal characteristics. As there were no major temporal or spatial changes in the availability of overstory trees in our study systems, an assessment of changes in habitat use alone should be informative for detecting seasonal shifts in forest habitat associations. Further studies could assess whether associations with (or selection of) other aspects of the habitat structure (e.g., cover objects, water availability, understory vegetation structure) vary seasonally, or whether turtles respond to thermal heterogeneity at broader spatial scales (i.e., macrohabitat or landscape scale distribution). It would also be instructive to determine if turtles in the fire-maintained longleaf forest exhibit different seasonal shifts in surface activity timing to avoid periods of extreme mid-day heat ($T_e > T_{set}$ from 1200 to 1800), as has been observed in other terrestrial turtles in thermally challenging habitats (Meek, 1988; Plummer, 2003). Because no turtles died from overheating nor showed any signs of heat stress (other than some that were burned by fire), we suspect that they exhibited some degree of thermoregulatory behavior, but our sampling design of tracking turtles only once per week was insufficient to detect such fine-scale temporal variation in activity.

Our results suggest that *T. carolina* does not exhibit a strong behavioral response to the thermal heterogeneity created by prescribed fire in our system at the spatial and temporal scales we examined. However,

we caution that our observations are from only on a single site where fire disturbance has long been a natural part of the system and where prescribed fire has been used in management for the last several decades. Turtle responses to other fire regimes, habitats, or in other parts of their broad geographic range may be different than observed here. Our study design was also limited in its ability to disentangle the many environmental factors other than temperature that can influence habitat use in turtles. Moreover, habitat associations and other behaviors could be affected by the direct risks imposed by fire, as *T. carolina* can suffer injury and mortality from burns (Babbitt and Babbitt, 1951; Platt et al., 2010), as well as decreased body condition following fire (Howey and Roosenburg, 2013). Fire could also indirectly affect habitat use behavior by altering understory vegetation structure, hydric conditions, or food availability (Rossell et al., 2006; Platt et al., 2009; Greenspan et al., 2015). It is clear that as fire becomes a more popular tool for habitat management, much more research is required to understand the responses of *T. carolina* and other terrestrial ectotherms to both wild and prescribed fires.

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