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

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A B S T R A C T

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 ± 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 × 50 cm × 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 × 85 cm × 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. Daytime 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