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Effects of gap-based silviculture on thermal biology of a terrestrial reptile

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Abstract

Context. Terrestrial reptiles require varied thermal environments to promote optimal physiological performance, growth, reproduction, and survival.

Aims. Our study was designed to determine whether gap-based silvicultural practices offer suitable thermal environments for eastern box turtles (*Terrapene carolina*) by examining environmental temperature variation and body temperature of eastern box turtles in, and adjacent to, canopy gaps.

Methods. We recorded box turtle body temperature from 20 radio-tracked turtles and environmental temperatures (canopy gaps and undisturbed habitat) using temperature loggers from June to September 2014 in a managed forest after canopy gaps (0.28–1.13 ha gap^{-1}) were created via gap-based silviculture.

Key results. Over the four-month study period, gap temperatures were generally higher than adjacent undisturbed microhabitats. Box turtle body temperatures were closely correlated with environmental temperatures in undisturbed habitat in June and July. Turtle body temperatures were, however, closely correlated with environmental temperatures in canopy gaps in August and September. In addition, box turtles in our study had activity areas that overlapped canopy gaps from 0 to 65%, depending on the individual. As percentage overlap of canopy gaps increased, turtle body temperatures were increasingly correlated with canopy gap temperatures. Furthermore, as percentage overlap of canopy gaps increased, daily mean body temperature records consistently stayed within the preferred box turtle body temperature range (20.2–26.2°C).

Conclusions. Our study suggests that gap-based silviculture can create thermally compatible environments for box turtles depending on the time of day and year, and that box turtles use these microhabitats to thermoregulate.

Implications. The application of relatively small-scale silvicultural practices ($\leq$1 ha gap^{-1}) that provide heterogeneity in forest structure, composition, and function may be a useful alternative to clearcutting and other intensive harvesting methods that are associated with declines in terrestrial reptile populations.

Additional keywords: forest dynamics, habitat modification, habitat use, radio telemetry, thermoregulation.

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Introduction

Canopy gaps created by natural disturbance (due to wind, tree fall, etc.) create heterogeneity in microclimatic conditions, forest structure, and resource availability (i.e. direct and diffuse solar radiation) (Greenberg 2001). Heterogeneity in microclimatic conditions also increases establishment, growth, and recruitment of numerous tree species (Elliott et al. 2002; Ritter and Bjørnlund 2005). Consequently, silvicultural systems that emulate natural disturbance by creating single-tree- to several-hectare-sized canopy gaps are often proposed as a forest management strategy (Greenberg 2001; Mitchell *et al.* 2005). Gap-based silviculture is being increasingly used in deciduous forests of the eastern and midwestern United States (Webster and Lorimer 2005; Kern *et al.* 2013; Lhotka 2013). These silvicultural practices create structural complexity at the stand level and yield a gradient of canopy conditions. Varying canopy structure resulting from gap-based silviculture can influence ecological processes and ecosystem function via increased light, temperature and moisture availability (Chen *et al.* 1999). Because of these ecological benefits, spatial variation in microclimatic conditions in and around canopy gaps are frequently studied in managed forests (Bauhus and Bartsch 1995; Bartsch 2000).

Several wildlife species, especially reptiles, may use canopy gaps due to increased light availability and intensity, and high soil-surface temperatures (Greenberg 2001; Greenberg and

Lanham 2001; Faccio 2003), although responses depend on physiological tolerances and how species respond behaviourally to changes in microclimatic conditions. Specifically, effects of reduced canopy cover can depend on a species' habitat preference and degree of selection or avoidance of direct sunlight (Pike *et al*. 2011*a*). Reptiles may use canopy gaps to access increased light and warmer temperatures required for optimal activity (Vitt *et al*. 1998). Furthermore, increased use of areas with reduced canopy has been linked to increases in abundance and diversity of reptiles in forests (i.e. Perison *et al*. 1997; Ross *et al*. 2000; Greenberg 2001; Renken *et al*. 2004; Todd and Andrews 2008; Felix *et al*. 2008; Cantrell *et al*. 2013). Greenberg (2001) noted greater reptile species richness in natural canopy gaps compared with non-harvested reference sites with dense canopy cover in the southern Appalachians (USA). Furthermore, Pike *et al*. (2011*a*) suggested that canopy removal benefits species that thrive in direct sunlight habitat with warmer temperatures. Conversely, if insolation and subsequent temperatures in canopy gaps exceed preferred body temperatures, some species may avoid them altogether due to limited dispersal and thermoregulatory capabilities. Thus, varying microclimatic conditions within harvested areas (i.e. understorey closure and substrate temperature) may positively or negatively alter reptile movement, thermoregulation, and habitat use (O'Bryan 2014; Currylow *et al*. 2012).

Although there is sufficient qualitative evidence to suggest a positive thermoregulatory response of ectotherms to gap-based silviculture (Messere and Ducey 1998), there is little quantitative evidence linking habitat heterogeneity created by gap-based silviculture to reptile thermoregulation and body temperatures. Eastern box turtles are useful species to assess the effects of timber harvest, as they are a common reptile in forests of the eastern USA and sensitive to environmental disturbance (Dodd 2001; Dodd *et al*. 2016). Currylow *et al*. (2012) notes that temperatures in harvested landscapes (i.e. clearcuts and group selection) often approached the critical thermal maximum (41.5–43.9°C: Hutchison *et al*. 1966) of eastern box turtles (*Terrapene carolina*) in southern Indiana, USA. Additionally, eastern box turtles often experienced higher body temperatures in areas exposed by timber harvesting (Currylow *et al*. 2012). Furthermore, varied thermal environments generated by timber harvests shortened and concentrated eastern box turtle movements to edges of harvested areas (e.g. limited mobility: Currylow *et al*. 2012). Finally, while box turtles can reach maximum walking velocity at warm temperatures (31.9°C: Adams *et al*. 1989), when given a thermal gradient, they often have a preferred temperature range of ~20−28°C (Boucher 1999; Currylow *et al*. 2012; do Amaral *et al*. 2002) or 27−31°C (Roe *et al*. 2017).

The objective of this study was to examine environmental temperatures and body temperatures of eastern box turtles during the day and throughout the active season in a managed forest that uses gap-based silviculture, and to determine whether environmental temperatures in canopy gaps are thermally compatible with preferred body temperatures of eastern box turtles. Thus, we may infer if gap-based silviculture may be a useful alternative to mitigate declines of forest reptiles in areas exposed to clearcut silviculture. Although the gaps were either 0.28 ha or 1.13 ha in our study area, man-made canopy gaps create markedly different thermal environments compared with nearby non-harvested forest stands (e.g. ambient temperatures significantly higher or lower than in non-harvested areas). In addition, box turtles may not have adequate physiological mechanisms to combat thermal stress (Hutchison *et al*. 1966; Sturbaum 1981) created by above-average temperatures in man-made canopy gaps (Currylow *et al*. 2012). Thus, we predicted that gap-based silviculture would create thermal environments (i.e. average environmental temperatures) that would not correlate with box turtle body temperatures. In addition, we expected that box turtles whose activity areas overlapped with canopy gaps would show carapace temperatures outside the range of preferred body temperatures throughout the main activity season (June–September).

Materials and methods

Study area

We conducted our study in the 3440-ha Berea College Forest (BCF) in Madison County, Kentucky, USA. The BCF (37°32′N, 84°14′W) is managed by Berea College and is used for experimental research studies, timber harvesting, recreation, and education. The BCF is a mature hardwood forest consisting of *Quercus* (*alba*, *coccinea*, *montana*, *velutina*), *Carya* (*glabra*, *ovata*), and *Pinus* (*echinata*, *virginiana*) (Patterson and Karcher 2013), and has been intermittently harvested for timber over the past century. The understorey is dominated by shade-tolerant species – sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*). The average canopy top height at BCF is 27.9 m at base age 50, and the average age of overstorey trees is 111 years old (Craig *et al*. 2014). The BCF is located on the western edge of the Northern Cumberland Plateau ecological section, and elevation ranges from ~200 to 500 m.

The current management plan at BCF includes the implementation of a variant of gap-based silviculture, known as the 'expanding gap method', in an effort to enhance direct sunlight levels needed for the survival and growth of oak seedlings (Raymond *et al*. 2009). In one watershed where this gap-based practice was completed, eight circular canopy gaps were created on east-facing slopes in autumn 2012 (Fig. 1). Four canopy gaps were created by felling all trees over 1.4 m tall within a 30-m radius of gap centre. An additional four canopy gaps were created using the aforementioned methods, and a deadening (herbicide treatment) of all understorey and overstorey trees (i.e. non-oak trees) within a 60-m radius of gap centre. Stems from deadened trees were cut into smaller pieces and left on the ground within or near plot boundaries. The total cut area of each gap was 0.28 ha where understorey tree removal was not applied, and 1.13 ha where understorey herbicide treatment tree removal was applied. In addition, adjacent gap edges were an average of 145 m distance from each other, to maintain forest canopy heterogeneity. See Stringer (2006), Patterson and Karcher (2013), and Craig *et al*. (2014) for further detailed information about BCF and methods of canopy gap creation.

Field techniques

From September 2013 to May 2014, we used time–area constrained searches to capture box turtles within and around

Fig. 1. Aerial view of eight canopy gaps, and view from within canopy gap (bottom right) in a managed forest in Madison County, Kentucky, USA.

canopy gaps throughout the entire study site (Walker 2012). We also located new box turtles opportunistically when they were encountered across the study area. Upon first capture, we recorded the sex, and measured (cm) straight-line carapace length, plastron length, carapace width, and shell depth (height). Additionally, we marked the marginal scutes of each turtle's carapace in a unique pattern using a triangular metal file (Cagle 1939), and determined maturity based on secondary sexual characteristics. In total, 20 adult turtles (10 males, 10 females) captured in or near canopy gaps were fitted with a radio-transmitter (SOPER-2190; Wildlife Materials, Inc., Murphysboro, IL). Radio-tracked individuals were also outfitted with Embedded Data Systems© Thermochron iButton temperature loggers (DS1922T-F5#) (hereafter referred to as temperature loggers) to monitor their carapace temperatures, which are generally highly correlated with internal body temperatures (Bernstein and Black 2005; Chen and Lue 2008; Dubois *et al*. 2009). To prevent water damage on temperature loggers, we covered each logger in plastic tool dip (Plasti-Dip International, Circle Pines, MN). Temperature loggers were programmed (using Thermodata Viewer 3.1.2 software) to record air temperature (accurate to ±1°C) every 30 min. Once the box turtle was marked, measured, and affixed with a radio-transmitter and temperature logger, it was released at point of capture. Radio-transmittered adults were located every 7–10 days from June to September 2014, and their location was recorded to the nearest 3 m using a handheld GPS. In addition, turtle temperature data from loggers were downloaded via Thermodata Viewer 3.1.2 software once every 30 days.

To investigate thermal characteristics of the various microhabitats within our study area, we measured ambient environmental temperatures using temperature loggers suspended in 15 × 15 × 15 cm open plastic containers ~10 cm aboveground (approximate height of box turtle carapace), and shaded via a blue plastic container cover to minimise direct sunlight exposure. The colour of the plastic cover was also selected to best mimic the reflectance of a box turtle carapace (Peterson *et al*. 1993). Temperature loggers were placed directly in the centre of each of the eight gaps; however, only six of the gap centre loggers remained functional throughout the study period. By placing temperature loggers in the centre of gaps, we best approximated strictly open canopy environmental temperatures. We also placed temperature loggers in four different closed-canopy forest areas using methods described before (i.e. above-ground control) and 15 cm below ground (i.e. below-ground control) ~200 m from canopy gap habitat, representing a non-harvested reference area and environmental temperature available to turtles. Environmental temperature loggers were programmed to record air temperature every 30 min, and data from these loggers were retrieved once every 30 days during the study period.

Spatial analysis

We used ArcGIS 10.1.1 (ESRI 2014), Hawth's Analysis Tools extension, and ArcGIS 3D Analyst extension, to create a 100% minimum convex polygon (MCP) using geographic coordinates for each radio-tracked turtle, and then estimated three-dimensional landscape activity area (in hectares) based on a 10-m digital elevation model (DEM). To create the study footprint (i.e. 37.28 ha; complete study area boundaries), we generated an MCP, incorporating a 10-m DEM, that included all radio-telemetry locations as well as gap plots. Mean MCP values (±standard error) were generated for adult males, females, and both groups combined. We ensured that the number of turtle relocations did not influence our results by using a simple linear regression of individual activity area sizes versus relocation numbers. We then determined the proportion of each MCP activity area that overlapped a canopy gap (i.e. percentage overlap). To conduct this analysis, we used the ArcGIS 3D intersect tool extension, which calculated mean percentage overlap for each individual's MCP. Using the median of all percentage canopy gap overlap values (32.5%), we partitioned individuals into two groups based on degree of overlap for further analysis (i.e. lower degree of overlap: ≤ median percentage canopy gap overlap; and higher degree of overlap: > median percentage canopy gap overlap). Finally, to visually interpret overall use of canopy gaps by box turtles with all capture locations (all capture–recapture and telemetry locations, $n = 504$), we used the ArcGIS point-density tool, which generated the density of capture locations (density per 3.5-m^2 cells) across our entire study site.

Thermal analysis

To address whether or not canopy gaps provided suitable environmental temperatures for eastern box turtles, we used three complementary approaches integrating both turtle body temperatures (T_b) and environmental temperatures (T_e) adjacent to and within canopy gaps. First, we analysed the relationship between gap habitat T_{e1} versus non-harvested reference habitat T_{e2} using multimodel selection. Second, we split turtle temperature data based on high versus low percentage overlap, and analysed the relationship between T_b and T_e in gaps and non-harvested reference microhabitats. This analysis allowed us to determine which microhabitat T_e best correlated with turtle T_b throughout the day and year in both high- and low-overlap groups. Third, we tested the relationship between percentage canopy gap overlap and the number of T_b records within the preferred T_b range to see whether box turtles with increased access to canopy gaps were able to reduce their temperature variance and acquire preferred body temperatures.

For our first approach, we retrieved 30-min T_e records from each microhabitat type during the complete study period. To analyse T_e variation throughout the day, we averaged temperatures in each microhabitat at different periods of the day (i.e. sunrise, late-morning, midday, early-afternoon, sunset). Specifically, we partitioned T_e records by microhabitat type and parsed data into five periods: (06:00–09 : 00 hours (P1), 09:00–12 : 00 hours (P2), 12:00–15 : 00 hours (P3), 15:00–18 : 00 hours (P4), and 18:00–21 : 00 hours (P5)). Because our study focussed on daytime behaviour, T_e records from before sunrise and after sunset, as determined by US Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/docs/RSOneYear.php), were removed. Using Program R 3.1.1 and 'nlme' package (Pinheiro *et al*. 2013), we fit generalised least-squares models (GLS) to compare T_e among different microhabitats (i.e. gap centre, below-ground control, above-ground control) during all five periods of the day – one model for each period of the day. To account for temporal autocorrelation, we fit out GLS models with an autoregressive (AR-1) correlation structure (Littell *et al*. 2000), which accounted for correlation between consecutive T_e records within each individual microhabitat. Our AR-1 correlation structure was a function of day of year (DOY) nested within each habitat type (DOY|microhabitat). Mean T_e in each microhabitat was calculated from the model coefficients, and confidence intervals were calculated using the standard errors for the prediction means. Coefficients were determined to be significant at $\alpha = 0.05$.

For our second approach, we used results from our activity area analysis, and split box turtle T_b records into three datasets: (1) all data combined, (2) high-degree canopy gap overlap (>32.5%), and (3) low-degree canopy gap overlap (≤32.5%). Using 'nlme' package, we fit linear mixed effects models (LME) (Faraway 2005) to assess the relationship between T_b and different microhabitat T_e in all datasets separately, including one model for each period of the day. The LME models were fit with a random coefficient (box turtle ID), and random effect (DOY) to allow the relationship between T_b and T_e to vary between individuals. We fit four models for each period of the day, each with a single set of T_e records (gap centre, above-ground control, below-ground control). To account for temporal autocorrelation between box turtle temperature records, we fit LME models with an AR-1 correlation structure. The AR-1 correlation structure was a function of DOY nested within turtle identification (DOY|ID). To address which microhabitat T_e best correlated with box turtle T_b in each dataset, models were compared and a top model selected using AIC (Burnham and Anderson 2002). Finally, with all datasets, we investigated monthly box turtle T_b associations with microhabitat T_e via LME models for each month in our study period (June, July, August, and September).

For our third approach, we first defined a preferred temperature range for eastern box turtles within the central region of Kentucky, USA. Using ~58 000 daytime T_b records collected from all animals over the course of our study, we generated lower (20.2°C) and upper (26.2°C) quartiles to identify the middle quartile of preferred T_b range in our study region. This preferred range of T_b in our study is congruent with and within the preferred range of box turtles in conspecific populations (Boucher 1999; do Amaral *et al*. 2002; Currylow *et al*. 2012), and best approximates the preferred range at our study site. For each monitored turtle, we calculated the proportion of days when daily mean T_b fell within this preferred T_b range (20.2–26.2°C). Using a linear regression, we related the proportion of days within the preferred T_b range with the percentages of canopy gap overlap in the activity area of each animal.

Results

Over the course of our study, we captured/recaptured and processed 77 unique adult box turtles, totalling 504 captures overall. Of the 77 adults, 20 were radio-tracked. On average, we obtained 18.5 (range = 7–37, s.d. = 11.41) locations per animal from the 20 radio-tracked turtles. Activity area size was not correlated with the number of measured locations per individual ($P = 0.39$, $r^2 = 0.04$). Mean activity area size was 1.33 ± 0.28 ha for females ($n = 10$) and 1.8 ± 0.43 ha for males ($n = 10$). For all individuals, mean activity area size was 1.57 ± 0.25 ha. Mean activity area overlap with canopy gaps was 25.4% (range = 0–65%, median = 32.5%, s.d. = 19.4%).

Over the entire study period, mean daily gap T_e (i.e. gap centre) was generally greater than T_e in all other microhabitats sampled (Fig. 2). When the data were parsed into five discrete periods of the day, our temperature modelling exercise revealed that the T_e relationship among different microhabitats varied

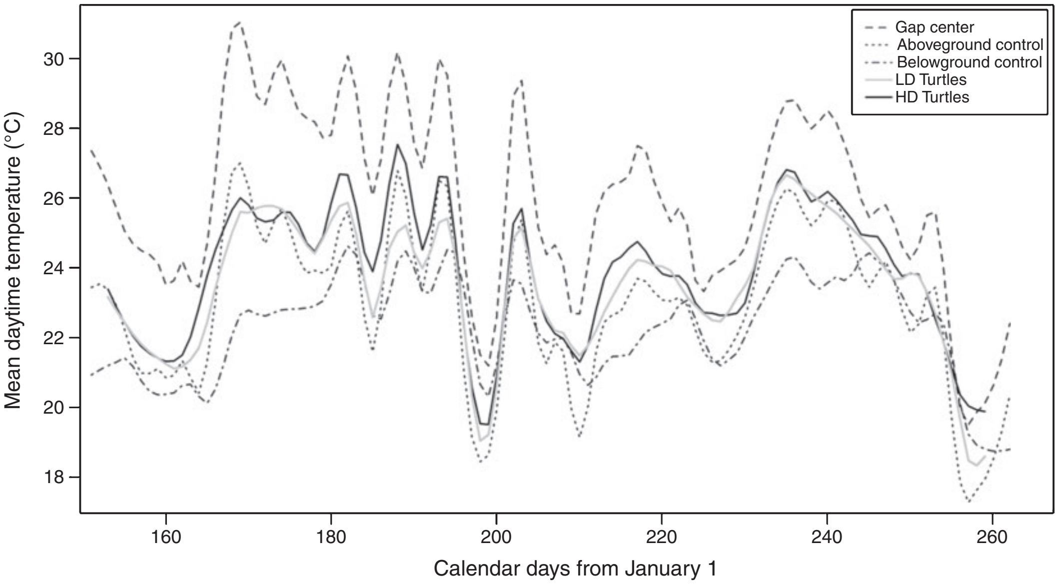

Fig. 2. Mean daytime temperature (°C) for different microhabitats and box turtles during the entire study period at Berea College Forest. High-degree-of-overlap turtles (>32.5%; HD Turtles) are denoted by a dark solid line, and low-degree-overlap turtles (≤32.5%; LD Turtles) are denoted by a light solid line.

(see Table 1 for period of day comparisons for the entire study period). Overall, when comparing box turtle T_b to microhabitat T_e, box turtle T_b closely correlated with above-ground control T_e in June and July. However, box turtle T_b was closely correlated with gap centre T_e in August and September. When separated into two discrete groups based on degree of canopy gap overlap, box turtles with a low degree of overlap (≤32.5%) had T_b that closely correlated with above-ground control T_e during all periods of the day and year (Fig. 3). In contrast, box turtles with a high degree of overlap (>32.5%) had T_b that closely correlated with gap centre T_e overall throughout the year; this relationship, however, varied depending on the period of the day (Fig. 3). From 06 : 00 to 12 : 00 hours, and from 18 : 00 to 21 : 00 hours (i.e. periods P1, P2, and P5), box turtles with a high degree of overlap with canopy gaps had T_b that closely correlated with above-ground control T_e. In contrast, in the afternoon periods 12:00–18 : 00 hours (P3 and P4), these same box turtles had T_b that closely correlated with gap centre $T_{e.}$ Furthermore, we show a positive, significant correlation between degree of overlap and proportion of T_b in the optimal range, suggesting that as an individual's activity area increasingly overlapped with canopy gaps, the proportion of T_b records that fell within the species' preferred range (20.2–26.2°C) also increased ($P = 0.04$) (Fig. 4). Finally, using an all-capture dataset and a point-density map, we show the highest densities of captures occurring at the peripheral of canopy gaps and near or adjacent to water sources (i.e. ephemeral ponds) (Fig. 5).

Discussion

Box turtles are presently declining throughout their range in North America due to human-caused habitat loss and alteration (Dodd *et al*. 2016). Consequently, disturbance of critical wildlife habitat caused by timber harvesting has become a theme of recent conservation research (Greenberg 2001; Todd and Andrews 2008; Currylow *et al*. 2012; Todd *et al*. 2014). To address potential impacts of timber harvesting on wildlife, our study aimed to better understand thermal impacts of silviculture on box turtles. On the basis of previous studies documenting environmental temperature changes caused by silviculture on box turtles (Currylow *et al*. 2013), we predicted that gap-based silviculture would create dramatic changes to the thermal environment (e.g. ambient temperatures significantly higher or

Table 1. Mean temperature comparison between adjacent microhabitats in a managed forest in Madison County, Kentucky, USA

GLS model comparison of mean temperature for entire study period between three different microhabitats – gap centre (GC), below-ground control (BC), above-ground control (AC) – during each period of the day (1–5). Habitat types not connected by the same letter are significantly different (α = 0.05)

Period of day	Habitat type	Comparison	Temperature (°C)	
			Mean	s.d.
P1 (06:00–09 : 00 hours)	GC	A	17.03	4.22
	BC	B	20.36	1.98
	AC	A	17.24	3.99
P2 (09:00–12 : 00 hours)	GC	A	23.09	4.11
	BC	B	20.52	2.03
	AC	B	20.89	3.32
P3 (12:00–15 : 00 hours)	GC	A	30.90	5.22
	BC	B	21.76	2.35
	AC	C	24.79	3.69
P4 (15:00–18 : 00 hours)	GC	A	30.32	4.66
	BC	B	23.07	2.82
	AC	C	25.68	3.62
P5 (18:00–21 : 00 hours)	GC	A	22.38	7.55
	BC	B	22.44	2.20
	AC	B	22.32	3.19

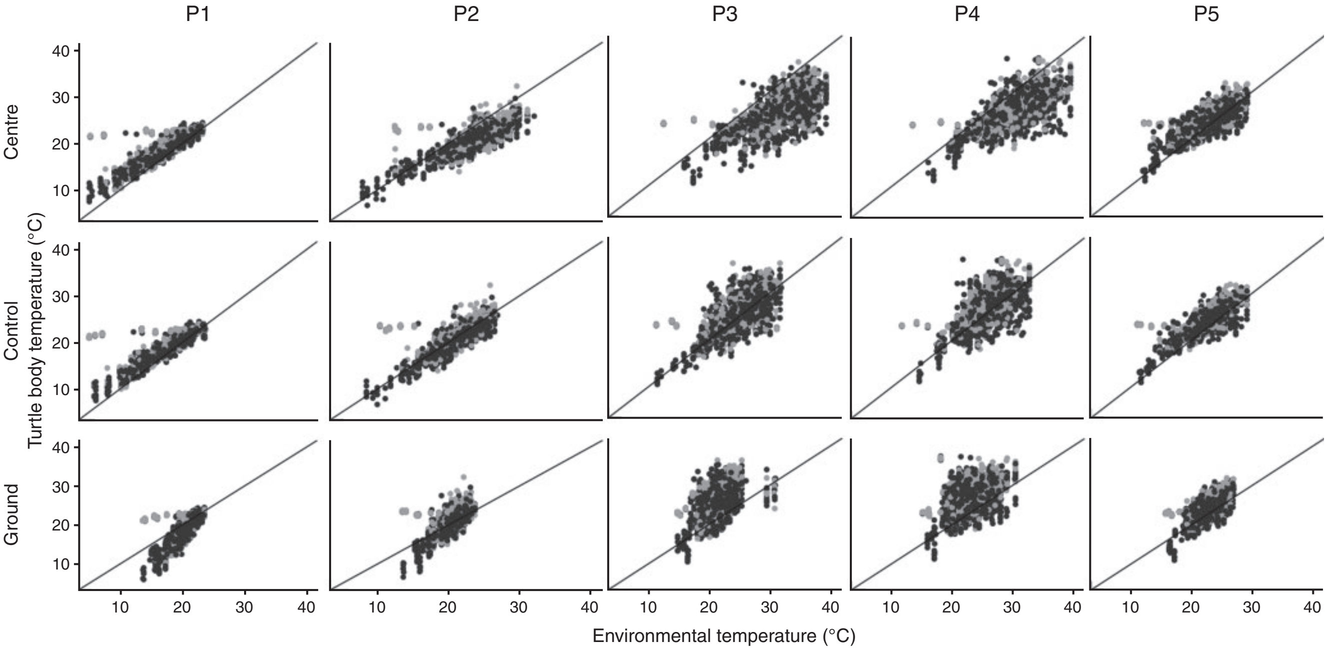

Fig. 3. Mean daytime temperature (°C) for different microhabitats versus box turtle body temperature during each of the five different periods of the day (P1: 06:00–09 : 00 hours; P2: 09:00–12 : 00 hours; P3: 12:00–15 : 00 hours; P4: 15:00–18 : 00 hours; P5: 18:00–21 : 00 hours), over the entire study period at Berea College Forest. High-degree-of-overlap turtles (>32.5%) are denoted by grey colour points, and low-degree-overlap turtles (≤32.5%) are denoted by black coloured points. The diagonal line represents a direct match or correlation of turtle body temperatures with environmental temperatures (1 : 1 ratio).

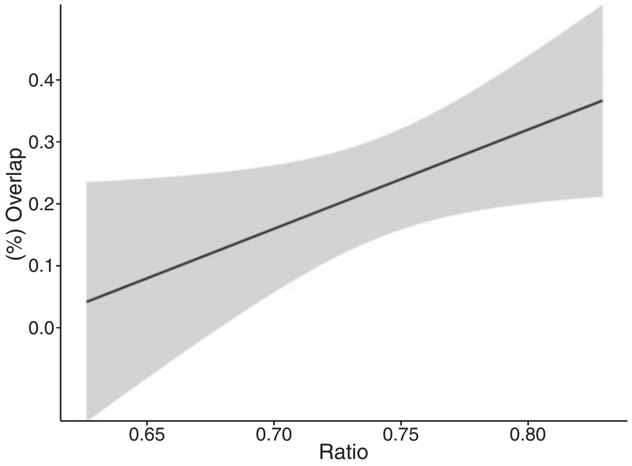

Fig. 4. Ratio of box turtle T_b within preferred range (20.2–26.2°C) versus percentage (%) home-range overlap with canopy gaps in Berea College Forest.

lower than non-harvested reference areas), and thus box turtle body temperatures would not correlate with canopy gap temperatures. However, our data provide support contrary to this prediction, and suggest that gap-based silviculture may offer suitable thermal environments that box turtles and similar ectotherms can use for optimal thermoregulation, physiological functions (i.e. metabolic rate), and fitness (Cunnington *et al.* 2008). For instance, while environmental temperature varied significantly between canopy gaps and adjacent non-harvested reference areas throughout the day and year at BCF, box turtle body temperatures were often highly correlated with canopy gap temperatures during various periods of the day. We hypothesise that this relationship could be due to the change in vegetative structure (e.g. rapid growth of *Quercus* seedlings and *Rubus*), and the scale of timber harvest (e.g. size of canopy gap: Currylow *et al*. 2013). Gaps with 0.28–1.13 ha per gap of the regeneration opening at BCF often retained microclimatic conditions that can be thermally suitable for box turtles. Conversely, silviculture practices that create larger canopy openings, such as clearcuts and group selection management (total cut area: 2.72–4.43 ha per gap), may create poor-quality habitat and can potentially expose box turtles to average temperatures near their critical thermal maxima (Currylow *et al*. 2012), with less opportunity for the animals to quickly retreat to cooler forests nearby.

Behaviour and physiology of reptiles are largely related to environmental variables such as air temperature and humidity (Angilletta *et al*. 2010); therefore, physiological performance is highly related to an animal's ability to behaviourally thermoregulate and physically locate thermally suitable habitat (Huey and Stevenson 1979). Again, due to the risk of box turtles quickly approaching their thermal maxima in open canopy gaps, our second prediction was that box turtles that had a high degree of activity area overlap with canopy gaps would show body temperatures outside their preferred range. In contrast, we documented that as a turtle's activity area encompassed a greater proportion of canopy gap area, the proportion of body temperature records (i.e. time spent) within the box turtle's preferred temperature range also increased, thereby rejecting our second prediction. Thus, canopy gaps may have provided

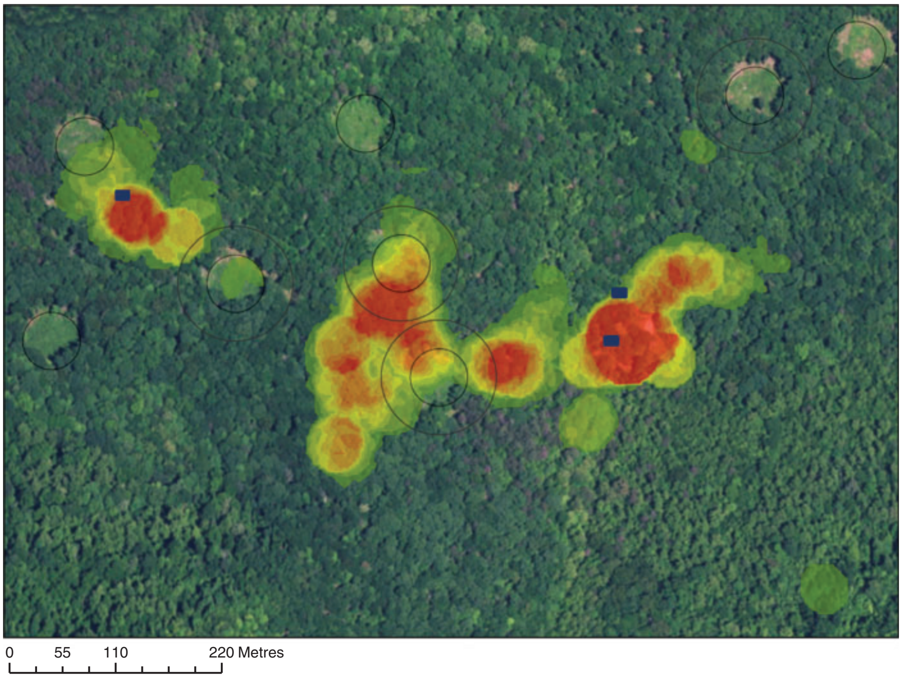

Fig. 5. Point density map of all box turtle captures ($n = 504$) over eight canopy gaps in a managed forest in Madison County, Kentucky, USA. Canopy gaps (0.28–1.13 ha gap^{-1}) are outlined by black circular lines, and ephemeral ponds are denoted by blue coloured rectangle boxes. Turtle capture density (density per 3.5 m^2) is represented by colour scale from high density (red) to low (green).

environmental temperatures that allowed animals to regulate body temperature within a preferred range, likely via behavioural thermoregulation and movement into and out of the relatively small canopy gaps at different times of the day when environmental temperatures were optimal (Boucher 1999; Ernst and Lovich 2009).

Temperature modelling of microclimates at BCF suggested that gap-based silviculture with relatively small-scale timber harvests can create a diverse microclimate matrix (e.g. significant ambient temperature variation among microhabitat types), but also maintain environmental temperatures within a preferable range for box turtles (20.2–26.2°C). Over the study duration, microclimatic differences between habitats varied over the course of the day. These differences were greatest during the early afternoon (P3), when gap centre, above-ground control, and ground temperatures were significantly different from each other (Table 1). During the early to late afternoon (P3 and P4), temperature within gap centre habitat averaged just above 30°C, and remained just under that temperature until sunset (P5). Relatively high temperatures in canopy gap habitats are attributable to direct insolation (Matlack 1993; Todd and Andrews 2008; Pike *et al.* 2011*b*). Below-ground temperatures at BCF were significantly cooler than all other habitats during all periods of the day except at sunrise (P1), when they were warmer than all other habitats. Warm below-ground temperatures in the early morning suggest that latent heat was retained in the soil overnight despite ambient air temperatures decreasing until after sunrise (Carlson and Groot 1997; Hashimoto and Suzuki 2004). We suspect that turtle body temperatures did not correlate with below-ground temperatures during our study because they may only access such insulated habitat types during winter (e.g. overwintering; Burke *et al.* 2016). However, in the event that a turtle was in a gap at sunset, it could retreat to an underground substrate in gap habitat to maintain optimal body temperatures. While environmental temperatures in canopy gap centres may have increased above those of unharvested forest during the middle of the day, they did not reach or exceed the thermal maxima for box turtles on a consistent basis. Rather, gap temperatures appeared suitable for box turtles throughout the study season, especially in August and September. For instance, our temperature modelling suggested that box turtles with greater access to canopy gaps had body temperatures that closely followed gap centre habitat temperatures during the afternoon periods of the day (P3 and P4).

Management implications

In North America, ~7.5 million ha of forests are disturbed by humans each year, and 6.1 million ha of this are due to timber harvesting (Masek *et al.* 2011). Although there are several benefits from commercial timber harvesting (Sims 2013), it is cited as one of the leading causes of the global decline of reptile species (Todd *et al.* 2010). While our study did not document negative thermal effects to available box turtle habitat, harvested landscapes can alter vegetation and form microclimates at local scales that potentially disrupt species richness patterns and thermal suitability (Lindenmayer *et al.* 2009; Martín-Queller *et al*. 2013). In addition, uncertainty regarding the intensity and pattern of forest harvesting can hamper effective habitat conservation and management (Kittredge *et al*. 2003). To mitigate potential declines in reptiles, the application of silvicultural practices that promote heterogeneity of forest structure, composition, and function may be needed. Additionally, relatively small-scale timber harvesting (≤1 ha per gap) could be implemented to allow for ectotherms to quickly seek adjacent forest habitat when environmental temperatures are above average within harvested areas. Furthermore, small-scale timber harvesting that maintains forest canopy heterogeneity via adequate spacing (>145 m distance between adjacent gap edges) may preserve habitat connectivity for terrestrial reptiles. Finally, while some silviculture-related mitigation techniques in managed forests have been successful for sensitive species in the past, further applied ecological research on animal/environmental temperature dynamics and gap-based silvicultural practices may help reduce negative impacts on reptile populations or reveal potential benefits from similar types of forest harvesting practices.

Conflicts of interest

The authors declare no conflicts of interest.

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