



Management and Conservation

Hibernal Thermal Ecology of Eastern Box Turtles Within a Managed Forest Landscape

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ABSTRACT Box turtles are being extirpated from much of their former range and remaining populations often live in association with anthropogenically altered habitats. This is particularly evident at the northern distributional limit of eastern box turtles (*Terrapene carolina carolina*) and is an important factor to consider during the winter months when their ability to respond to microclimatic change is limited. Using temperature dataloggers, we studied the hibernal microclimate of box turtles and associated habitat following timber harvests. We monitored the body temperatures of 38 eastern box turtles and collected detailed air and soil profile temperatures of 12 box turtle hibernacula, 6 clearcuts, and 6 adjacent forested areas during the hibernal season (winter 2009–2010). We partitioned the hibernal season into 2 biologically significant thermal periods: hibernation and emergence. The mean hibernation body temperature averaged (3.28°C , $\text{SE} = 0.09$) and corresponded to an average depth of 10 cm. Clearcuts were consistently colder ($\bar{x} = 1.91^{\circ}\text{C}$) than forests ($\bar{x} = 2.68^{\circ}\text{C}$) and hibernacula ($\bar{x} = 2.77^{\circ}\text{C}$) during hibernation, but became the warmest areas during emergence ($\bar{x} = 9.96^{\circ}\text{C}$). We found that in the average clearcut, turtles could burrow to approximately 20 cm to attain the average hibernation body temperature or to approximately 15 cm to attain a body temperature no different than those overwintering on colder, northeast-facing slopes in the forest ($\bar{x} = 2.83^{\circ}\text{C}$). Alternatively, we found that southwest-facing slopes were warmer and if turtles chose to overwinter only in clearcuts on those slopes, they could remain shallower. All but 1 turtle overwintered in forested areas; however, our study suggests that some timber harvested areas offer various microhabitats exploitable by hibernating box turtles based on soil profile temperatures, slope aspect, and depth of hibernation. © 2012 The Wildlife Society.

KEY WORDS box turtle, clearcut, hibernacula, hibernation, Midwest, silviculture, *Terrapene carolina*, timber harvest.

Among all threats to the perseverance of wildlife populations, habitat loss and alteration are considered the most pervasive and deleterious (White et al. 1997, Gibbons et al. 2000, Lawton et al. 2001, Todd and Andrews 2008). Consequently, uses of natural resources through sustainable practices such as timber harvesting are increasingly becoming the focus of conservation study (Perison et al. 1997, Fredericksen et al. 2000, Li et al. 2000, Gitzen et al. 2007). A variety of vertebrate taxa (including birds, small mammals, and some herpetofauna) benefit, at least temporarily, from the canopy openings and clearings created by certain silvicultural techniques (Fredericksen et al. 2000, Goldstein et al. 2005, Semlitsch et al. 2009). However, other

taxa (particularly frogs) have been found to respond negatively to timber harvests (Fredericksen et al. 2000, Cushman 2006, Semlitsch et al. 2009). Still, many more species have not been studied and their response to timber harvests is not known. Thus, effects of timber harvests can differ both across taxa and within species based on changing habitat requirements throughout the year.

Changes in habitat selection are known to occur during biologically significant events including mating, nesting, and the selection of overwintering sites (Madden 1975, Spencer and Thompson 2003). Although our general knowledge of habitat selection for many species is plentiful for both mating and nesting events, we have far less information for the hibernal season (winter). Moreover, we lack information regarding the impacts on wildlife associated with silvicultural practices during the hibernal season. For non-migratory species, hibernal season habitat selection is critical to survival, especially for poikilotherms whose body temperature is regulated by the physical environment. Herpetofauna are particularly affected by changes to habitat in that they

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must adjust behaviorally to environmental flux (Johnston and Bennett 1996). Many herpetofaunal species sustain regular cycles of dormancy to acclimate to changing environmental conditions (Gregory 1982). Cold winter conditions will cause many taxa to retreat to hibernacula for extended periods (e.g., squamates up to 8 months, anurans up to 11 months; Aleksziuk 1976, Zug et al. 2001). Therefore, empirical evaluation of habitat selection during the hibernal season is crucial to gain a more complete picture of the effects of timber harvests on forest-dependent wildlife species.

The eastern box turtle (*Terrapene carolina carolina*) is a forest-dwelling species whose population is declining throughout its range (Stickel 1978, Williams and Parker 1987, Hall et al. 1999, Dodd 2001, Indiana Department of Natural Resources 2007). This species is protected in most states within its range and its survival may be compromised by habitat proximity to anthropogenic disturbances (Currylow et al. 2011). Box turtles select habitats based on a combination of factors, including cover and temperature (Reagan 1974). Canopy cover influences temperature by regulating light intensity, a factor known to be critical for turtles during activity periods (Gould 1957, Rose and Judd 1975). Ground and air temperature play key roles in the activity of box turtles, even in winter months (Congdon et al. 1989). Eastern box turtles may hibernate for a significant proportion of the year (up to 9 months); however, much in situ work with this species involves only active season monitoring. Studies that examine hibernal behavior are often limited by unnatural settings, do not address thermal environments, or are narrow in scope (few records and lack of habitat variables such as slope aspect or canopy). Alterations of temperature due to canopy removal and the concomitant use by box turtles have not been studied during hibernal seasons.

Thermoregulation is ostensibly an influential factor in hibernaculum selection and overwintering behavior in box turtles. Box turtles have a natural mechanism that enables them to endure sub-zero temperatures when more than 58% of their body fluids are frozen, with minimal deleterious effects (Costanzo and Claussen 1990). Though super-cooling and natural freeze-tolerance allows eastern box turtles to survive below freezing temperatures, mortality due to prolonged exposure is not uncommon (Claussen et al. 1991). Box turtles burrow to avoid extreme temperatures during the hibernal season (Nov through Apr), and may burrow deeper as the seasonal temperatures decrease (Carpenter 1957). The majority of studies have found box turtles to overwinter at an average depth of only 5 cm, and no more than 18 cm (Carpenter 1957, Dolbeer 1971, Madden 1975, Congdon et al. 1989, Claussen et al. 1991, Minton 2001). Depth to which turtles burrow may also depend on slope aspect. Slope aspect and elevation can significantly affect the amount of penetrating solar radiation, vegetative cover, precipitation, and consequently, the temperature of a particular location (Holland and Steyn 1975, Schulze 1975). Slopes that face the sun low on the horizon will remain warmer than slopes facing away from the sun. Therefore, management considerations must include evaluations of

slope aspect, especially in areas completely exposed such as in timber-harvested areas.

In this study, we expanded upon the limited knowledge pertaining to hibernal season impacts of timber harvests on a hibernating forest ectotherm. Specifically, we aimed to investigate whether clearcut areas offer suitable habitat for overwintering eastern box turtles. The goals of this study were to 1) characterize hibernal thermal behavior of eastern box turtles, 2) determine the available thermal habitat in clearcuts relative to forests on various slope aspects, and 3) evaluate the effect of clearcuts on actual and theoretical hibernal habitat use.

STUDY AREA

We conducted our study within approximately 35,000 ha of Morgan–Monroe and Yellowwood State Forests in Morgan, Monroe, and Brown Counties, Indiana. Both forests were characterized by hills and ravines of hardwood, deciduous forests with scattered timber harvest areas. The majority of canopy species were *Quercus* spp., such as chestnut oak (*Q. montnana*), and butternut (*Carya cordiformis*) and shagbark hickory (*C. ovata*; Summerville et al. 2009).

Morgan–Monroe and Yellowwood State Forests were managed for multiple uses, including recreation, education, research, and timber. The study site comprised a relatively contiguous forest and population of free-ranging box turtles, and timber harvests were recently implemented within the box turtle habitat as part of the Hardwood Ecosystem Experiment (HEE). The HEE is a long-term (100-yr), landscape-scale timber and wildlife research and management collaborative designed for the study of ecological and social impacts of various silvicultural methods (Kalb and Mycroft in press). We focused on 6 of the 9 HEE study sites (Fig. 1), each with similar vegetative species, slope aspects, and elevations. The 6 study sites encompassed approximately 400 ha each and were randomly assigned a management type: clearcut treatments (2 clearcuts approx. 4 ha each) or control (no timber removal), each with 3 replicates. The clearcut treatments were implemented over the winter of 2008–2009 within 90-ha centers of each unit to allow the remaining forest to act as buffer areas.

METHODS

Turtle Monitoring

To locate hibernaculum sites for hibernal monitoring, we used standard radiotelemetry homing methodology. As part of a concurrent radiotelemetry study, we epoxied radio transmitters (Holohil RI-2B, Carp, Ontario, Canada; 14.5 g each representing <5% of the animal's total body weight) to the carapaces of 38 adult box turtles (19 M and 19 F) throughout the HEE sites (Fig. 2). We followed turtles 3 times a week until most were consistently found underground for hibernation (5 Nov 2009). We defined, a posteriori, the initiation of hibernation as the first date each turtle was consistently observed buried underground provided that it was subsequently found at that location for at least 1 week before regular tracking ceased. To represent the

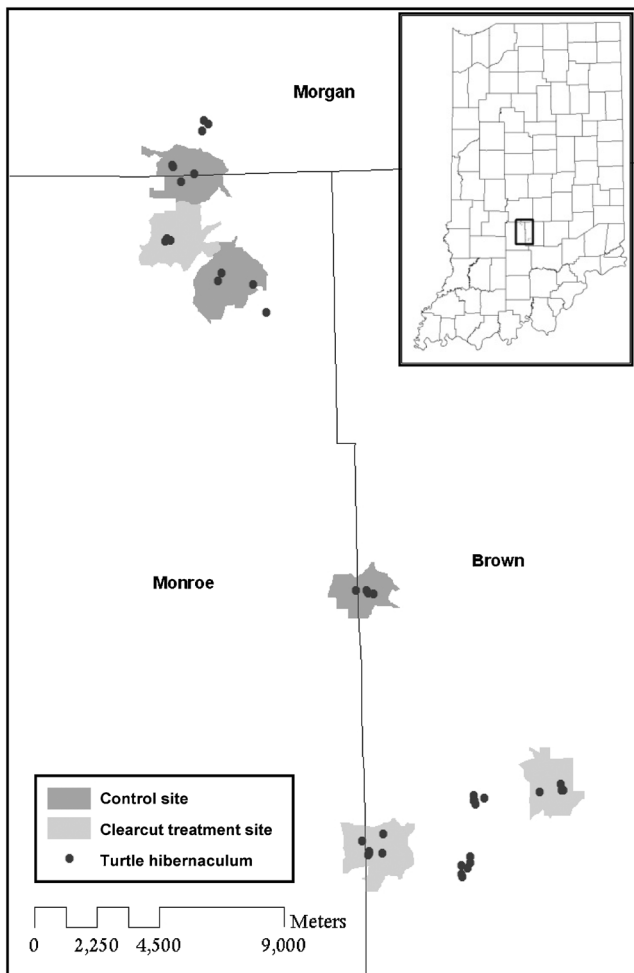


Figure 1. Map of Indiana (inset) with study area in Morgan, Monroe, and Brown Counties outlined and the 6 study sites (3 clearcut sites and 3 control sites) as part of the Hardwood Ecosystem Experiment in south-central Indiana, 2009–2010. All radiotelemetered box turtle hibernacula are indicated as dark dots.

temperatures turtles chose over time, we affixed temperature dataloggers, accurate to 0.5° C (Thermochron iButtons, model number DS1921G-F5, Maxim Integrated Products, Inc., Sunnyvale, CA) to each turtle’s carapace prior to hibernation. Carapacial temperature measurements have been found to correlate well with turtle core body and cloacal temperatures (Peterson 1987, Congdon et al. 1989, do Amaral et al. 2002, Bernstein and Black 2005). We programmed temperature dataloggers to record turtle body temperatures every 180 minutes throughout the hibernational season. We used these temperatures to then align with soil thermal profile temperatures (described below) to inform turtle burrowing depth. These activities were permitted under Purdue Animal Care and Use Protocols and amendments (PACUC 07-037).

Experimental Design and Habitat Monitoring

To document hibernational microhabitats available to burrowing animals, we monitored temperatures at multiple soil depths using thermal profile stakes (hereafter TPSs) at 24 locations throughout the study sites. The TPSs consisted of 5 temperature dataloggers affixed at 10-cm intervals along the

length of a 1.3-cm × 5-cm × 51-cm wooden stake, and sunk into the forest floor. The profile intervals spanned from 10 cm above soil surface (in the leaf litter at turtle height), at the soil surface (0 cm), and at 10 cm, 20 cm, and 30 cm below the soil surface. We programmed the temperature dataloggers to logging intervals of 180 minutes and they recorded soil profile temperatures throughout the landscape for 22 weeks from 8 November 2009 through 10 April 2010.

We compared thermal environments between forested habitats (forests) and treatments (clearcuts) to evaluate their suitability as box turtle hibernational habitat. We placed a TPS mid-slope at each of the 6 replicate clearcuts and the 6 replicate forested habitats (Table 1). We used ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA) to assign the random locations of the TPSs within the designated habitats. We placed the remaining 12 TPSs at a selection of turtle hibernacula to characterize soil profile temperatures where turtles chose to overwinter. Each of these hibernacula TPS replicates were sunk into the forest floor within 1 m of hibernating turtles, but no closer than 0.33 m to avoid disturbing the turtle. We radiotracked hibernating turtles monthly to ensure turtles maintained consistent proximity to hibernacula TPSs over the hibernational season. We selected the 12 turtles associated with hibernacula TPSs based on a variety of factors including their association with clearcuts, sex, slope aspect, and elevation. We equally divided hibernacula TPSs by sex and active season home range association with clearcuts or controls. We used replicates of north-to-east- and of south-to-west-facing slopes to the greatest extent possible (Table 1). On all slopes, we selected elevations to most closely match the average turtle hibernaculum (approx. 260 m).

Analyses

We analyzed thermal data at multiple levels in an attempt to characterize the hibernational ecology of box turtles and detect specific patterns of temperature in the landscape relative to clearcut and forested habitat. We processed raw logged data using program R (R Version 2.10.1, www.r-project.org, accessed Apr 2010), which is capable of handling and managing very large datasets, and calculated daily minimum, maximum, and mean temperatures for all temperature loggers. We analyzed all temperatures weekly to determine biologically significant periods over the season. Although the daily range in temperature (daily max. – daily min.) is known to affect reptile behavior during the active season, daily ranges during the hibernational season are very small and often within the range of datalogger accuracy (averaged 1° C). Therefore, we determined these data difficult to justify as biologically significant and opted to use actual temperature values in our analyses. We combined temperatures recorded from each of the 38 turtles to obtain an average hibernational body temperature at which turtles spend the majority of their time. To determine the depths to which turtles burrow overwinter, we compared body temperatures to hibernacula TPS temperatures on specific slopes.

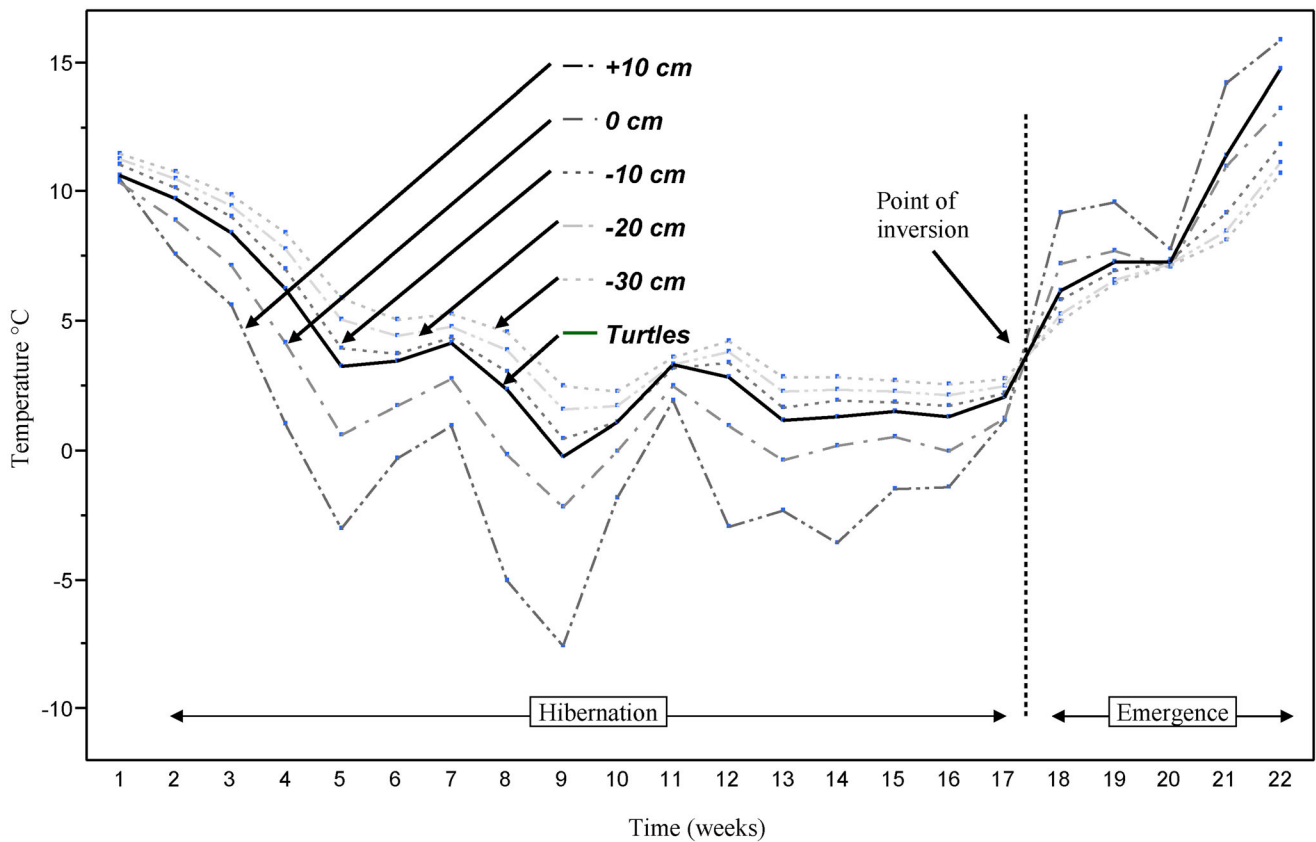


Figure 2. Mean hibernaculum temperatures recorded by week at various depths (+10 cm, 0 cm, -10 cm, -20 cm, and -30 cm) and mean box turtle body temperatures recorded in south-central Indiana, 2009–2010. Figure illustrates the point of inversion (between 23 Feb and 7 Mar 2010), demarcating the hibernation period (weeks 2 through 17) and emergence period (weeks 18 through 22).

We determined overwintering microclimates throughout the landscape using comparisons of the TPS temperatures. We tested for differences in TPS temperatures at varying depths and slopes for each of the TPS types (clearcut, forest, and hibernaculum) across time. We used restricted maximum likelihood (REML) for fitting our mixed model designs for each test. We used temperature logger identification number as a repeated measures random effect with sex, slope, period, depth, and associated location as fixed or interacting effects, depending on the scenario. Following those analyses, we conducted Least Squares Means Tukey-Kramer post hoc pairwise comparisons or Student's *t* tests where appropriate to detect significant differences in mean temperatures. We carried out all statistical analyses using JMP statistical software (SAS Institute, Inc., Cary, NC;

Environmental Systems Research Institute, Inc.). We considered values significant where the *P* values were less than 0.05 and differences in mean temperature values were greater than 1° C.

RESULTS

Over the 22-week period, we recorded 191,200 temperatures on a variety of slope aspects associated with clearcuts, forests, and turtles. Because of the volume of data, many of the comparisons were statistically significant; however, the accuracy of the temperature dataloggers ($\pm 0.5^\circ\text{C}$) is an additional criterion that must be considered. Here we report all statistical significance with both of these considerations in mind (i.e., $P < 0.05$ and $\Delta^\circ\text{C} > 1$).

Table 1. Number and location of temperature dataloggers in harvest openings (H) and forested habitats (F) in south-central Indiana, 2009–2010. We attached dataloggers to box turtles and to thermal profile stakes (TPSs) in random locations and near turtle hibernacula. Slope aspect represents the slope for which the logger was assigned or that the overwintering turtle chose (N/A indicates the turtle was in a hibernaculum on flat land or began hibernation after tracking ceased).

	Total	Slope aspect														N/A
		NW		NE		E		SE		S		SW		W		
		H	F	H	F	H	F	H	F	H	F	H	F	H	F	
Turtle	38		7	1	5		2		4		3		2		6	8
TPS	12			3	2		1					3	2		1	
Hibernaculum TPS	12		2		3			1		2		1			3	

Temporal analysis of all TPS temperatures revealed 2 biologically significant time periods within the 22 weeks of monitoring: hibernation and emergence. Mean temperatures of these periods were different ($F_{1, 45} = 1,059$, $P < 0.001$, $\Delta^{\circ}C = 6.56$) and were divided by the time at which inversion of soil and surface temperature occurs (point of inversion). For example, early in the season, we recorded the coldest hibernacula temperatures at the surface and temperatures were progressively warmer at increasing depths (Fig. 2). However, between the 17th and 18th week of monitoring (28 Feb–7 Mar 2010), that trend reversed and the warmest temperatures were found at the surface. We refer to the thermal period between weeks 2 and 17 as hibernation and between weeks 18 and 22 as emergence (Fig. 2).

Box Turtle Thermal Behavior

All 12 TPS-associated turtles remained within 3 m of their hibernaculum TPS (i.e., no turtles made significant lateral movements over the hibernation period from their last known location the previous fall). Most turtles (89%) chose hibernacula between 14 October and 29 October 2009 and the vast majority of turtles (97%) overwintered in forested habitats. A single female turtle (706F) overwintered within an unmonitored 2.56-ha harvest opening associated with a separate aspect of the HEE.

Mean hibernation body temperature ($3.28^{\circ}C$) of all turtles differed from emergence body temperature ($9.32^{\circ}C$; $F_{1, 72} = 1,297$, $P < 0.001$, $\Delta^{\circ}C = 6.04$; see Table S1, available online at www.onlinelibrary.wiley.com). Turtle 706F maintained body temperature values that were comparable but warmer ($\bar{x} = 3.73^{\circ}C$) than the mean hibernation body temperature. In addition, the mean depth of hibernation for all turtles averaged slightly less than 10 cm. Turtles began to decrease their depths and emerge (as evidenced by higher temperatures) after the point of inversion (28 Feb–7 Mar 2010). Although we found no statistically significant differences in mean body temperature between the sexes over the hibernal season, we observed several trends in those data. Females averaged slightly warmer body temperature ($3.34^{\circ}C$) than males ($3.22^{\circ}C$) during the hibernation

period. Moreover, differences between sexes were even more striking for the subset of 12 turtles in monitored hibernacula. Male hibernation body temperature matched that of depths just below the soil surface ($2.55^{\circ}C$) with the shallowest overwintering turtle consistently above the soil surface ($\bar{x} = 1.81^{\circ}C$). Monitored females, in contrast, had body temperatures matching depths of 10 cm ($3.51^{\circ}C$) with the deepest burrowing to 20 cm ($\bar{x} = 4.44^{\circ}C$, $SE = 0.09$). These 2 extreme cases constitute the minimum and maximum mean hibernation body temperature, respectively (see Table S1, available online at www.onlinelibrary.wiley.com).

We were unable to use 8 of the 38 turtles in analyses involving slopes. Four of these turtles did not meet the criteria for determining if they selected a hibernaculum site before tracking ceased and 4 overwintered in flat locations such as hilltops or creek-beds. No turtles chose to overwinter on north-facing slopes and we did not monitor these slopes. Body temperature varied somewhat by slope during both hibernation ($P = 0.613$) and emergence periods ($P = 0.262$; Table 2). Before the point of inversion at week 17, the overall warmest slope aspect was southeast (\bar{x} all depths = $3.49^{\circ}C$) and the overall coldest was northeast (\bar{x} all depths = $2.47^{\circ}C$). Turtles overwintering on the warmer, southeast-facing slopes did not burrow as deeply as other hibernating turtles, but were able to remain as warm ($\bar{x} = 3.31^{\circ}C$). The mean hibernation body temperature ($3.28^{\circ}C$) was found just below the surface on southeast-facing slopes ($\bar{x} = 3.06^{\circ}C$ at a depth of 0 cm) and was not significantly different from the mean body temperature found deeper on most other slopes ($\bar{x} = 3.33^{\circ}C$ at a depth of 10 cm). Turtles overwintering on colder, northeast-facing slopes also did not burrow as deeply as most other turtles, but the colder slope aspect resulted in relatively cold mean body temperature ($\bar{x} = 2.65^{\circ}C$). After the point of inversion, the warmest slope aspects were south (\bar{x} all depths = $9.28^{\circ}C$) and southwest (\bar{x} all depths = $9.25^{\circ}C$), whereas the coldest remained on northeast slope aspects (\bar{x} all depths = $8.29^{\circ}C$). The turtles that hibernated shallowly on both southeast- and northeast-facing slopes emerged earlier than the average on other slopes. Additionally, those turtles that overwintered on southwest-facing slopes averaged

Table 2. Mean body temperatures (T_b) and standard errors for box turtles during hibernation (H) and emergence (E) in south-central Indiana, 2009–2010. Unknown slopes indicate turtles did not select hibernacula by the final tracking date. The 12 turtles associated with hibernaculum thermal profile stakes (TPSs) are also listed separately in the last row.

Hibernaculum slope	No. of records	Hibernation T_b		Emergence T_b	
		\bar{x} ($^{\circ}C$)	SE	\bar{x} ($^{\circ}C$)	SE
Northeast	7,038	2.83	0.20	8.58	0.22
East	2,346	3.20	0.35	9.20	0.37
Southeast	4,692	3.31	0.25	9.38	0.26
South	3,519	3.21	0.29	9.82	0.30
Southwest	2,346	3.23	0.35	9.00	0.37
West	7,039	3.23	0.20	9.63	0.22
Northwest	8,211	3.52	0.19	9.09	0.20
Flat	4,692	3.34	0.25	9.33	0.26
Unknown	4,692	3.61	0.25	10.11	0.26
Total	H: 34,048 E: 10,527	3.28	0.09	9.32	0.09
Select 12 total	H: 10,752 E: 3,325	3.10	0.16	9.00	0.17

emergence body temperatures that matched soil depths between 0 cm and 10 cm (body temperature \bar{x} = 9.00° C, 0 cm = 10.60° C, 10 cm = 8.52° C), suggesting that they were still below the surface during the emergence period despite those slopes being among the warmest.

Microclimates of Forests Versus Clearcuts

We evaluated the thermal habitat in clearcuts versus forested areas by comparing mean temperatures from TPSs within the clearcuts (n = 6), the forest (n = 6), and at turtle hibernacula (n = 12). We found no difference between mean TPS temperatures of habitat or slope comparisons during the entire 22-week hibernal season ($F_{2, 21}$ = 1.7, P = 0.209, $\Delta^{\circ}C$ = 0.36). However, when separated by hibernation and emergence periods, the clearcuts maintained more extreme daily temperatures. During hibernation, the range of temperatures was greatest in clearcuts ($F_{2, 47}$ = 9.32, P < 0.001) meaning these areas were more variable in temperature. However, clearcuts were consistently colder (\bar{x} all depths = 1.91° C) than forests (\bar{x} all depths = 2.68° C) and hibernacula (\bar{x} all depths = 2.77° C) during hibernation ($F_{2, 21}$ = 9.60, P = 0.001), but were warmest during emergence (\bar{x} all depths = 9.96° C; $F_{2, 21}$ = 6.70, P = 0.006; Table 3). Although ambient (+10 cm) temperatures during the hibernation period were nearly identical in all locations, comparable soil temperatures in clearcuts were found approximately 10 cm deeper than in forests and hibernacula (i.e., clearcut hibernation temperatures at a depth of 10 cm were more similar to forest hibernation temperatures at 0 cm; Fig. 3). During the emergence period, hibernaculum locations were generally cooler than other locations at all depths, and significantly so from clearcuts on most slopes (see Table S2, available online at www.onlinelibrary.wiley.com).

Slope aspect influenced microclimates in clearcuts and forests (Table 3; see also Table S2, available online at www.onlinelibrary.wiley.com). During hibernation, southwest-facing slopes in forests were the warmest overall (\bar{x} all depths = 3.16° C), but during emergence, southwest-facing slopes in clearcuts became the warmest (\bar{x} all depths = 10.50° C). On average, the coldest slopes were northeast facing during hibernation (\bar{x} all depths = 2.11° C) and northwest facing during emergence (\bar{x} all depths = 8.42° C).

Nonetheless, when depth is taken into account, northeast-facing slopes showed the greatest differences in mean temperatures across habitats (from +10 cm during hibernation at -0.88° C to +10 cm during emergence at 11.02° C; see Table S2, available online at www.onlinelibrary.wiley.com).

DISCUSSION

Forest management practices change the vegetative structure and local environmental conditions, which in turn may alter species use of available habitat (Renken et al. 2004). Many forest dwelling vertebrates (both endothermic and poikilothermic) will prefer to use certain types of available habitat throughout the year for thermoregulation, nesting, and dormancy (Schwartz and Schwartz 1974, Madden 1975). The current study provides key insights into the hibernal thermal behavior of eastern box turtles and the microclimates of habitats within timber-harvested areas versus those within adjacent forests.

Data from TPSs within clearcuts, adjacent forests, and at turtle hibernacula revealed several general patterns. First, the emergence of box turtles was correlated with an inversion of surface and deep soil temperatures. Once the point of inversion occurs, turtle hibernacula are no longer warmer than soil surface temperatures. Previous studies attribute rising air, surface, and rough estimates of subsurface temperatures as the triggers for box turtles to emerge in the spring (Grobman 1990, Bernstein and Black 2005). Our data suggest proximity to the surface is also a key factor to timing of emergence. Turtles that burrowed deeper during winter months emerged later in the spring. Premature emergence has been implicated in the death of box turtles and other ectotherms exposed to inclement weather (Schwartz and Schwartz 1974, Claussen et al. 1990, Nazdrowicz et al. 2008). In anuran species, tolerating cold temperatures for long periods is known to come with energetic costs, even during low metabolic periods such as hibernation (Swanson and Graves 1995, Irwin and Lee 2003). Therefore, if box turtles remain underground long after the point of inversion, when soil temperatures are colder than surface temperatures, they will not replenish energy reserves, may eventually emerge undernourished, and consequently be unprepared in the competition for resources. Conversely, if early emergence occurs late enough in the

Table 3. Mean thermal profile stake (TPS) temperatures (°C) and standard error from all depths combined during hibernation and emergence thermal periods for box turtles in south-central Indiana, 2009–2010. Temperatures are separated by locations (forests, hibernacula, and clearcuts) and by slope aspects. Starred (*) values are different (P < 0.05 and $\Delta^{\circ}C$ > 1) from others across habitat types for associated thermal period and slope aspect. Total recordings (n) and mean values are reported for each habitat type in the last row.

Slope	n	Hibernation						Emergence					
		Forests		Hibernacula		Clearcuts		Forests		Hibernacula		Clearcuts	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
NW	11,736			2.68	0.12					8.42	0.14		
NE	46,945	2.44	0.17	2.49	0.14	1.53	0.14	8.72	0.18	8.00*	0.15	9.42*	0.15
E	3,528	2.24	0.10					9.20	0.17				
SE	5,858			3.49	0.06					8.60	0.11		
S	11,734			2.92	0.12					9.28	0.14		
SW	35,179	3.16	0.32	2.60	0.45	2.29	0.26	9.19	0.33	9.36	0.46	10.50	0.27
W	23,460	2.65	0.31	2.81	0.18			8.79	0.33	9.10	0.19		
Total	138,440	2.69	0.17	2.77	0.12	1.91	0.17	8.94	0.18	8.71	0.12	9.96*	0.18

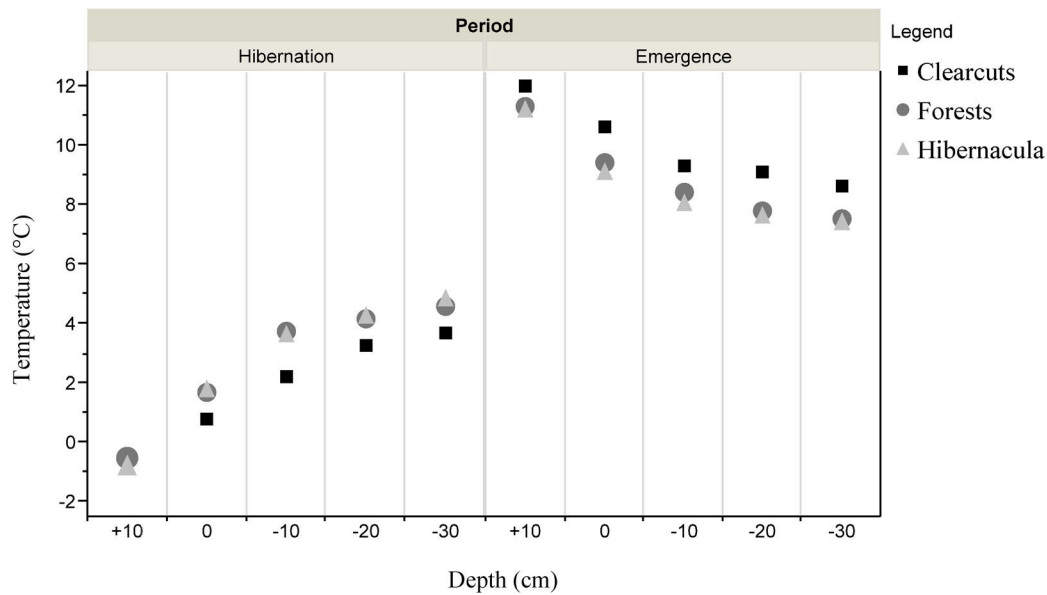


Figure 3. Mean thermal profile stake (TPS) temperatures (°C) by location and depth (cm) during the hibernation and emergence periods for box turtles in south-central Indiana, 2009–2010. Temperatures at hibernacula and forests were not significantly different at varying depths. However, temperatures in clearcuts were significantly colder (hibernation period) or warmer (emergence period) at nearly all depths.

winter when spring is arriving, turtles may have the advantage of first access to renewed foraging resources and be better physically prepared to mate.

The second general pattern to emerge was that nearly all turtles chose hibernacula that were in forested habitats. Only a single radiotelemetered turtle overwintered within a HEE-associated timber harvest opening. The question of whether box turtles find suitable habitat in forest openings such as clearcuts during the hibernal period is central to this project. Few turtles overwintered within clearcuts possibly because the total area of openings was small relative to that of forested habitat and thus, if habitat is selected in accordance with its availability the likelihood of turtles overwintering in clearcuts is low. Although the clearcut treatments do represent a relatively small proportion of the overall study site (<1.5%), associated radiotelemetry data clearly demonstrates that timber harvest openings are used by many of these same turtles during the active season (Currylow et al. 2012), averaging 8.2% of their home ranges (A. F. Currylow, Purdue University, unpublished data). Therefore, the lack of overwintering sites within clearcuts may reflect habitat selection based on simple energetics.

With little leaf litter or canopy cover to buffer harsh weather, the microclimate of the clearcuts often exhibited temperature extremes that overwintering turtles were expected to avoid. Freezing temperatures are known to cause mortality in even hardy, freeze-tolerant taxa such as frogs and salamanders, as well as box turtles (Carpenter 1957, Metcalf and Metcalf 1979, Storey and Storey 1986). During intermittent warm periods, however, hibernal soil temperatures in clearcuts temporarily increased above those found in adjacent, uncut forests. Higher soil temperatures in mid-winter can trigger early emergence and the subsequent freezing death of overwintering turtles (Neill 1948, Schwartz and Schwartz 1974, Ultsch 2006). Nearly all turtles in this study

(37 of the 38) chose hibernacula in forested areas where forest debris, such as leaf litter, was greater than in clearcuts. Dolbeer (1971) noted that turtles selected areas with a thick mat of leaf litter and rotting logs for hibernacula. Based on soil profile data among clearcuts and forests, turtles overwintering in a clearcut would need to burrow an average of 10 additional centimeters to achieve the warmer body temperature. However, burrowing more deeply is likely associated with energetic costs.

The third general pattern that emerged from temporal analyses of temperatures was that most turtles chose temperatures of 3.28° C for hibernation. This body temperature corresponded to a depth of approximately 10 cm, which is within the range (5–18 cm) found in other studies (Carpenter 1957, Dolbeer 1971, Madden 1975, Congdon et al. 1989, Claussen et al. 1991, Minton 2001, Converse et al. 2002). We found that females maintained slightly warmer body temperatures than males and generally burrowed deeper throughout hibernation. Many males burrowed to just below the soil surface with only leaf litter shielding them from harsh winter weather conditions. Whether this observation is due to variation caused by slope aspect is unclear. One explanation is that certain adult males could be physiologically more tolerant of the cold, although studies on hatchling turtles showed no sex differences in cold tolerance (Costanzo et al. 1995, Packard and Janzen 1996). A blood chemistry panel from a subset of turtles in the present study showed that males generally had higher freeze-resistant glucose levels than females and the turtle that was at the surface for a majority of the hibernal season had comparable levels to other males (Kimble and Williams 2012). In contrast, females undergoing follicle development may select warmer sites to speed the process or because their increased mass would cause them to recover from freezing temperatures more slowly (Shine 1980). Despite numerous

laboratory studies on freeze tolerance in this species, the reported sex difference herein is novel and warrants further investigation.

Slope aspect appears to affect habitat selection for many burrowing animals during the hibernation season. Black rat snakes (*Elaphe o. obsoleta*) and eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) in Ontario prefer to hibernate on south-facing slopes that remain warmer and thaw earlier, likely ameliorating the effects of freezing winter temperatures (Prior and Weatherhead 1996, Harvey and Weatherhead 2006). Similarly, toads (*Bufo boreas*) in the Pacific Northwest chose to inhabit south-facing slopes and burrow to just below the frost line (Bull 2006). Yellow-bellied marmots (*Marmota flaviventris*) in Colorado generally chose burrows on either southwest- or northeast-facing slopes year-round, but chose those with deep, insulating snow cover overwinter (Svendsen 1976). In contrast, Claussen et al. (1991) found that eastern box turtles in Ohio's woodlands prefer nearly level ground or west-facing slopes for hibernacula, but we found no such trend among the 38 turtles in this study. However, we did observe patterns in the burrowing behavior (depth of hibernacula) depending on the slope of the selected hibernaculum site. As with the aforementioned studies, many of our animals burrowed deeper to reach warmer temperatures overwinter. However, the conflicting behavior we noted on the colder, northeast-facing slopes indicated timber harvests may be appropriate hibernaculum habitat, as the temperatures available in the clearcuts were overall equally as cold. The clearcuts offered temperatures most often used by overwintering turtles, but at greater depths (depending on slope) than forested areas and hibernacula. Therefore, these areas could theoretically be inhabited by burrowing animals during the winter months.

Forest floor temperatures have been shown to affect the burrowing activity of small mammals, amphibians, reptiles, and invertebrates (Vernberg 1953, Byers 1984, Landry-Cuerrier et al. 2008). Temperatures collected in this study can be used to predict the hibernation use of clearcuts. If overwintering animals choose clearcuts for hibernaculum sites, they must behaviorally adjust as found in some amphibians (Storey and Storey 1996). Turtles must burrow twice as deep (20 cm) to attain a mean body temperature of 3.28° C, or tolerate the colder hibernation temperatures of 2.83° C (at 15 cm). Alternatively, they could choose to overwinter in clearcuts only on warmer slopes (such as southwest facing) and burrow 10 cm to attain the mean hibernation temperature. However, burrowing depth could be an issue in that animals would need to expend more energy digging down and emerging while navigating possible hazards such as roots and rocks.

Turtle 706F was the only turtle to overwinter in a timber-harvest opening. This female was able to maintain above average hibernation temperature, despite being in an opening and on a northeast-facing slope. Using the temperatures obtained from TPSs that we placed in other northeast-facing clearcut slopes, we determined that this female would have had to burrow to depths greater than 30 cm to attain her hibernation temperatures in that habitat. Even the north-

east-facing slopes of forested habitats only offered temperatures comparable to her mean at depths of nearly 20 cm. A comparison of 706F daily mean temperatures to corresponding TPS temperatures suggests this turtle regulated body temperature by rising to the surface on warmer days and burrowing deeper on colder days. These depth adjustments are frequently seen in three-toed box turtles (*T. c. triunguis*), which burrow deeper as winter temperatures decrease (Carpenter 1957, do Amaral et al. 2002). Still, we did not observe this behavior to such extremes in any of the 12 hibernacula monitored turtles or the remaining 25 turtles until the emergence period.

Data from this and other studies indicate that site fidelity may play a role in hibernaculum selection. Cook (2004) observed that several individuals exhibited hibernaculum site fidelity with inter-hibernaculum changes of less than 100 m over successive years. Doroff and Keith (1990) found that 8 of 14 ornate box turtles (*T. ornata*) tracked in Wisconsin overwintered within 1 m of their previous hibernation sites. Analysis of the concurrent radiotelemetry study data of the same turtles herein indicate that in 2010, turtles chose overwinter locations averaging 123 m from the 2009 site (see Table S3, available online at www.onlinelibrary.wiley.com). Most turtles appeared to choose sites within 61 m of their 2009 hibernaculum (median = 41 m, min. = 5.8 m, max. = 1,801 m). Thus, if previous hibernacula were not located in the areas that were later clearcut, simple site fidelity might explain why animals did not select clearcuts for overwintering. However, given the range in site fidelity distances, turtles would not likely return to the exact location of an earlier hibernaculum if habitat alteration made it undesirable. Instead, the animal could choose a more desirable site adjacent to that location. None of the turtles appeared to choose 2010 overwintering locations within the clearcuts, although some were relatively close. Turtle 706F was last located in 2010 within 16 m of the edge of the harvest opening in which she hibernated previously; and the turtle that maintained the warmest hibernation temperatures in 2009–2010, was within 20 m of a clearcut in October 2010. Ultimately, the reasons why most animals failed to overwinter within clearcuts is unknown and further investigation into the costs or benefits of these sites should be investigated.

MANAGEMENT IMPLICATIONS

Our data suggest that the effect of relatively small-scale timber harvests on overwintering microclimates is not likely to exclude eastern box turtles from using clearcuts during the winter months. We suggest using the typical harvest size implemented in the Midwest (0.5–5 ha) in a forest matrix, where clearcuts are small enough in proportion to adjacent forest and to animal home ranges that alternative habitat could be selected for hibernation if required. Because temperatures in clearcuts were more variable than in forested habitats and this may cause inconsistency in the warmer temperatures typically offered on south-facing slopes, we suggest implementing harvests on a variety of slope aspects. Using these 2 factors, timber harvests can be implemented in

a way that may mediate their overall impact on forest-dwelling wildlife. Further research should focus on investigating the longer-term physiological costs and energy requirements for burrowing deeply or early emergence.

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Table S1: Average body temperatures (T_b) of 38 adult eastern box turtles during hibernation and emergence (sorted by hibernation temperature). The mean values are totaled at the bottom of the table. Starred (*) individuals are the chosen 12 associated with hibernacula TPS. The four turtles who did not select hibernacula by the time tracking ceased have “unknown” slopes.

ID# & Sex	Slope	n	Hibernation T_b		Emergence T_b	
			Mean ($^{\circ}$ C) & SE		Mean ($^{\circ}$ C) & SE	
605M*	NE	1173	1.82	0.11	10.15	0.43
1350M*	NE	1173	2.33	0.10	7.62	0.19
1206F	S	1173	2.34	0.11	9.73	0.39
506F	E	1173	2.52	0.10	9.20	0.34
406M*	W	1173	2.56	0.10	9.90	0.40
615M*	NW	1173	2.68	0.11	10.37	0.45
800F	0	1173	2.70	0.09	8.74	0.32
806M	W	1173	2.77	0.11	9.56	0.36
1357F*	NE	1173	2.81	0.09	7.27	0.16
1100M*	S	1173	2.85	0.10	9.49	0.35
704M	NE	1173	2.98	0.10	8.58	0.33
1403F	0	1173	3.01	0.09	10.15	0.44
402M*	SE	1173	3.08	0.10	8.54	0.17
714F	SW	1173	3.13	0.10	9.27	0.36
1252F	SE	1173	3.13	0.10	9.33	0.30
904M	W	1173	3.15	0.10	8.75	0.25
100F	SE	1173	3.17	0.10	10.09	0.41
500M	NE	1173	3.30	0.10	9.29	0.35
1455F*	SW	1173	3.33	0.10	8.74	0.29
1360F*	NW	1173	3.34	0.09	6.93	0.14
1150M	NW	1173	3.34	0.10	9.03	0.32
900F*	W	1171	3.34	0.10	9.89	0.37
504M	Unknown	1173	3.41	0.10	10.45	0.38
885F	Unknown	1173	3.52	0.10	10.75	0.44
503F	Unknown	1173	3.60	0.10	8.69	0.26
708M	NW	1173	3.69	0.09	8.31	0.23
680F	NW	1173	3.72	0.10	9.32	0.34
706F	NE	1173	3.73	0.10	8.58	0.31
814M	NW	1173	3.76	0.10	9.38	0.35
1602F*	W	1176	3.78	0.10	9.99	0.30
700M	W	1173	3.79	0.10	9.70	0.36
848M	0	1173	3.81	0.10	9.66	0.41
603F	0	1173	3.85	0.10	8.78	0.37
1207M	SE	1173	3.86	0.10	9.58	0.31
1253M	E	1173	3.87	0.09	9.19	0.24
880F	Unknown	1173	3.92	0.10	10.56	0.39
607M	NW	1173	4.09	0.10	10.25	0.38
906F*	S	1173	4.44	0.09	10.24	0.35

Table S2: Mean temperatures and standard errors (SE) recorded from each depth along TPS during the hibernation and emergence periods. Temperatures are separated by stake habitat types (forests, hibernacula, & clearcuts) and by slope aspects. Starred (*) values are different ($P < 0.05$ and $\Delta^{\circ}\text{C} > 1$) of mean values across habitats (forests, hibernacula, & clearcuts) for associated thermal period (hibernation/emergence), slope aspect, and depth.

			Hibernation						Emergence					
Slope	Depth	# of Records	Forests		Hibernacula		Clearcuts		Forests		Hibernacula		Clearcuts	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
NE	10	9387	-0.56	0.33	-1.17	0.27	-0.80	0.27	11.15	0.52	10.25*	0.43	11.71*	0.43
	0	9390	0.89	0.33	2.01*	0.27	0.80	0.27	9.88	0.52	8.37*	0.43	10.00	0.43
	-10	9388	3.46	0.33	3.40	0.27	1.73*	0.27	7.92	0.52	7.41*	0.43	8.77*	0.43
	-20	9390	4.07	0.33	3.94	0.27	2.77*	0.27	7.41	0.52	7.08*	0.43	8.63*	0.43
	-30	9390	4.33	0.33	4.27	0.27	3.16*	0.27	7.24	0.52	6.89*	0.43	7.98*	0.43
E	10	1176	-0.81	0.47	11.64	0.74
	0	Failed
	-10	1176	3.42	0.47	8.07	0.74
	-20	1176	4.11	0.47	7.89	0.74
	-30	Failed
SE	10	1172	.	.	-0.22	0.47	11.01	0.74	.	.
	0	1172	.	.	3.06	0.47	8.93	0.74	.	.
	-10	1172	.	.	4.46	0.47	7.96	0.74	.	.
	-20	1170	.	.	4.78	0.47	7.55	0.74	.	.
	-30	1172	.	.	5.38	0.47	7.51	0.74	.	.
S	10	2346	.	.	-0.33	0.33	11.90	0.52	.	.
	0	2346	.	.	1.91	0.33	9.58	0.52	.	.
	-10	2346	.	.	3.72	0.33	8.83	0.52	.	.
	-20	2348	.	.	4.34	0.33	8.24	0.52	.	.
	-30	2348	.	.	4.97	0.33	7.87	0.52	.	.

Slope Depth # of Records			Hibernation						Emergence					
			Forests Mean & SE		Hibernacula Mean & SE		Clearcuts Mean & SE		Forests Mean & SE		Hibernacula Mean & SE		Clearcuts Mean & SE	
SW	10	7035	-0.22	0.33	-1.06	0.47	-0.22	0.27	11.50	0.52	12.00	0.74	12.30	0.43
	0	7035	2.26*	0.33	0.88	0.47	0.88	0.27	9.09*	0.52	10.60	0.74	11.31	0.43
	-10	7035	4.34	0.33	3.69	0.47	2.69*	0.27	9.22	0.52	8.52*	0.74	9.93*	0.43
	-20	7038	4.39	0.33	4.37	0.47	3.79	0.27	8.16	0.52	8.01	0.74	9.65*	0.43
	-30	7036	5.01	0.33	5.14	0.47	4.29	0.27	7.97	0.52	7.71	0.74	9.32*	0.43
W	10	4690	-0.56	0.47	-0.80	0.27	.	.	11.15	0.74	11.83	0.43	.	.
	0	4693	2.15	0.47	1.47	0.27	.	.	9.29	0.74	9.57	0.43	.	.
	-10	4693	3.45	0.47	3.75	0.27	.	.	8.28	0.74	8.40	0.43	.	.
	-20	4691	3.96	0.47	4.47	0.27	.	.	7.85	0.74	7.94	0.43	.	.
	-30	4693	4.24	0.47	5.14	0.27	.	.	7.41	0.74	7.75	0.43	.	.
NW	10	2342	.	.	-0.80	0.33	11.05	0.52	.	.
	0	2349	.	.	1.67	0.33	8.57	0.52	.	.
	-10	2349	.	.	3.44	0.33	7.71	0.52	.	.
	-20	2349	.	.	4.22	0.33	7.53	0.52	.	.
	-30	2347	.	.	4.86	0.33	7.26	0.52	.	.

Table S3: Pairwise comparisons of mean distances between turtle hibernacula since 2007 ('07) as part of a radiotelemetry study at the Hardwood Ecosystem Experiment in south-central Indiana. Turtles often returned to locations used previously but not necessarily consecutively.

Turtle ID	'07 to '08	'07 to '09	'07 to '10	'08 to '09	'08 to '10	'09 to '10
402M	9.22	247.16	41.00	250.24	34.53	234.83
404F	55.00
406M	.	3062.80
500M	.	155.72	146.29	.	.	9.43
503F	544.82	55.04	60.03	580.55	354.22	6.40
504M	36.50	54.57	20.12	25.50	36.12	44.28
506F	.	12.73	11.05	.	.	22.36
603F	.	38.08	98.90	.	.	75.24
605M	.	483.92	398.53	.	.	91.02
607M	.	42.54	34.01	.	.	9.22
615M	47.10
680F	155.13
700M	47.17
704M	39.56	47.27	55.03	10.82	15.65	13.93
706F	88.84	89.99	57.04	5.00	36.06	39.05
708M	45.54	166.00	156.42	132.65	124.48	11.00
787F	13.89
800F	.	12.04	20.62	.	.	18.44
806M	.	85.00	87.09	.	.	89.05
814M	132.62
848M	5.83
880F	97.05
885F	538.03
900F	.	236.14	227.73	.	.	37.58
904M	.	69.63	43.01	.	.	22.36
906F	200.81	58.05	35.23	230.78	213.56	26.63
908M	.	71.70	9.22	.	.	23.60
1206F	129.31
1207M	10.44
1252F	8.54
1253M	47.43
1350M	1800.64
1357F	43.01
1360F	43.86
1455f	264.70
1602F	24.70
Average	127.54	277.13	88.31	176.51	116.37	123.06
St. Dev.	178.49	704.67	99.43	205.44	126.37	313.89
Median	50.27	70.67	55.03	132.65	36.12	41.03