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Thermoregulation of spotted turtles (*Clemmys guttata*) in a beaver-flooded bog in southern Ontario, Canada

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ABSTRACT

Body temperature has a major influence on the physiological processes, growth, reproductive output, and overall survival of ectotherms. When a habitat is altered as a result of natural or anthropogenic influences, the available temperatures in the habitat can change, thus affecting an animal's ability to thermoregulate. We studied thermoregulation in response to habitat change in a population of spotted turtles (*Clemmys guttata*) in Southern Ontario, Canada. Historically, the study site was ditched to draw down water levels to facilitate peat mining, and the resulting drainage ditches were the only habitat containing surface water and turtles were restricted to these drains. Recent colonization of the site by beaver (*Castor canadensis*) caused increases in water level and water surface area. We followed spotted turtles ($N=16$) outfitted with radio transmitters and iButtons to estimate body temperatures (T_b) continuously throughout the active season post-flooding. Turtle models outfitted with iButtons ($N=50$) were deployed in the nine available habitat types to record environmental temperatures (T_e). Turtles ($N=13$) were tested in a thermal gradient under laboratory conditions to determine preferred body temperature range (T_{set}). The T_{set} for the population ranged from 20 °C to 26 °C. In the field, T_b was within the T_{set} range 28% of the time from March to October, and 67% of the time from July to August. Efficiency of thermoregulation was calculated to be highest in July and August. The habitat type with the highest thermal quality was the shallow flooded zone created by beaver damming, and the habitat with the lowest thermal quality was the drain bottom, the drains being the only aquatic habitat available prior to flooding. This study confirms that beaver flooding provided a wide variety of preferable thermal opportunities for spotted turtles. Further investigation is needed to determine the effects of flooding on spotted turtle thermoregulation during nesting and hibernation.

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1. Introduction

Physiological processes are strongly influenced by temperature (Dorcas et al., 1997; Du et al., 2000; Ojanguren et al., 2001), and dependence on available temperatures governs the behaviors exhibited by ectotherms (Huey, 1982; Hertz et al., 1993; Peterson et al., 1993). Environmental temperature selection by means of thermoregulatory behavior (i.e., body orientation towards the sun, moving away from cold towards warm temperatures) is a key factor that affects survivorship, growth, and physiological function of reptiles (Huey, 1982; Brooks et al., 1991; Tamplin, 2006; Edge et al., 2009). The degree to which reptiles behaviorally regulate their body temperature (T_b) varies greatly (Boyer, 1965; Christian and Bedford, 1995; Diaz, 1997; Schauble and Grigg, 1998), and they display a variety of thermoregulatory strategies, ranging from thermoconformity to thermoregulation (Ruibal,

1961; Hertz et al., 1993; Rummery et al., 1994; Ibarquengoytia et al., 2010). Thermoconformity describes an animal that does not thermoregulate such that their T_b matches the temperatures of their thermal environment, whereas thermoregulation describes an animal changing their behavior to achieve T_b within a range of optimal temperatures (Hertz et al., 1993). There are benefits associated with thermoregulation by ectotherms (Huey and Slatkin, 1976). For example, performance is improved when T_b approaches an optimum temperature range, which is generally close to the species' preferred or target T_b range (T_{set}) (Hertz, 1992; Angilletta, 2001; Blouin-Demers et al., 2003). T_{set} has been used extensively to estimate the T_b that maximizes physiological performance (Hertz et al., 1993; Schauble and Grigg, 1998; Dubois et al., 2008).

Behavioral thermoregulation can incur costs for the animal by reducing the energy spent on other important behaviors such as feeding, reproduction, and predator avoidance (Sears, 2005). A primary cost of thermoregulation is related to the time and energy expended in seeking thermoregulation opportunities (Huey and Slatkin, 1976). Environmental thermal quality is a

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measure of how much time and energy an ectotherm needs to invest into thermoregulation so that their T_b meets T_{set} (Edwards and Blouin-Demers, 2007). When the thermal quality of the environment is low, environmental temperatures deviate far from T_{set} , and the cost of thermoregulation is high because more energy and time are required to get T_b closer to T_{set} (Edwards and Blouin-Demers, 2007). In thermally optimal environments, ectotherms do not need to spend time and energy thermoregulating because environmental temperatures do not deviate far from T_{set} (i.e., thermoconformity; Shine and Madsen, 1996; Blouin-Demers and Nadeau, 2005).

Spotted turtles (*Clemmys guttata*) are semi-aquatic and occupy a variety of small wetlands including fens, bogs, swamps, ponds, and small woodland streams (Ernst and Lovich, 2009). The species is classified as Endangered in Ontario and Canada (COSEWIC, 2004), and globally. Threats include habitat loss and fragmentation, road mortality, pollution, predation, and illegal collection by humans for the pet trade (COSEWIC, 2004). Temperature selection by spotted turtles has been given some attention (Ernst, 1982; Litzgus and Brooks, 2000; Rasmussen and Litzgus, 2010a); however, thermoregulation has not been analyzed. Spotted turtles are known to prefer cool environmental temperatures, emerging from hibernation in the spring at water temperatures as low as 2 °C (Ernst, 1982; Litzgus and Brooks, 2000). Foraging behavior has been observed at water temperatures as low as 7.7 °C (Rasmussen et al., 2009), 14.2 °C (Ernst, 1982), and 17 °C (Litzgus and Brooks, 2000). Aestivation behavior has been observed when air temperatures reach 33 °C (Litzgus and Brooks, 2000) and when water temperatures reach 32 °C (Ernst, 1982).

The purpose of our study was to examine the thermoregulatory behavior and efficiency of thermoregulation of spotted turtles in a bog that was historically mined for peat and that was recently flooded by beaver (*Castor canadensis*) activity. We assumed that the historical conditions at the study site, namely the drained peat bog, represented thermally degraded and sub-optimal habitat for spotted turtles based on our finding that spotted turtles preferred the newly flooded zones (Yagi and Litzgus, 2012). We hypothesized that flooding would create habitats with high thermal quality, and predicted that temperatures in the new habitat would not deviate far from the preferred temperature range (T_{set}) for spotted turtles. We also predicted that spotted turtles would be most efficient at thermoregulating within the new aquatic habitats.

2. Methods

2.1. Study site

We studied an isolated population of spotted turtles located within a partially mined peatland located in Southern Ontario (the exact location is not given to prevent collection of the turtles). The mean level of annual precipitation in the region is 1003.2 mm, and the mean daily temperature in January is -4.2 °C and increases to 21.6 °C in July (Environment Canada, 2010). The study site covers an area of 1460 ha and is situated within the prehistoric floodplains of Lake Erie, making the surrounding region optimal for cropland, and susceptible to flooding (Gayler, 1994; Pengelly et al., 1997). This site was used as a peat-mining location for over 60 years (Yagi and Frohlich, 1998). The impacts from mining include the placement of drainage ditches within and around the site, which caused significant water loss to the interior of the wetland. As a result, the only standing water available to turtles was in the drainage ditches (Yagi and Frohlich, 1998). The wetland has been undergoing recovery management since it was purchased in 1997 by the Niagara Peninsula

Conservation Authority (NPCA), Nature Conservancy of Canada (NCC), and the Ontario Ministry of Natural Resources (OMNR).

In fall 2005, beaver dispersed back into the local watershed, and into the drainage system of the study site. Significant flooding occurred in the interior of the study site, changing the appearance and potential biodiversity in the recovering wetland. Dominant plant species changed rapidly in all flooded zones; for example, European birch (*Betula pendula*) started dying off while other wetland species became abundant, including reeds (*Phragmites* sp.), sedges (family Cyperaceae), rushes (*Juncus* sp.), and tickseed (*Bidens* sp.).

2.2. Radio telemetry and turtle body temperatures (T_b)

In 2009, 19 spotted turtles (eight males, nine females, and two sub-adults) outfitted with 3 g Advanced Telemetry Systems (ATS) radio transmitters (Model R1680, Isanti, MN) were located 2–3 times/week from emergence from hibernation (March) until entrance into hibernation (November). See Yagi and Litzgus (2012) for a detailed description of transmitter attachment and radio telemetry methodology.

Turtle body temperature (T_b) was estimated by attaching small temperature data loggers (iButtons; Maxim model DS1922L-F5 and DS1923-F5, accuracy ± 0.5 °C, Dallas Semiconductor, Sunnyvale, CA), to the carapaces of spotted turtles outfitted with transmitters to obtain the distribution of T_b s they experienced in the field. The iButtons were waterproofed using PlastiDip (Performix Brand, Blaine, Minnesota), and attached to the carapace in the same way the transmitters were attached (Yagi and Litzgus, 2012). Waterproofing iButtons has been found to be a reliable method of preventing device failure while minimally affecting temperature readings (Roznik and Alford, 2012). The combined mass of both the radio transmitter and the iButton did not exceed 7% of turtle body mass to ensure the equipment did not negatively affect locomotion. iButtons were initially attached to the radio-tagged turtles in March 2009 and were set to record temperatures once every 60 min. Because the iButtons were only able to store about 2200 temperature recordings, the iButtons were replaced once in the middle of the field season.

T_b data were collected from radio-tagged spotted turtles from May to October 2009. The data were pooled by sex, creating mean temperature profiles for male and female spotted turtles for the duration of the active season. If T_b data were not normally distributed, \log_{10} transformations were made in order to meet the assumption of normality for parametric analyses. T_b data were analyzed for the whole active season and by season (spring, summer, and fall; Table 1). A repeated measures ANOVA (rmANOVA) was used to determine whether there were any differences in T_b between males ($N=8$) and females ($N=8$), and among seasons (spring, summer, and fall).

2.3. Thermal gradient trials to determine T_{set}

In order to calculate the temperature range that turtles target in the field (T_{set}), 13 individual spotted turtles were exposed to a range of temperatures under laboratory conditions in thermal

Table 1
Definitions of the three seasons, spring, summer, and fall. Spotted turtle (*Clemmys guttata*) behaviors associated with each season are indicated.

Season	Time period	Associated turtle behaviors
Spring	1 May – 30 June	Mating, nesting, foraging
Summer	1 July – 31 August	Foraging, aestivating
Fall	1 September – 26 October	Searching for hibernacula

gradient trials conducted in facilities provided by the OMNR. The turtles used in the trials were located using radio-telemetry (Yagi and Litzgus, 2012) and captured by hand or using a dip net. There have not been any previous T_{set} studies on spotted turtles; therefore, we exposed turtles to a wide range of temperatures over three gradient trials in a 72 day time frame during the summer (Table 2). The overall available temperature range for all gradient trials combined was approximately 10–33 °C. The thermal gradient consisted of a copper plate (91.4 cm × 10.2 cm × 0.6 cm) inside a plywood enclosure (107 cm × 23 cm × 41 cm) with solid state thermoelectric devices (Peltier cell; WATRONIX Inc., model inb.31-5.0-1.5, West Hills, CA) mounted at either end to establish the temperature gradient. Digital controllers at each end of the gradient allowed temperature adjustment to within 0.5 °C. One of the Peltier-cells malfunctioned during the third gradient trial; therefore, an air-conditioner was attached to the heat exchanger on the cool end of the gradient to maintain the cooler temperature extreme. Two UV lights were placed at either end of the gradient to provide homogenous illumination, and little to no radiant heat, of the enclosure interior. The lights were set to a photoperiod that reflected the natural summer conditions (Table 2). The gradient was divided into 10-cm sections, which corresponded to the approximate length of a spotted turtle, resulting in the gradient being divided into nine same-sized sections. iButtons were placed in the center of each section to record temperature once every 20 min for the duration of the gradient trials. Turtles positioning themselves along the gradient were assumed to be selecting a T_b that was represented by the temperature of the gradient in that section.

We conducted preliminary pilot trials in the gradient, using three small (spotted turtle-sized) painted turtles (*Chrysemys picta*), before data were collected on spotted turtles. When turtles showed minimal movement in the gradient during the photo-phase, it was assumed that the turtles were selecting temperatures within the gradient. Painted turtles showed minimal movements after approximately 24 h in the gradient; therefore, we allowed spotted turtles approximately 24 h to acclimate to the lab in a semi-aquatic tank followed by 24 h to acclimate to gradient conditions before we recorded any temperature selection data.

The gradient trials were run after spotted turtle nesting season to ensure that reproductive status did not affect temperature selection. Turtle movements in the gradient were recorded in 1 min intervals, using an infrared closed circuit television camera (model DS-2CC512N-IR1, 10 m range, 6 mm lens) and digital video recorder (DVR model DRX-50-16-500, resolution 2560 × 1920; CAMACC Systems Inc., Victoria, BC, Canada). Each gradient trial lasted 24 h, or 1440 min. Because each observation was equivalent to a time interval of 1 min, the selected temperature was calculated by tallying the number of observations of each

Table 2

Three separate temperature gradients trials were done, marked by the different dates they were run, number of turtles tested (N), photoperiod and the temperature range established in each gradient. The photoperiod was set to mimic the natural photoperiod in the field. In June and July, lights were turned on at 6:10 AM and turned off at 9:20 PM. In August and September, lights were turned on at 6:30 AM and off at 8:00 PM.

	Run date	N	Photoperiod (L:D)	Temperature range
Gradient 1	26 June – 10 July	4	15.2:8.8	18.2–33.4 °C
Gradient 2	13 July – 20 July	5	15.2:8.8	9.5–26.1 °C
Gradient 3	31 August – 6 September	4	13.5:10.5	10.8–25.8 °C

turtle in each section of the gradient during the trial. Each turtle was considered independent for the analyses of the gradient data.

2.4. Operative environmental temperatures

Operative temperatures (T_e), or available environmental temperatures, are typically quantified by the use of inanimate objects (i.e., thermal models) that approximate the study animal in size, shape, and color (Bakken, 1992). Pilot work comparing models constructed from several materials concluded that models constructed of PVC pipe and plexiglass best represented the T_b of live turtles in the field. Fifty models were placed throughout the available habitats within the population range (Yagi and Litzgus, 2012; Fig. 1). Each model was outfitted with two waterproofed iButtons (Plastidip; Performix Brand, Blaine, Minnesota). One iButton was attached to the external surface of the model and one was attached to the inside of the model. The iButtons were fastened using 5-min curing epoxy glue (Lepage Speed-Set Epoxy). iButtons were set to record temperatures once every 60 min, and the two readings from each model were averaged for the analyses.

Thermal models were placed in the field to estimate available temperatures to the turtles, and to determine whether turtles were actively thermoregulating or thermoconforming to the temperatures available in certain habitat types (Fig. 1). Nine habitat types within the turtle population range were defined based on relative water depth (Table 3). The models were placed in three different zones (A, B, and C) that represented replicates of the nine habitat types; 20 models were placed in zone A, 16 in zone B, and 14 in zone C. The temperature data collected from the replicate models from each of the nine habitat types were averaged together to obtain a mean T_e for each habitat type. The temperature data were divided into three time periods, representing three seasons (spring, summer, and fall; Table 1). A rmANOVA was used to examine differences in mean temperatures among seasons and among habitat types; the models ($N=50$) represented replicates and seasons ($N=3$) represented the repeated measurement.

2.5. Analysis of T_{set} data

The temperatures turtles selected from the gradient in the 24 h period were used in the analysis. Data were collected from the time lights turned on to the minute before lights turned on again

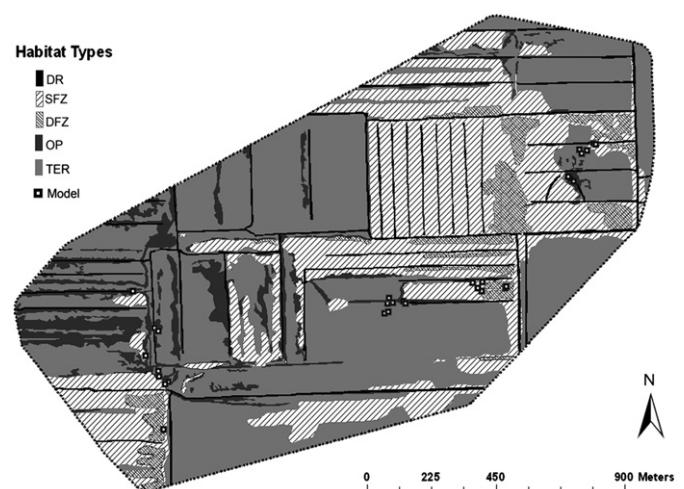


Fig. 1. Map of study site showing the habitat types (see Table 3 for definition of acronyms) and thermal model locations within the spotted turtle (*Clemmys guttata*) population range.

Table 3
Descriptions of the habitats in which temperatures were measured using thermal models. Nine available habitat types were defined based on a gradient of water depth. Drain bottom had the deepest water, the flooded zones had medial water depths, and terrestrial sites had no water. Fifty turtle models were placed throughout these habitat types and recorded temperatures hourly from 18 May to 11 October 2009. Habitat types marked with an * indicate those types that were also present before the flooding event.

Habitat type	Key	Definition
*Drain bottom	DR bottom	Model secured at a water depth > 80 cm
*Drain surface	DR surface	Model secured at the surface of the drain water
Deep flooded zone bottom	DFZ bottom	Model secured at a water depth between 50 cm and 80 cm
Deep flooded zone surface	DFZ surface	Model secured at the surface of the deep flooded zone water
Shallow flooded zone bottom	SFZ bottom	Model secured at a water depth between 20 cm and 50 cm
Shallow flooded zone surface	SFZ surface	Model secured at the surface of the shallow flooded zone water
Saturated peat	SAT peat	Model secured in areas of mainly exposed peat and some vegetation, close to flooded zones where surface water is no longer visible
*Open peat	OP peat	Model secured in areas of predominately dry, exposed peat, with little to no vegetation cover
*Terrestrial	TER	Model secured in upland areas, including shrub zones and mature forests

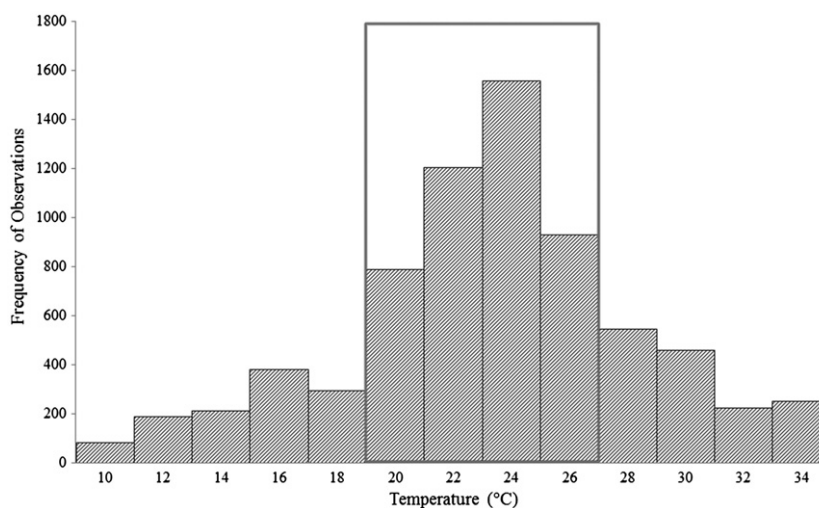


Fig. 2. Data for all three gradient trials combined showing the frequency of turtles ($N=13$) observed resting at each temperature along the thermal gradient. Observations during both the photophase and scotophase were included. Due to the unequal number of turtles represented in each gradient, this distribution was standardized to represent the mean frequency distribution per turtle. The central 50%, or T_{set} , of this distribution is a temperature range from 20 °C to 26 °C, outlined here with a gray rectangle.

the next day (Table 2). This was done to account for the effect of photoperiod on temperature selection, and reflected what turtles experience in the field. The T_b data from the turtles in the field included temperatures experienced during the photophase and scotophase, so we retained both photophase and scotophase in the analysis of the T_{set} data.

The T_{set} range was calculated by determining the central 50% of the distribution for all the temperatures selected by all turtles that participated in the three gradient trials. The 25% and 75% quartiles (or central 50%) of the frequency distribution of temperatures selected in the gradient were 19.5 °C and 25.8 °C for females, and 19.9 °C and 26.3 °C for males, respectively. A t-test indicated that temperatures selected by males and females were not significantly different ($t=-0.14$, $df=11$, $P=0.89$), therefore we used an overall T_{set} range of 20–26 °C for both sexes combined (Fig. 2).

2.6. Deviations from T_{set} (d_e and D_b)

The thermal quality of the nine habitat types at the study site were assessed by calculating the absolute mean deviation of T_e from T_{set} (mean d_e) (Hertz et al., 1993). Values of zero indicated

habitats of perfect thermal quality, as all recorded temperatures attained from those habitat types were within the calculated T_{set} range. The accuracy of thermoregulation is the absolute mean difference that T_b deviated from T_{set} (mean d_b). For example, 26 °C was subtracted from any values above the upper T_{set} limit, and 20 °C was subtracted from values below the lower T_{set} limit, and any values in between the range were given a value of zero. Values of zero indicated perfect accuracy of thermoregulation, as all recorded T_b s of turtles were within the T_{set} range. Both d_e and d_b values were calculated for the whole active season (May to October), and separately for the three seasons (spring, summer, and fall).

2.7. Efficiency of thermoregulation

The effectiveness of thermoregulation is calculated using the formula $d_e - d_b$ (Blouin-Demers and Weatherhead, 2001). Values that approach zero indicate that turtles were thermoconforming to the temperatures available within the indicated habitat types. This means that turtles were being efficient at thermoregulating when in these habitat types because little to no energy would be expended in searching for thermally preferable habitats (i.e.,

basking locations; Huey and Slatkin, 1976; Withers and Campbell, 1985). When $d_e - d_b$ results in a positive value, this indicates that animals are successfully thermoregulating within a habitat of low thermal quality (high d_e value and low d_b value; Blouin-Demers and Weatherhead, 2001). When values are negative, this suggests that animals are avoiding thermally preferable habitat types (Blouin-Demers and Weatherhead, 2001; Blouin-Demers and Nadeau, 2005). A rmANOVA was used to determine how close male and female turtles were to achieving thermoconformity (i.e., $d_e - d_b = 0$). The efficiency of thermoregulation values from all nine habitat types for males and females were compared to a vector of zeros, which represented perfect thermoconformity to the temperatures available in each habitat type. Differences between males and females were analyzed separately among seasons. Tukey's (HSD) *post hoc* analyses for homogenous groups were used to determine in which habitat types turtles were thermoconforming. All statistical analyses were performed using Statistica 6.1 (Tulsa, OK).

3. Results

3.1. Radio telemetry and turtle body temperatures (T_b)

During the 2009 active season, turtles were found basking out of the water on only 4.1% of the total observations for all turtles ($N=455$). Most observations (85.3%) were of turtles carrying out aquatic activities such as cryptic basking, swimming, and courtship in the surface vegetation of aquatic habitats.

A total of 50,288 temperatures were recorded from all adult turtles outfitted with iButtons ($N=17$). However, one iButton failed (attached to an adult female), thus those temperature data were excluded from the analysis, leaving 16 turtles with viable iButtons. From May to October, the mean T_b for males was 18.7 °C (SE=0.2), and mean T_b for females was 18.1 °C (SE=0.2) (Table 4). The difference in T_b between males and females over the whole active season was almost significant ($F_{1, 14}=4.0, P=0.07$). T_b differed among seasons ($F_{2, 28}=252.8, P<0.001$). There was no interaction effect between season and sex ($F_{2, 28}=0.67, P=0.52$). The highest mean T_b was recorded from males in the summer (26.3 °C, SE=0.2), and the lowest mean T_b was recorded from females in the fall (5.7 °C, SE=0.3).

3.2. Operative environmental temperatures (T_e)

A total of 176,850 temperatures were recorded from the 50 models placed in nine habitat types throughout the population range. Temperatures (T_e) differed significantly among habitat types ($F_{8, 41}=44.5, P<0.001$) and among seasons ($F_{2, 82}=637.8, P<0.001$). There was also a significant interaction between season and habitat type ($F_{16, 82}=20.2, P<0.001$). DR bottom had the lowest mean T_e during the spring and summer, and OP had the lowest mean T_e in the fall. Conversely, OP had the highest mean T_e in the spring and summer, and SFZ surface had the highest mean T_e in the fall (Table 3; Fig. 3).

Table 4
Mean \pm SE body temperature (T_b) of male and female spotted turtles (*Clemmys guttata*) in three seasons; spring, summer and fall.

Season	Male T_b (°C)	Female T_b (°C)
Spring	19.9 \pm 0.4	19.7 \pm 0.3
Summer	21.9 \pm 0.4	21.1 \pm 0.3
Fall	14.3 \pm 0.4	13.4 \pm 0.3

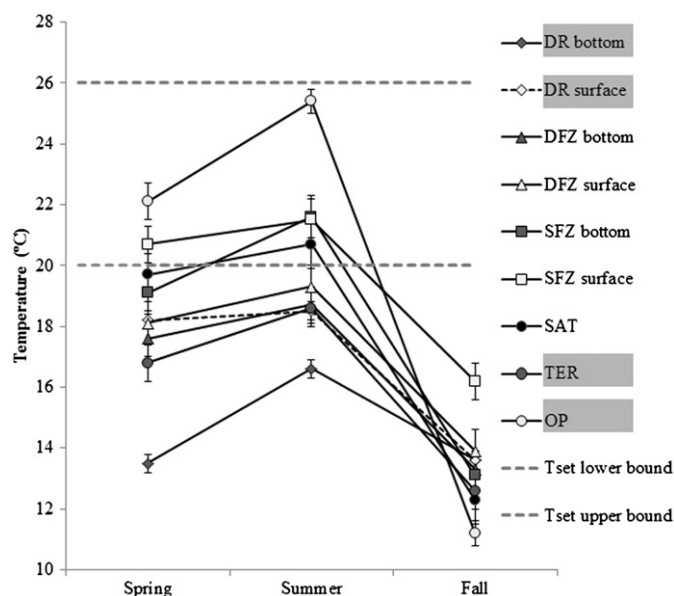


Fig. 3. Mean operative environmental temperatures (T_e) of each habitat type in three seasons; spring, summer and fall. DR bottom had the lowest mean T_e during the spring and summer, and OP had the lowest mean T_e during the fall, whereas OP had the highest mean T_e during the spring and summer and SFZ surface had the highest mean T_e during the fall. Error bars represent standard error. Habitat acronyms shaded with gray represent habitat types that were also present prior to flooding.

3.3. Deviations from T_{set} (d_e and d_b)

The thermal quality of the habitats (d_e) available to spotted turtles differed significantly among habitat types ($F_{8, 41}=122.23, P<0.001$) and among seasons ($F_{2, 82}=1396.2, P<0.001$), and the interaction between habitat type and season was significant ($F_{16, 82}=66.8, P<0.001$). All habitats were generally of higher thermal quality in the summer than in spring and fall (Fig. 4). Tukey's (HSD) *post hoc* analyses indicated that the habitat types with the highest thermal quality (low d_e) were SFZ (surface and bottom), DFZ (surface and bottom), DR surface, OP, and SAT in summer; and OP and SFZ surface in spring (Table 3; Fig. 4). The habitat types with the lowest thermal quality (high d_e) were SFZ bottom, DFZ (surface and bottom), DR (surface and bottom), OP, and TER in the fall, and DR bottom in the spring (Table 3; Fig. 4).

The accuracy of thermoregulation (d_b) differed between males and females ($F_{1, 14}=7.9, P<0.01$), and differed among seasons ($F_{2, 28}=97.3, P<0.001$). Tukey's (HSD) *post hoc* analysis indicated that males and females were both more accurate at thermoregulating in the spring and summer compared to the fall ($MS=1.05, df=41, P<0.001$). During the spring, mean d_b for males was 0.6 °C (SE=0.3) and mean d_b for females was 0.9 °C (SE=0.3). During the summer, accuracy of thermoregulation improved such that male mean d_b was 0.1 °C (SE=0.01) and female mean d_b was 0.4 °C (SE=0.1). During the fall, accuracy of thermoregulation declined; male mean d_b was 4.1 °C (SE=0.5) and female mean d_b was 5.9 °C (SE=0.4). Overall, male accuracy of thermoregulation ($d_b=1.6$ °C) was lower than that of females ($d_b=2.4$ °C).

3.4. Efficiency of thermoregulation

During the spring there was a significant difference in thermoregulatory efficiency between males and females ($F_{1, 28}=6.51, P<0.01$), and a significant interaction effect between efficiency and habitat type ($F_{8, 224}=2774.2, P<0.001$). In summer, there was a significant difference in thermoregulation efficiency between males and females ($F_{1, 28}=7.43, P<0.01$), and a

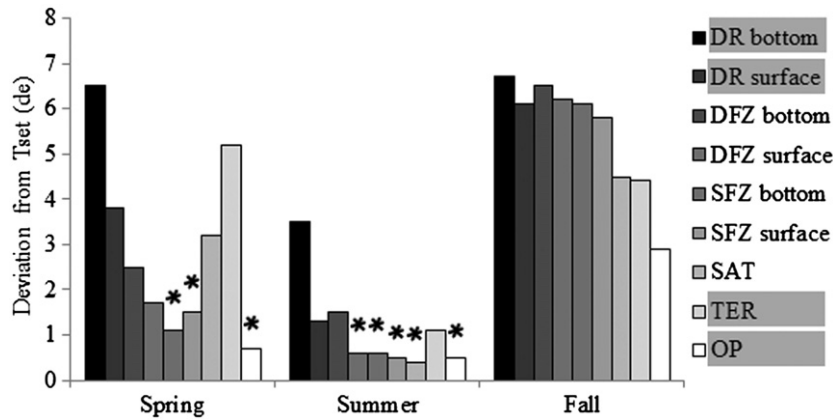


Fig. 4. The mean d_e of each habitat type in three seasons; spring, summer and fall. DR bottom had the lowest thermal quality for all three seasons. Habitat types with the highest thermal quality are indicated with an *. Habitat acronyms shaded with gray represent habitat types that were also present prior to flooding.

significant interaction between efficiency and habitat type ($F_{8, 224} = 2209.7, P < 0.001$). Finally, during the fall there was an almost significant difference in thermoregulation efficiency between males and females ($F_{1, 28} = 4.05, P = 0.06$), and there was a significant interaction between efficiency and habitat type ($F_{8, 224} = 3804.7, P < 0.001$).

Tukey's (HSD) *post hoc* analyses indicated which habitat types male and female spotted turtles were likely thermoconforming with; P -values above $\alpha = 0.05$ indicate efficiency values that are not different from thermoconformity ($d_e - d_b = 0$) and are therefore the best habitats (i.e., the least energetically expensive) in which to maintain preferred T_b (Fig. 5). During the spring and summer, there was variation in efficiency values between the sexes and among habitat types (Fig. 5). During the fall, all efficiency values did not differ from thermoconformity ($d_e - d_b = 0$); all efficiency values were close to zero for all habitat types (Fig. 5). Overall, females (F) were more efficient at thermoregulating than males (M) in the spring ($F = 1.02^\circ\text{C}, M = 1.17^\circ\text{C}; P < 0.05$) and summer ($F = 0.34^\circ\text{C}, M = 0.50^\circ\text{C}; P < 0.01$), and there was an almost significant difference between the sexes in the fall ($F = -0.20^\circ\text{C}, M = 0.67^\circ\text{C}; P = 0.06$).

4. Discussion

4.1. T_{set}, T_b and T_e

The T_{set} range calculated for spotted turtles in our study population ranged from approximately 20°C to 26°C for both males and females. Ours was the first study to calculate T_{set} for spotted turtles, and the range of values we found generally agrees with temperature data collected in previous studies of spotted turtle thermal ecology in the wild. Ernst (1982) recorded mean T_b s of spotted turtles in Pennsylvania to be 21.5°C while turtles were basking, 19.29°C when they were moving in water, and 23.5°C while females were nesting. Litzgus and Brooks (2000) recorded mean T_b s of spotted turtles in northern Ontario to be 25.3°C while turtles were basking, and 21.8°C while turtles were aestivating.

Males had slightly warmer T_b s than females for most of the active season, suggesting that males are selecting the upper end of the calculated T_{set} and females are selecting the lower end of the T_{set} . Reasons for this sex difference may be the fact that males were generally more active, having larger daily movements and larger activity areas (Yagi and Litzgus, 2012). Being more active implies the need for higher T_b s to facilitate higher metabolic rates to meet greater energy requirements (i.e., foraging and mate

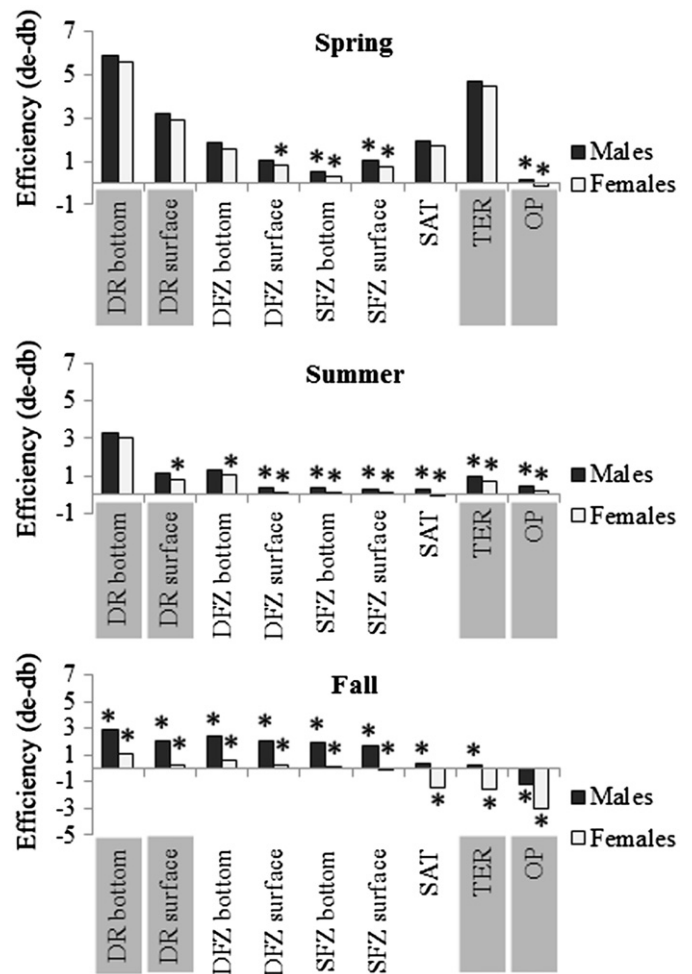


Fig. 5. Mean efficiency of thermoregulation ($d_e - d_b$) during spring, summer and fall, for male and female spotted turtles (*Clemmys guttata*). The efficiency values that are not different from zero ($d_e - d_b = 0$) are the habitats the turtles were found to be thermoconforming with, suggesting that they are the best habitats (i.e., least energetically expensive) to occupy during the active season (indicated with an *). Habitat acronyms shaded with gray represent habitat types that were also present prior to flooding.

searching; Huey and Slatkin, 1976; Withers and Campbell, 1985; Dubois et al., 2009). Females may have been slightly cooler than males because they were remaining within their smaller activity areas after the nesting season, and not moving large distances

(Yagi and Litzgus, 2012). Smaller movements and a more latent behavior would not require a large amount of energy and so would not require very warm temperatures (Huey and Slatkin, 1976). It is also possible that females were re-gaining their fat stores lost from egg development (Bjorndal, 1985) by foraging and not expending energy by moving large distances or having high metabolic rates (i.e., avoiding high T_b).

The data collected from the models in the nine habitat types showed that our study site is thermally heterogeneous. The habitat type with the largest daily temperature fluctuations was the open peat (OP), and drain (DR) bottom had the smallest daily temperature fluctuations. The availability of a relatively stable environmental temperature would be beneficial for an ectotherm if they were unable to move from that habitat type for an extended period of time, such as during hibernation periods, and indeed most of the turtles in our study hibernated in the drains (Yagi and Litzgus, 2012). The presence of thermally preferable habitat may allow spotted turtles to remain active throughout what would usually be their aestivation period, and indeed we found a low proportion of turtles aestivating during flooding conditions compared to pre-flooding conditions (Yagi and Litzgus, 2012).

4.2. Deviations from T_{set} (d_e and d_b)

All flooded habitats (DFZ bottom and surface, SFZ bottom and surface, and SAT; Table 3) were of the highest thermal quality. Based on radio telemetry observations, turtles spent most of their time within aquatic habitats during the active season; however, turtles showed selection for drains during hibernation (Yagi and Litzgus, 2012) even though DR bottom had the poorest thermal quality. The drain surfaces were of higher thermal quality than the drain bottoms, and this difference in thermal quality within a single habitat type based on water depth appears to provide microhabitat heterogeneity from which turtles can select preferred temperatures in the field.

Male spotted turtles were more accurate at thermoregulating (i.e., maintaining T_b within T_{set}) than females. This is interesting and somewhat surprising because females would need to regain their energy stores after egg production (Congdon and Tinkle, 1982; Rollinson and Brooks, 2007; Carriere et al., 2008), and having a T_b that maximizes physiological function would likely maximize the rate at which they regain their energy stores (Huey and Slatkin, 1976; Huey and Stevenson, 1979). It is possible that female T_{set} is slightly different than male T_{set} , and that the differences were not detected in our gradient study due to factors such as small sample size. According to the seasonal analyses, the accuracy of thermoregulation for both males and females was greatest in the spring and summer, and lowest in the fall. T_e also decreased in fall, although temperatures within T_{set} were still available, so turtles could have regulated their T_b within T_{set} by basking. The fact that accuracy was low in the fall suggests that T_{set} may have shifted to a lower temperature range. It would be beneficial for turtles to have a high metabolism when there is a large supply of food available and when they need to expend large amounts of energy (Huey and Slatkin, 1976; Huey and Stevenson, 1979; Carriere et al., 2008). This usually happens in the spring (i.e., when mate searching and egg production occur) and summer (i.e., when females nest and subsequently regain fat stores) when ambient temperatures are high (Schwartzkopf and Brooks, 1987; Rollinson and Brooks, 2007). In the fall however, turtles are preparing for hibernation by fasting and enduring a temperature-induced torpor as ambient temperatures decrease (Gregory, 1982; Row and Blouin-Demers, 2006). It would be beneficial to reduce metabolism if there are limited resources

and temperatures to fuel activity, thus a lower T_{set} would be established in fall.

4.3. Efficiency of thermoregulation

Male and female spotted turtles appeared to be thermoconforming to the temperatures available in some aquatic habitat types during spring and in many habitats in summer. This corresponds with the results of a simultaneous spatial ecology study which showed that turtles selected primarily SFZ habitat over all others (Yagi and Litzgus, 2012). Because turtles were not located in concordance with every temperature reading, we cannot rule out the possibility that turtles were sometimes actively thermoregulating in poor quality habitats. However, this scenario is unlikely because turtles were located the majority of the time within large areas of good quality habitat (Yagi and Litzgus, 2012) and individuals would have had to move large distances to be situated in poor quality habitat. In the spring, turtles tended to aim for higher T_b , which would increase their metabolism (Huey and Slatkin, 1976). For many reptiles, during spring (emergence from hibernation to the nesting/gestation period), optimal physiological function would be advantageous because the physiological processes related to reproductive output would be maximized (Brown et al., 1994). Brown and Weatherhead (2000) found that gravid female snakes thermo-regulate differently from non-gravid females and males, likely due to gravid females aiming to increase their body temperature for gestation. Wapstra (2000) found that female lizards (*Niveoscincus ocellatus*) thermoregulate to increase their T_b in order to increase the rate of egg development. A study on a population of painted turtles in northern Ontario suggested that the energetic demands of female egg production resulted in an increased basking duration (Carriere et al., 2008).

The cost-benefit model states that thermoconformity is expected when climatic extremes make thermoregulation too expensive (Huey and Slatkin, 1976; Withers and Campbell, 1985). However, rather than having to deal with extreme temperatures in their environment, spotted turtles in the new aquatic habitat encountered preferable temperatures, thus thermoconformity for these turtles would be the most efficient option. Similarly, Blouin-Demers and Nadeau (2005) found that lizards thermoconformed to their habitat when the thermal quality of the habitat was high.

In the fall, it appeared that females were thermoconforming to all habitat types; however, their d_b and the d_e for each habitat type were high. That is, both habitat and turtle temperatures were far from T_{set} (not accurate), resulting in low (close to 0) efficiency values. Because both d_e and d_b were far from T_{set} , this suggests that the preferred temperature range for spotted turtles in fall may have shifted to a cooler temperature range. Seasonal shifts in thermoregulatory effort suggest that there are seasonal shifts in T_{set} (Huey and Slatkin, 1976; Hertz et al., 1993; Schauble and Grigg, 1998; Glanville and Seebacher, 2006). Similarly, milksnakes (*Lampropeltis triangulum*) were shown to thermoregulate most effectively in the spring and summer, and the least effectively in the fall when thermal quality of the habitat was very low (Row and Blouin-Demers, 2006).

4.4. Conclusions

Our study confirmed that the available habitat for the spotted turtles in the population we studied was thermally heterogeneous and that a large proportion of the habitat was of high thermal quality, especially the newly flooded zones that resulted from beaver activity. Spotted turtles were most likely thermoconforming to the new aquatic habitat during the summer season,

indicating a positive benefit for turtles as a result of the habitat change. Future experiments on spotted turtle thermoregulation should focus on seasonal changes in T_{set} and how these relate to specific behaviors such as nesting and hibernation. Understanding the seasonal changes in preferred temperatures will help to understand which habitats would be of higher thermal quality at different times during the active season. If optimal temperatures are available for turtles during all times of the year and nest site quality is acceptable (energy is put towards reproduction and growth rather than searching for preferable habitat or temperatures), then over time we may see a positive response in population size due to an increase in recruitment (Rasmussen and Litzgus, 2010b).

These results have important implications for conservation and management plans for this population and other freshwater turtle populations living in degraded habitats. This study showed how an increase in water levels caused by beaver dams introduced a variety of thermal opportunities that benefit a population of endangered turtles. Increasing the presence of water can increase biodiversity by providing habitat for new plant biota, attracting water fowl, and providing refuge for many aquatic organisms. This is important to consider because human impacts have decreased biodiversity worldwide. Because temperatures tend to fluctuate less in water than in air, the presence of water becomes more important when considering the effects of global climate change. The importance of maintaining and rehabilitating sustainable wetlands, especially by natural methods like beaver damming, could become an important tool in management plans for conservation and population recovery purposes.

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