The Effects of Sex and Season on Patterns of Thermoregulation in Blanding's Turtles (*Emydoidea blandingii*) in Ontario, Canada

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ABSTRACT. – When preparing management plans for species at risk, conservation practitioners need information on the habitat requirements of those species. In environmental extremes, the fitness of ectotherms is tightly linked to thermoregulation, as all physiological processes are temperature dependent. In an effort to better quantify the habitat requirements of Blanding's turtles (*Emydoidea blandingii*), a species at risk, at the northern extreme of their range, we quantified the thermoregulation patterns of adult males and gravid females during the active season. Turtles exploited their thermal environment significantly more in early season than in late season. Although basking allowed turtles to reach the highest daytime temperatures, surface water was the habitat with the highest thermal quality overall. Although not statistically significant, gravid females tended to maintain higher mean and maximum shell temperatures throughout the active season. Our results highlight the importance of stratifying field observations and thermoregulation data by reproductive classes and time. Differences in behavior and thermal habitat requirements between reproductive classes and season must be considered in management plans for conservation efforts to be effective.

KEY WORDS. – Reptilia; Testudines; thermal ecology; *Emydoidea blandingii*; indices of thermoregulation; basking behavior; Chelonia

Because all physiological processes are temperature dependent, variation in the body temperature (T_b) of ectotherms greatly affects their development, physiology, and behavior (Dawson 1975; Huey 1982; Peterson et al. 1993). Despite some physiological control of T_b (Weathers and White 1971; Seebacher and Franklin 2005), most ectotherms depend on behavioral thermoregulation to maintain T_b within a certain range permitting optimal performance (Cowles and Bogert 1944; Huey and Kingsolver 1989; Huey et al. 1989). The benefits of increased metabolic and physiological performance realized when T_b is maintained within the optimal range must be weighed against the loss of time and energy spent shuttling between microclimates and increased exposure to predators (i.e., basking behavior).

Huey and Slatkin (1976) predicted that ectotherms, in particular reptiles, should thermoregulate less precisely in low-quality environments, where temperatures are far from the optimal range, because of the high energetic costs associated with thermoregulation in such environments. However, recent studies have shown that reptiles invest more in thermoregulation in thermally challenging climates than in thermally benign climates, probably because the disadvantages of thermoconformity are much higher when the thermal quality of the environment is low (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Nadeau 2005; Row and Blouin-Demers 2006; Bulté and Blouin-Demers 2010; Picard et al. 2011).

We investigated patterns of thermoregulation in Blanding's turtles (*Emydoidea blandingii*) in Ontario, a

thermally challenging region near the northern extreme of the species' range. The Blanding's turtle is a semiaquatic freshwater turtle and is considered at risk in 17 of the 18 state/provincial jurisdictions across its range (NatureServe 2009). In Canada, Blanding's turtles are considered threatened, save for one population that is considered endangered, and their critical habitat must be identified (COSEWIC 2005). Because of the strong link between habitat use and thermoregulation in reptiles (Blouin-Demers and Weatherhead 2002), climatic differences throughout the global range of this species have the potential to impact critical habitat determination. Regional differences in Blanding's turtle habitat use are apparent (Rowe and Moll 1991; Hamernick 2000; Piepgras and Lang 2000; Edge et al. 2010; Millar and Blouin-Demers 2011) and some of the variation could be attributed to differences in climate.

In an effort to determine the thermally critical habitat of Blanding's turtles at the northern extreme of their global range, we had three objectives: 1) to describe turtle T_b and basking behavior, 2) to investigate how turtles respond to seasonal changes in temperature, and 3) to compare thermoregulation of males and gravid females throughout the active season.

Because past studies have demonstrated that ectotherms in thermally challenging climates invest more in thermoregulation (Blouin-Demers and Weatherhead 2001; Blouin-Demers and Nadeau 2005; Row and Blouin-Demers 2006), we expected Blanding's turtles in Ontario to bask regularly to elevate and maintain T_b above ambient temperatures. We also expected differences in thermoregulatory behavior among months. More specifically, the study area is temperate and therefore temperatures during spring and fall are considerably lower than in summer. Thus, we expected Blanding's turtles to invest more in thermoregulation in spring and fall than in summer, as thermal quality should be highest in summer.

Reproductive activities, including mate searching, courtship, and mating, occur in water in Blanding's turtles and are initiated by adult males (Baker and Gillingham 1983). Thus, reproductive activities can be in direct competition with thermoregulatory behaviors (e.g., aerial basking). Although Blanding's turtles do not have a welldefined mating season, 2 studies report a high number of copulations prior to and following overwintering (Newton and Herman 2009; Edge et al. 2010). Furthermore, the additional energetic requirements associated with follicular development and egg bearing in gravid females may lead to differing thermoregulatory strategies between adult males and gravid females (Congdon 1989; Lefevre and Brooks 1995; Sarkar et al. 1996). Accurate thermoregulation should entail high reproductive benefits for gravid females, especially at northern latitudes where the active season is short. Thus, identifying and protecting high-quality thermal habitats for gravid females may be essential for the long-term survival of Blanding's turtles at the northern extreme of their range. Given the potential reproductive benefits of elevating T_b by basking, many researchers have suggested that female turtles should exhibit more basking behavior than male turtles (Congdon 1989; Lefevre and Brooks 1995; Sarkar et al. 1996); however, results have been mixed (Hammond et al. 1988; Nutting and Graham 1993; Krawchuk and Brooks 1998; Chen and Lue 2008). Similarly, we expected gravid females to thermoregulate more accurately and to bask more often than males during follicular development and ovulation (May-June).

METHODS

Study Area. — We conducted this study from May to October 2008 on Grenadier Island (ca. 600 ha). Grenadier Island is located in the St. Lawrence River south of Mallorytown, Ontario, Canada. It is one of the largest islands in St. Lawrence Islands National Park and harbors several beaver ponds and wetlands that are used by Blanding's turtles. Our main study site was a marsh (ca. 28.4 ha) surrounded by a mixed deciduous forest.

Radiotelemetry and Data Collection. — We captured Blanding's turtles by hand, with dip-nets and in submerged hoop nets baited with canned sardines. We determined sex by plastron concavity, head and upper neck markings, and preanal tail length. We determined female reproductive status by palpation during the eggbearing period (May to early June). Blanding's turtles were fitted with temperature-sensitive radio-transmitters (Holohil SI-2FT 17 g, battery life of 36 mo). We bolted transmitters to the rear marginal scutes of the carapace using stainless steel screws, washers, and nuts. We used marine silicone to cover screws and transmitter edges, thus preventing detritus and macrophytes from catching on the transmitters. Transmitters (including screws, nuts, and silicone) represented at most 5% of the turtle's body mass and were removed at the end of the study.

Shell Temperature (T_s) . — We did not measure internal T_b of Blanding's turtles. Instead, we measured shell temperature (T_s) as others have done (Grayson and Dorcas 2004; Picard et al. 2011). In addition, Sajwaj and Lang (2000) have shown that external transmitter temperatures are highly correlated to internal T_b of submerged freshwater turtles; because of the high thermal conductivity of water, freshwater turtles are unable to maintain an important temperature differential with the water when submerged. Blanding's turtles in our study area spent more than 70% of their time underwater (Millar and Blouin-Demers 2011). It is important to note, however, that T_s is generally 5°–10°C higher than internal T_b when turtles are basking (Sajwaj and Lang 2000; Edwards and Blouin-Demers 2007).

The pulse rates of each temperature-sensitive transmitter attached to turtles were recorded up to 3 times per hour by 2 automated radiotelemetry data loggers (SRX 400, Lotek Engineering Inc, Newmarket, Ontario, Canada) strategically placed within the study area. Transmitter pulse rates were converted to temperatures by fitting a polynomial equation to the calibration points (provided by the manufacturer) for each transmitter.

Environmental Operative Temperatures (T_e) . — To describe accurately the variety of thermal microhabitats available to turtles throughout the study period, we placed small temperature data loggers (Thermochron iButton DS1921, Dallas Semiconductor, Sunnyvale, CA) at several locations in the study area. We attached 6 data loggers, in pairs, to an anchored buoyed rope positioned at 3 depths (surface, 0.5 m, and 1 m) in open water. In addition, we placed 4 data loggers at the surface of the water between mats of thick vegetation and 30 cm below mats of thick vegetation. Finally, we placed 4 iButton temperature data loggers centered inside 2 water-filled copper models attached to a fallen log. The copper models represent the range of temperatures available to a basking turtle (Shine and Kearney 2001; Edwards and Blouin-Demers 2007; Dubois et al. 2009).

Thermoregulatory Set-Point Range (T_{set}). — We did not measure T_{set} ; however, the published values for freshwater turtles at temperate latitudes indicate that T_{set} is a conserved trait (Nutting and Graham 1993). Therefore, we used the same estimate of T_{set} proposed by Picard et al. (2011). Picard et al. (2011) estimated T_{set} by using the mean 75% and 25% quartiles of the distribution of T_b selected by 7 species of temperate turtles placed in a thermal gradient (28.0° ± 0.8°C SE and $24.4^{\circ} \pm 1.0^{\circ}$ C SE; Gatten 1974; Graham and Hutchison 1979; Schuett and Gatten 1980; Williamson et al. 1989; Knight et al. 1990; Nebeker and Bury 2000; Edwards and Blouin-Demers 2007; Ben-Ezra et al. 2008).

Indices of Thermoregulation. — Using the indexes proposed by Hertz et al. (1993), we measured the accuracy of thermoregulation (d_b; mean absolute deviation of T_b from T_{set}) and the thermal quality of each habitat (de; mean absolute value of deviation of Te from T_{set}). As explained above, T_s was used as a substitute for T_b. Furthermore, we also measured the effectiveness of thermoregulation using the $d_e - d_b$ index proposed by Blouin-Demers and Weatherhead (2001). Finally, we calculated a modified version of the thermal exploitation index (Ex) proposed by Christian and Weavers (1996). This Ex represents the amount of time a reptile's T_b is within T_{set} when T_e indicates that T_{set} is available in the environment (i.e., ideal environmental conditions). Thus, we calculated Ex by determining the percentage of time T_{s} was within T_{set} when T_{set} was available using hourly means for each turtle.

Basking Behavior. — We defined the percentage of time spent basking as the percentage of time when T_s exceeded the maximum surface water temperature (S_{max} ; Bulté and Blouin-Demers 2010). We determined if a turtle was basking by calculating the difference between T_s and S_{max} for each hour of the day (Bulté and Blouin-Demers 2010). Positive values indicated that the turtle was basking and negative values indicated that the turtle was submerged.

Statistical Analyses. — We performed all statistical analyses with JMP version 8.0 (SAS Institute, Cary, NC) and R version 2.7.2 (R Development Core Team 2008). We report all means \pm SE and we considered tests significant at $\alpha = 0.05$. We transformed data as needed to meet assumptions of homogeneity of variance, normal distribution, and sphericity. When assumptions of variance could not be met by transformation, we report nonparametric test results.

RESULTS

We studied 19 turtles (13 males, 6 gravid females) from May to October 2008 and collected 117,369 T_s measurements. Due to incomplete environmental and turtle data for the months of May and October, we did not include these months in the main statistical analyses. Thus, we used data from 15 turtles (9 males, 6 gravid females) in 2-way repeated measures analyses of variance (ANOVAs) to test for the effects of month and reproductive class and their interaction on T_s , d_b , and $d_e - d_b$. We ran additional statistical analyses for T_s and d_b for 10 turtles (6 males, 4 gravid females) radio-tracked in May.

Environmental Operative Temperatures. — We collected 22,151 T_e measurements from the 6 thermal microhabitats: the copper model (n = 2857), surface water in thick mats of vegetation (n = 3858), surface

water in open water (n = 3860), 0.5 m below the surface in open water (n = 3860), 1 m below the surface in open water (n = 3858), and 0.5 m below the surface under thick mats of vegetation (n = 3858). Mean T_e never reached T_{set} in any given month, suggesting that the habitat of Blanding's turtles in Ontario is thermally challenging. In fact, water temperatures 1 m below the surface never reached T_{set} during the active season. This aquatic habitat, 1 m below the surface, was the most constant and had the coldest temperatures during the day. Although basking provided the highest daytime temperatures, surface water was the habitat with the highest thermal quality throughout the active season (Table 1).

Two 1-way Welch's ANOVAs assuming unequal variances revealed that month had a significant effect on T_e ($F_{3,399} = 97.24$, p < 0.0001) and d_e ($F_{3,388}$ 72.72, p < 0.0001). A Tukey-Kramer honestly significant difference test demonstrated that T_e values were highest in June and July and lowest in September (Fig. 1). Similarly, d_e values were lowest in June and July and highest in September (Fig. 2).

Patterns of Body Temperature. — A 2-way repeated measures ANOVA revealed that mean T_s varied significantly among months ($F_{3,39} = 252.23$, p < 0.0001), but not by reproductive class ($F_{1,13} = 2.08$, p = 0.173) from June to September. The interaction between the 2 terms was not significant ($F_{3,52} = 5.24$, p = 0.67). Bonferronicorrected contrasts revealed that mean T_s values were significantly higher in June and July than in later months and lowest in September (Fig. 1). In May, the average daily T_s tended to be higher for gravid females ($22.4^{\circ} \pm 0.8^{\circ}$ C SE) than for males ($21.0^{\circ} \pm 0.5^{\circ}$ C SE), although the difference was not significant (t₈ = 1.46, p = 0.18).

A 2-way repeated measures ANOVA revealed that mean daily maximum T_s also varied significantly among months $(F_{1.67,21.7} = 159.86, p < 0.0001)$ and marginally nonsignificantly among reproductive classes($F_{1,13} = 4.52$, p = 0.053) from June to September. The interaction between the 2 terms was not significant $(F_{1.67.24.7} = 0.616)$, p = 0.52). Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2_5 = 13.89$, p = 0.017), therefore we corrected degrees of freedom with the Huynh-Feldt estimate of sphericity ($\epsilon = 0.557$). Bonferroni-corrected contrasts revealed that maximum T_s was significantly higher in June (33.2° \pm 0.7°C SE) and July (31.1° \pm 0.5°C SE) than in any other month and lowest in September $(21.5^{\circ} \pm 0.3^{\circ}\text{C SE})$. Furthermore, gravid female max T_s was consistently higher than male max Ts throughout the study period. In May, the average daily maximum T_s tended to be higher for gravid females $(37.1^{\circ} \pm 1.3^{\circ}C \text{ SE})$ than for males $(33.8^{\circ} \pm 1.3^{\circ}C \text{ SE})$, although the difference was not significant ($t_8 = 1.66, p = 0.135$).

Hourly patterns of T_s plotted against T_e demonstrate that Blanding's turtles spent much less time with T_s within T_{set} than what was possible given environmental conditions, except in June (Fig. 2). In June, throughout a 24-hr period, Blanding's turtles were as warm as their

Table 1. Monthly averages (\pm SE) of the daily mean and daily maximum operative environmental temperatures (T_e) recorded in 4 habitats available to Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada. Also, the monthly mean (\pm SE) deviation of environmental temperatures from the preferred body temperature range (d_e) and the percentage of time where environmental temperatures are within the preferred body temperature range ($\% d_e = 0$) are reported.

Month/habitat	T _e		d _e	
	Mean	Maximum	Mean	% = 0
June				
Copper model Open, surface water Open, 0.5 m below ^a Open, 1 m below ^b	$\begin{array}{r} 24.53 \pm 0.78 \\ 23.93 \pm 0.17 \\ 22.97 \pm 0.14 \\ 18.32 \pm 0.07 \end{array}$	$\begin{array}{r} 36.4 \pm 1.26 \\ 26.73 \pm 0.58 \\ 24.8 \pm 0.45 \\ 18.43 \pm 0.24 \end{array}$	$\begin{array}{c} 6.03 \ \pm \ 0.21 \\ 1.63 \ \pm \ 0.11 \\ 1.89 \ \pm \ 0.11 \\ 6.08 \ \pm \ 0.07 \end{array}$	10.7 54.5 43.4 0.0
July				
Copper model Open, surface water Open, 0.5 m below ^a Open, 1 m below ^b	$\begin{array}{l} 25.91 \ \pm \ 0.37 \\ 24.52 \ \pm \ 0.13 \\ 22.42 \ \pm \ 0.05 \\ 19.21 \ \pm \ 0.01 \end{array}$	$\begin{array}{r} 39.32 \pm 1.00 \\ 27.89 \pm 0.40 \\ 23.48 \pm 0.17 \\ 19.24 \pm 0.06 \end{array}$	$\begin{array}{l} 5.70 \ \pm \ 0.19 \\ 1.07 \ \pm \ 0.06 \\ 2.01 \ \pm \ 0.05 \\ 5.19 \ \pm \ 0.01 \end{array}$	21.6 48.2 7.6 0.0
August				
Copper model Open, surface water Open, 0.5 m below ^a Open, 1 m below ^b	$\begin{array}{l} 24.05 \pm 0.47 \\ 23.07 \pm 0.13 \\ 20.64 \pm 0.04 \\ 18.58 \pm 0.02 \end{array}$	$\begin{array}{r} 40.65 \pm 1.05 \\ 27.02 \pm 0.38 \\ 21.45 \pm 0.13 \\ 18.61 \pm 0.06 \end{array}$	$\begin{array}{r} 6.73 \ \pm \ 0.22 \\ 1.96 \ \pm \ 0.09 \\ 3.76 \ \pm \ 0.04 \\ 5.82 \ \pm \ 0.02 \end{array}$	12.0 30.5 0.0 0.0
September				
Copper model Open, surface water Open, 0.5 m below ^a Open, 1 m below ^b	$\begin{array}{l} 19.25 \pm 0.32 \\ 19.60 \pm 0.17 \\ 18.17 \pm 0.38 \\ 17.26 \pm 0.05 \end{array}$	$\begin{array}{r} 35.53 \pm 1.29 \\ 22.56 \pm 0.64 \\ 19.17 \pm 0.38 \\ 17.35 \pm 0.17 \end{array}$	$\begin{array}{l} 8.17 \pm 0.18 \\ 4.98 \pm 0.15 \\ 6.23 \pm 0.11 \\ 7.14 \pm 0.05 \end{array}$	13.9 7.1 0.0 0.0

^a Similar to temperatures recorded in surface water surrounded by thick mats of vegetation

 $^{\rm b}$ Similar to temperatures recorded below thick mats of vegetation, approximately 0.5 m from the surface.

environment permitted without significantly surpassing the upper limit of T_{set} . In July and August, thermal optima were only reached during the day despite environmental temperatures within T_{set} being available at night. In September, however, turtles did not seek to maintain T_s within T_{set} when T_{set} was accessible, suggesting thermoconformity.

A 2-sample Kolmogorov-Smirnov test confirmed that the distribution of mean monthly hourly T_e, when all habitats are included in the analysis, was significantly different from the distribution of mean monthly hourly T_s (D = 0.338, p < 0.0001; Fig. 3). T_s fell within the range of T_{set} 19.1% of the time whereas T_e fell within this range only 5.8% of the time. Blanding's turtles avoided low temperatures and maintained temperatures above the mean T_e .

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Indices of Thermoregulation. — A 2-way repeated measures ANOVA revealed that d_b varied significantly among months ($F_{3,39} = 286.5$, p < 0.0001) but not by reproductive class ($F_{1,13} = 0.141$, p = 0.71). The interaction between the 2 terms was not significant ($F_{3,52} = 0.874$, p = 0.46). Bonferroni-corrected contrasts revealed that d_b was significantly greater in September than in any other month. In May, the average d_b of gravid females ($3.5^{\circ} \pm 1.2^{\circ}$ C SE) was less than that of males



Figure 1. Mean shell temperature ($T_s \pm 1$ SE) of gravid female ($n = 6, \bullet$) and male ($n = 9, \bullet$) Blanding's turtles (*Emydoidea blandingii*) and mean environmental temperatures ($T_e \pm 1$ SE, \bigcirc) throughout the active season in Ontario, Canada.



Figure 2. Maximum and minimum mean hourly environmental temperatures (\bigcirc) and hourly mean shell temperature of gravid female ($n = 6, \bullet$) and male ($n = 9, \blacksquare$) Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada, from June to September. The preferred body temperature range is represented by the horizontal lines.



Figure 3. Frequency distributions of the monthly hourly mean operative environmental temperatures (T_e) and the monthly hourly mean shell temperatures (T_s) of 15 Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada, from June to September. The range of preferred body temperatures (T_{set}) is shaded.

 $(4.1^{\circ} \pm 1.2^{\circ}\text{C SE})$, however the difference was not significant (t₈ = 0.82, p = 0.43).

A 2-way repeated measures ANOVA revealed that $d_e - d_b$ varied significantly among months ($F_{3,39} = 20.08$, p < 0.0001), but not by reproductive class ($F_{1,13} = 0.141$, p = 0.71; Fig. 4). The interaction between the 2 terms was not significant ($F_{3,52} = 0.874$, p = 0.46). Thermoregulatory effectiveness peaked in August and was significantly lower in September than in any other month. Furthermore, gravid females tended to have higher thermoregulation effectiveness ($4.2^{\circ} \pm 1.2^{\circ}C$ SE) than males ($3.5^{\circ} \pm 1.2^{\circ}C$ SE) in May, however this difference was not significant ($F_{1,14} = 0.82$, p = 0.43).

The Ex averaged across all individuals throughout the active season was $19.3\% \pm 1.4\%$ SE. The proportion of time T_s was above T_{set} was $12.8\% \pm 1.4\%$ SE and the proportion of time T_s was below T_{set} was $68.1\% \pm 2.6\%$ SE. A 2-way repeated measures ANOVA revealed that Ex was significantly different among months ($F_{2.5,31.9} = 62.12$, p < 0.0001) but not between reproductive classes ($F_{1,13} = 0.46$, p = 0.51; Fig. 5). The interaction between the 2 terms was not significant ($F_{2.5,40.6} = 0.77$, p = 0.49). Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2_5 = 11.62$, p = 0.041), therefore we corrected degrees of freedom using the Huynh-Feldt estimate of sphericity ($\varepsilon = 0.819$). Bonferroni-corrected contrasts revealed that monthly Ex values were significantly higher in June and July and lower in September.

Basking Behavior. — A 2-way repeated measures ANOVA revealed that the percentage of time spent basking varied significantly among months ($F_{3,39} = 16.00$,



Figure 4. Monthly mean $(\pm SE)$ absolute deviations of operative temperatures from the preferred body temperature range (d_e, \bigcirc) , deviations of field shell temperatures from the preferred body temperature range $(d_b, dashed line)$, and thermoregulation effectiveness $(d_e - d_b, solid line)$ for male (\blacksquare) and gravid female (\bullet) Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada.

p < 0.0001), but not by reproductive class ($F_{1,13} = 1.31$, p = 0.27; Fig. 6). The interaction between the 2 terms was not significant ($F_{3,52} = 0.353$, p = 0.79). The percentage of time spent basking decreased as the active season progressed with the highest mean percentage of basking in June and the lowest in September. Although the difference was not significant, gravid females tended to spend more time basking than males throughout the active season (gravid female: $40.0\% \pm 4.5\%$ SE, male: $33.3\% \pm 3.7\%$ SE).

Figure 5. Mean (\pm SE) thermal exploitation index [percent time spent with shell temperatures within (white), above (gray), or below (black) the preferred body temperature range when the preferred body temperature range is available] for male (\circ) and gravid female (φ_g) Blanding's turtles in Ontario, Canada.

DISCUSSION

Environmental Operative Temperatures. — Blanding's turtles in Ontario inhabit a thermally challenging and dynamic environment. Environmental temperatures were rarely within the optimal range and the quality of thermal microhabitats varied seasonally. During the early (May–June) and late portions (September–October) of the active season, turtles had to actively thermoregulate by basking at the water's surface or basking on floating vegetation or on logs during the day to reach optimal T_b . During the midsummer months (July and August), however, thermal quality peaked and, on average, turtles had the possibility of maintaining optimal temperatures for most of the day and night.

Surface water provided the most consistent highquality thermal habitat for Blanding's turtles from June until the end of August. Blanding's turtles were often found at the surface of the water during these months

Figure 6. Monthly mean $(\pm SE)$ percentage of time spent basking $(\%T_s > S_{max})$ for gravid female $(n = 6, \bullet)$ and male $(n = 9, \bullet)$ adult Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada.

(Millar and Blouin-Demers 2011). Hartwig and Kiviat (2007) proposed that Blanding's turtles may conserve energy by simultaneously basking and foraging while in the neuston. Furthermore, the neuston may effectively hide Blanding's turtles (Ross and Lovich 1992; Hartwig and Kiviat 2007), thereby reducing the predatory costs associated with basking.

Patterns of Thermoregulation. — Similar to past studies on turtles at the northern edge of their range (Edwards and Blouin-Demers 2007; Bulté and Blouin-Demers 2010), we observed important seasonal variations in T_s , d_b , $d_e - d_b$, and Ex. The highest T_s , $d_e - d_b$, and Ex and the lowest d_b were recorded during the summer months (June–August). Our results are unsurprising, as the thermal quality of the environment peaked during these months. In snakes, when thermal quality is high, d_b is typically low and the percentage of time T_b is within T_{set} is high (Blouin-Demers and Weatherhead 2001).

Interestingly, from late June to August, turtles were able to maintain relatively high T_s without aerial basking. Sajwaj and Lang (2000) observed that the proportion of thermoregulating Blanding's turtles on sunny days dropped from > 90% in April and May to 33% in July and August. Similar to Sajwaj and Lang (2000), as the active season progressed, our turtles spent more time underwater and less time basking (Millar and Blouin-Demers 2011). Bulté and Blouin-Demers (2010) demonstrated that the maximal daily thermal gain associated with aerial basking decreases substantially as the active season progresses. As water temperatures increase, the thermoregulatory constraints decrease and individuals are free to spend more time performing other important activities, such as foraging.

Beginning in September, turtles stopped exploiting their thermal environment. Sajwaj and Lang (2000) observed a similar behavior in Minnesota: thermoconforming T_b patterns increased from ca. 10% in April–August to ca. 20%–40% in September–October. This thermoconformity toward the end of the active season could be indicative of entrance into hibernation.

Blanding's turtles exploited their thermal environment similarly to northern map turtles (Graptemys geographica) in Ontario (Bulté and Blouin-Demers 2010). Despite inhabiting the same region, however, Blanding's turtles exploited their thermal habitat less than eastern musk (Sternotherus odoratus) and painted turtles (Chrysemys picta) in Ontario (Edwards and Blouin-Demers 2007; Picard et al. 2011). Blanding's turtles and adult female northern map turtles (Bulté and Blouin-Demers 2010) are much larger than adult eastern musk and painted turtles. Because thermal inertia increases with body size, larger ectotherms have a more restricted range of possible daily T_b (Stevenson 1985). In a study by Bulté and Blouin-Demers (2010) on northern map turtles, larger turtles were not able to thermoregulate as accurately as smaller turtles, despite spending more time basking. They suggested that body size limits the rate of heating and the maximum daily T_b , which in turn affects the ability of larger turtles to reach T_{set} .

Sex Differences. — Various studies on aquatic turtles have attempted to identify sex differences in thermoregulation; however, results from these studies have been mixed (Nutting and Graham 1993; Krawchuk and Brooks 1998; Lefevre and Brooks 1998; Sajwaj and Lang 2000). Similar to observations by Sajwaj and Lang (2000), the effect of reproductive class on thermoregulation in Blanding's turtles was not significant. Unlike the results from Sajwaj and Lang (2000), however, mean and maximal T_s of gravid females were consistently higher than male T_s throughout the active season.

In a parallel study on the spatial ecology of this population of Blanding's turtles, gravid females were found to have significantly different movement patterns, home range sizes, and behavior than males and nongravid females (Millar and Blouin-Demers 2011). Concomitant to the results from our study, where gravid females on average spent a greater percentage of time basking than males, gravid females were also observed basking significantly more often than males (Millar and Blouin-Demers 2011). Furthermore, basking behavior was greatest in May, decreasing progressively thereafter. This pattern may be accounted for by the increased energy requirements during the early active season associated with egg development in adult females and the additional energetic costs associated with preparing for mating in adult males (Krawchuk and Brooks 1998).

In a study on the yellow-margined box turtle (Cuora flavomarginata), Chen and Lue (2008) found evidence that gravid females maintained significantly higher shell temperatures during the nesting season (May to July). Following the nesting season, however, there were no significant differences in shell temperatures between males and females (Chen and Lue 2008). Bulté and Blouin-Demers (2010) and Carrière et al. (2008) also found that gravid female northern map turtles and painted turtles spent more time basking than males prior to and during the nesting season (May and June). Interestingly, Nutting and Graham (1993) also found that female nongravid Blanding's turtles selected significantly higher temperatures (24.8°C; p < 0.05) than males (22.5°C) in a laboratory aquatic thermal gradient. Although this pattern was based on only 4 individuals, Nutting and Graham (1993) proposed that these observed differences in preferred mean $T_{\rm b}$ may be due to the higher energy investment required of females for the preparation of ovarian follicles for the next reproductive year.

Methodological Considerations. — Similar to Grayson and Dorcas (2004) and Picard et al. (2011), T_b was estimated using external temperature-sensitive radiotransmitters. Previous studies have shown that although internal and carapace temperatures are highly correlated (Sajwaj and Lang 2000; Edwards and Blouin-Demers 2007), there are significant differences between the 2 measurements. Generally, the internal T_b of basking turtles is overestimated when using externally mounted radio-transmitters. In addition, thermal inertia could also be responsible for differences between internally and externally recorded temperatures.

Conservation Implications. - To the best of our knowledge, this is the first study in which quantitative indices of thermoregulation have been applied to Blanding's turtles. Our results suggest that the thermal habitat requirements of gravid female and male Blanding's turtles differ among months. Specifically, identifying and protecting high-quality thermal habitats for gravid females during follicular development and egg bearing may be essential for the long-term survival of Blanding turtle populations located at the northern extreme of their global range. More generally, management plans should take into account the effects of season and reproductive class on thermal habitat use of Blanding's turtles. The information collected during this study represents an important step toward better characterization of the thermal habitat of Blanding's turtles and can help in the determination of critical habitat.

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