Thermal ecology of Blanding's Turtles (*Emydoidea blandingii*) on Grenadier Island: the influence of thermal quality of the environment on habitat selection

by

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Abstract

The numerous biological and physiological life processes that underlie an organism's basic functioning are dependent on temperature. Also, behaviours dictated by the thermal quality of an environment play a large role in the repertoire of day to day reptilian activities. Blanding's turtles (*Emydoidea blandingii*), a species of freshwater turtle, inhabit a thermally challenging environment. They are found in the northern states of the U.S.A., and within the Great Lakes region and south-west Nova Scotia in Canada. This study aims to study the thermoregulatory behaviours of a population of Blanding's turtles found on Grenadier Island in the St. Lawrence River. Twenty two turtles in this population were monitored from May to October 2008 using temperature sensitive radiotransmitters. Since this species is found in a thermally challenging environment, I expected that the thermal quality of the environment plays a largely influential role in habitat selection. In this study I use turtle body temperatures (T_b), and operative environmental temperatures (T_e) measured in the field along with the preferred range of body temperatures (T_{set}) to calculate several indices of thermoregulation. The accuracy of T_bs (d_b), the thermal quality of the environment (d_e), the effectiveness of thermoregulation ($d_e - d_b$), and the thermal exploitation index (Ex) were all assessed. Using these indices, it can be seen that the overall quality of the environment is thermally challenging; at no point in the active season does the environment as a whole offer temperatures within T_{set}, however during the warm months, selected few thermal microhabitats allow T_{set} to be attained. We see that the Blanding's turtles use their environment in a non-random manner and are relatively effective thermoregulators from May to August, choosing either aerial basking or surface water positions. By September and October, when the environment ceases to offer T_{set} temperatures Blanding's turtles' thermoregulatory strategy shifts to a more thermoconforming one. By looking at the exploitation

index it was determined that whenever the environment offers T_{set} values, Blanding's show a high amount of thermal exploitation, suggesting Blanding's behaviours and microhabitat selection are highly dictated by the thermal quality of their environment.

Introduction

It is commonly agreed upon that the numerous biological and physiological life processes that underlie an organism's basic functioning are dependent on temperature (Seebacher, 2005; Dubois, Blouin-Demers, and Thomas, 2008; Seebacher and Franklin, 2005). Furthermore, it is well accepted that behaviours dictated by the thermal quality of an environment play a large role in the repertoire of day to day reptilian activities. However, what is not as well understood is the extent in which individual species behaviourally thermoregulate. Not all *Reptilia* spend the same amount of time, energy, and effort actively thermoregulating and searching out thermally favourable environments. In fact, a spectrum of behaviours can be seen by all major groups of reptiles incorporating behaviours from both ends of a continuum of thermoconforming and thermoregulating behaviours in an attempt to decrease overall costs and produce the optimal strategy (Seebacher, 2005). Amongst the variety of thermoregulatory behaviours a large range of variation can be seen, from adult leatherback sea turtles (*Dermochelys coriacea*) that do not normally thermoregulate by selectively exploiting their thermal environment (Bostrom and Jones, 2007) to painted turtles (*Chrysemys picta*) that are well known to regularly thermoregulate across their distribution, exploiting their environment through such means as basking and strategically moving between microhabitats of varying temperatures (Krawchuk and Brooks, 1998).

This study focuses on the thermal ecology of a freshwater temperate turtle, the Blanding's turtle (*Emydoidea blandingii*). Blanding's turtles are distributed in Canada's southern Great Lakes and St. Lawrence region, Nova-Scotia, and the northern U.S.A., a range considered to be thermally challenging (Schofield *et al.*, 2009). As environments become more and more thermally constraining and thermally dynamic, due to latitudinal and altitudinal extremes, it becomes increasingly important for individuals to actively thermoregulate to maintain day to day physiological processes (Schofield *et al.*, 2009). It is due to the temperature dependence of physiological processes along with the thermally challenging nature of Blanding's turtles' range that I expect to see a strong link between thermoregulatory behaviour and habitat selection.

When trying to describe and quantify an individual's thermoregulatory behaviour there is no single question that can fully address the topic. Instead, it is more appropriate to ask a series of questions to more thoroughly understand how an individual behaviourally thermoregulates (Hertz, *et al.*, 1993). Hertz, *et al.* (1993) first came up with a set of quantitative indices to look at the precision and accuracy of body temperatures, as well as the effectiveness of thermoregulation. These three indices take into account the set of observed body temperatures (T_b) of the organism of interest, the range of temperatures available to individuals in the field (operative environmental temperatures, or 'null distribution of T_bs', T_e), and lastly the preferred range of temperatures (thermoregulatory set-point range, T_{set}). The first term defined by Hertz, *et al.* (1993) describes the accuracy of thermoregulation, how closely T_b values are maintained within the bounds of T_{set}; accuracy is represented as the absolute values of deviation of T_b values from the bounds of T_{set} and is denoted as d_b. If a turtle maintains its T_b within T_{set} at all times, then d_b would equal 0, and it can be said that the accuracy of temperature maintenance is high. High accuracy does not necessarily imply active regulation and no inference as to behaviours themselves can be made solely based on d_b. The next term described by Hertz, *et al.* (1993) describes the thermal quality of the habitat and how suitable the habitat is based on the organism of interest's thermal requirements. The thermal quality of the environment denoted by d_e is calculated as the absolute values of deviation of T_e values from the bounds of T_{set}. A d_e of zero indicates a temperature which falls within T_{set} and is thermally ideal for the organism of interest. Using these two indices, Hertz, *et al.* (1993) proposed a third index, the effectiveness index (E), in an attempt to give further insight into the thermoregulatory behaviour of the organism. This index has since been critiqued and a new method of calculating the effectiveness of thermoregulation has been proposed by Blouin-Demers and Weatherhead (2001). This new effectiveness index ($d_e - d_b$) uses the difference between d_e and d_b to describe the extent to which individuals depart from perfect thermoconformity. Perfect thermoconformers are individuals that do not select specific microhabitats based on the thermal quality and will have a $d_e - d_b$ value of zero. If individuals actively avoid microhabitats of superior thermal quality $d_e - d_b$ will be a negative value. Lastly, positive values of $d_e - d_b$ indicate some degree of thermoregulation. Larger positive values indicate a greater departure from thermoconformity.

Furthering the indices of Hertz, *et al.* (1993), Christian and Weavers (1996) introduce another quantitative thermal index known as thermal exploitation (Ex). The thermal exploitation index looks at the proportion of time that turtle T_bs fall within T_{set} with respect to the amount of time the environment allows for T_{set} temperatures to be attained. Therefore this index looks at the extent to which individuals exploit their environment when their environment offers ideal conditions.

In this study I will be using the above mentioned indices to provide a detailed assessment and description of the thermoregulatory behaviour of a population of Blanding's turtles in order to describe the link between Blanding's turtles' thermal environment and habitat selection. Based on Blanding's turtles' natural history and considering their distribution, I expect to see clear indication of active thermoregulation, as well as a high degree of exploitation when ideal temperatures are available. Due to the thermally dynamic and challenging nature of the environment in which Blanding's turtles are found, overall I expect to see a large amount of behavioural regulation of temperature and consequently preferential selection of thermally optimal environments. Additionally, due to the large seasonal variation in temperatures present in Blanding's turtles' northern range, I expect to observe increased behavioural regulation of temperature earlier and later on in the active season (May and October) when environmental temperatures are less favourable. Furthermore, I will take a preliminary look to see if, in a natural setting, there are basic differences in thermoregulatory behaviour between males and females, and between gravid and non-gravid females. Previous studies have suggested that a difference does exist (Nutting and Graham, 1993, and Sajwaj and Lang, 2000); however, these studies are limited and lack an adequate sample size.

Methods

Study Site and Population

All data for this study were collected between May and October of 2008 during Blanding's turtles' active season. The population used for data collection is found in St. Lawrence Islands National Park in the central swamp on Grenadier Island, located just south of Mallorytown, ON. Being located in a national park, this site is protected under the Canada National Parks Act, and provides an idealistic population of turtles in a natural environment with minimal anthropogenic disruption. The study site encompasses an area of approximately 28.4 ha. The sample population consists of adult males (n = 13; mean carapace length = 23.1 ± 1.1 SD; mean mass = 1580.4 ±

227.3 SD), gravid adult females (*n* = 6; mean carapace length = 21.8 ± 1.0 SD; mean mass = 1432.5 ± 154.7 SD), and non-gravid adult females (*n* = 3; mean carapace length = 21.8 ± 1.0 SD; mean mass = 1303.3 ± 310.6 SD).

Turtle body temperatures (T_b) and radiotelemetry techniques

The turtles used in this study were captured during the months of May and June either by hand or by using a hoop net trap baited with sardines. GPS points were taken at the site of capture, and the turtles were taken back to a Parks Canada laboratory for processing. At this point, both quantitative and qualitative observations, including weight, carapace dimensions, and overall physical health were recorded. Each individual turtle was given a unique identity code by drilling small holes into the marginal scutes of the carapace. Turtles were subsequently fitted with an external temperature sensitive radiotransmitter (model SI-2FT manufactured by Holohil Systems Ltd.), 50mm long by an 11mm radius, and weighing approximately 17g, to the posterior end of the carapace. Although the accuracy of using externally fitted transmitters to estimate internal T_b was not assessed in this study, the use of externally attached transmitters has been used in many cases of highly aquatic turtles before in which their reliability as a means of estimation has been assessed (Grayson and Dorcas, 2004). Transmitters were first painted fluorescent orange (and additionally a white triangle was painted on the center of the carapace) to facilitate locating turtles in the field during the study season. Next, the transmitters were attached to the marginal scutes by two stainless steel nuts and bolts to minimize transmitter loss, and any gaps between the transmitter and the shell were filled with a silicone sealant to avoid the accumulation of debris.

Following the lab processing, the turtles were returned to the GPS point at which they were captured. The turtles usually only remained in the lab overnight before being returned to the field. Once returned to the field, the turtle temperatures were recorded by two automated radiotelemetry data logger towers (Lotek Wireless Inc.) placed within the swamp. The rate of transmitter signal emission was automatically recorded and stored. Recordings for each turtle were taken up to three times per hour, depending on the location of the turtle to the data logging towers. The transmitter rates were subsequently converted to temperature values by using the transmitter calibration points provided by Holohil Systems Ltd. to produce a polynomial standard curve for each transmitter. Using the equations of the standard curves, derived using JMP8 software, all recorded rates were converted to temperatures.

At the end of the field season, the turtles were brought back to the lab, transmitters were removed and the turtles were returned to the field to the same location they were caught.

Quantifying Environmental Operative Temperatures (T_e)

To provide a survey of the environmental operative temperatures (T_es) available to the turtles in the field, small temperature data loggers, iButtons (Maxim Integrated Products) were placed in the field in the following locations: in open water at the surface (n = 1), 0.5 m below the surface (n = 1), and 1 m below the surface (n = 1), in surface water found on the bog mat (n = 1), under the bog (n = 1), and within a large copper model (n = 1), mimicking a basking turtle. The choice of sampling sites, or thermal microhabitats, encompasses all locations available to the turtles in their habitat and selects thermal microhabitats based on considerations such as the medium (i.e. water or air), water depth, and amount of solar radiation available. The copper model was filled with water and the iButton was placed within the model. Although the accuracy and efficiency of the copper model to represent actual basking turtle temperatures was not assessed in this study in particular, many past studies have used similar models to represent basking temperatures of ectotherms, and have also assessed the use of these tools of estimation to be valid (Edwards and Blouin-Demers, 2007, Dubois, *et al.*, 2009, and Shine and Kearney, 2001).

Thermoregulatory set-point range (T_{set})

Since no previous laboratory study has been done to determine the thermoregulatory set-point range (T_{set}) of Blanding's turtles in particular, this value has been approximated by surveying primary literature and calculating a T_{set} value from all primary literature values determined in a laboratory setting for temperate freshwater turtles that had a sample size of 10 individuals or greater. This approximation for T_{set} was calculated by Gabriel Picard (2008) and no new values were discovered and added since this original compilation of literature values was produced. Picard used the mean bounds of the central 50% of the distributions (i.e. from the 25th to 75th quartile) of temperatures from each past case and used the average over all cases to approximate the range of temperatures of T_{set}. The T_{set} range was estimated to be between 24.4 ± 0.98^{o}C and 28.02 ± 0.78^{o}C. A full list of primary data sources used in calculating this estimate is found in 'Annex I' of this paper.

Indices of Thermoregulation

A more thorough explanation of the indices of thermoregulation may be found in the introduction and in Table 1.

d_b – mean d_b values were calculated for each month and for day time (06h00 to 17h59) and night time (18h00 to 05h59) hours. Individual deviations were calculated for each individual temperature data point. If T_b temperatures were greater than the maximal bound of T_{set} (28.02 ^{o}C), $d_b = T_b - 28.02$, if T_b fell within Tset, d_b was assigned a value of 0, and if T_b temperatures were below the lower bound of T_{set} (24.4 ^{o}C), d_b = 24.4 - T_b. Following the individual d_b calculations, the values were grouped and averaged first for individual hours of the day, each month and then these values were averaged over the appropriate criteria (i.e. May day time average d_b, May overall average d_b, etc.).

d_e – mean d_e values were calculated for each month and for day time (06h00 to 17h59) and night time (18h00 to 05h59) hours. Individual deviations were calculated for each individual temperature data point. If T_e temperatures were greater than the maximal bound of T_{set} (28.02 ^{o}C), d_e = T_e - 28.02, if T_e fell within Tset, d_e was assigned a value of 0, and if T_e temperatures were below the lower bound of T_{set} (24.4 ^{o}C), d_e = 24.4 - T_e. Following the individual d_e calculations, the values were grouped and averaged first for individual hours of the day, each month, and then these values were averaged over the appropriate criteria (i.e. month/time of day) for each of the six thermal microhabitats (see 'Quantifying Environmental Operative Temperatures' above). Averages were first obtained for individual microhabitats due to the fact that uneven numbers of data points were recorded for each separate microhabitat, and to therefore control for this variable arbitrarily altering the final d_e value. The six microhabitat values were then averaged within the month/time of day category.

In calculating d_e values in this manner, I must assume that each unique microhabitat quantified in the field is equally accessible to the turtles and the turtles can freely move from one microhabitat to the next with negligible costs. I concede that the assumption that all microhabitats are equally spatially (relative dimensions) available is unrealistic, however, due to the following three reasons I have chosen to make this assumption: 1) surface area (i.e. in the case of the aerial basking microhabitat) and volume (i.e. in the case of water temperatures) cannot be directly compared mathematically, 2) after qualitative observation one microhabitat does not appear to dominate the range, and 3) all microhabitats are within close proximity to each other, facilitating ease of movement between them.

d_e - d_b – d_e– d_b values were calculated for each month overall, and for day time (06h00 to 17h59) and night time (18h00 to 05h59) hours by using the appropriate d_e and d_b values previously calculated and determining the difference between these two values.

Ex – The thermal exploitation index (Ex) was obtained by superimposing plots of T_b, T_e, and the range of T_{set} across a day. Sets of data points were connected in a linear fashion and the amount of time T_b fell within the range of T_{set} as well as the amount of time that at least one of the six thermal microhabitats provided a temperature above the lower limit of T_{set} was extrapolated from the plots (Fig. 2). The extrapolation of these time values for each individual turtle was done using Excel. The percentage of time T_b was within T_{set} to the time T_{set} was available was then calculated to give the Ex value. The values used for T_b were obtained by calculating hourly averages of all data points available per individual turtle and for all turtles (as appropriate for the corresponding calculation and analyses), and the environmental temperatures were calculated in a similar manner for each individual thermal microhabitat. A separate plot and Ex calculation was performed for each individual month.

Data Analyses

Before any data analyses or calculations were performed on the field data, T_b outliers were removed. Data points were considered to be outliers if they fell into one or more of the following categories, temperatures greater than 55 ^{o}C, a single data point showing a large (>10^{o}C) jump while all other points before and after show steady values, or unrealistic values when considering the time of day (i.e. 40^{o}C recorded at 1:00am). The 55^{o}C cut off was chosen after determining the maximal recorded temperature of the full-sun basking model to be 50^{o}C at the centre of the model; although an internal T_b of such an extreme would be lethal to the turtles, these values were kept in the data in the slight chance that the *externally* fixed transmitters may have briefly reached this temperature. Ultimately, the final decision for removing outliers was decided with the following philosophy in mind: "When unsure, keep the data point in the data set." Data analyses and calculations were performed using either JMP8 or Microsoft Excel 2007.

Results

Data Collection

Throughout the field season, a total of 117369 T_b measurements were collected from the 22 turtles sampled (see Methods, 'Study Site and Population' for details). A total of 22151 T_e measurements were collected from the six thermal microhabitats, the basking copper model (n = 2857), the bog surface (n = 3858), open water surface (n = 3860), open water 0.5 m below surface (n = 3860), open water 1 m below surface (n = 3858), and under the bog (n = 3858). It should be noted that T_b values for May were only recorded starting on May 22, and thus month averages will be warmer than if an entire month of data collection was done. Similarly, October T_bs were recorded until October 15, and month averages will theoretically be warmer than if the entire month data was collected. T_e measurements were recorded for every month in its entirety except for May, in which recordings began on the 22nd and therefore month averages will be warmer than if recordings were taken throughout the month.

Indices of Thermoregulation:

Table 1 provides a summary of the indices used in this study as well as a list of the abbreviations used within this paper.

Accuracy of Thermoregulation (d_b)

The accuracy of thermoregulation values of the entire population of Blanding's turtles are summarized in Table 2. It is worth noting that a smaller d_b value is actually indicative of a more accurate (smaller deviation from T_{set}) temperature. The overall trend in the accuracy of T_bs follows the same trend as the thermal quality of the environment (Fig. 1), starting off being less accurate (higher d_b values) and becoming more accurate towards mid-season when the environment is most favourable, until finally, as the cold season approaches, the accuracy of thermoregulation decreases once again. During each month, mean d_b values were always below d_e values suggesting that the turtles always maintained T_bs closer to T_{set} than the mean T_e range, with random microhabitat selection, allowed. Furthermore, it can be noted that for the start of the field season (May) and the later months of the season (August-October) day-time T_bs are more closely maintained to T_{set} than at night-time, while during June and July, when correspondingly the thermal quality of the environment is more favourable, night-time T_bs are closer to T_{set}.

Thermal Quality of the Habitat (d_e)

The thermal quality of the habit values are summarized in Table 2. The quality of the habitat increases over the season until it reaches its highest quality during the month of July. In July, T_e values on average only fall 3.42 ^{o}C from T_{set} range. From this maximal habitat quality, the quality steadily drops reaching its most unfavourable point by the end of the field season in October, when T_e values on average fall 13.20 ^{o}C outside of the T_{set} range. The mean hourly temperatures provided by each thermal microhabitat each month is provided in Fig. 2, while the quality of individual thermal microhabitats is summarized in Table 4.

In the month of July it is interesting to note that the majority of the time the basking model temperatures either fall above or below the T_{set} range. While the aerial basking does not provide an ideal microhabitat for optimal temperature maintenance during July, the surface water provides T_{set} temperatures over a broad time period during the day and it can be seen that mean T_bs almost perfectly match the T_e values for the surface of the open water microhabitat.

Effectiveness Index (d_e - d_b)

The effectiveness index calculations are summarized in Table 2. The turtles' effectiveness is highest at the beginning and end of the season, showing lower values in the warmer months of the active season and dropping down to the lowest value in September.

Thermal Exploitation (Ex)

The thermal exploitation indices for each month for the entire population of turtles are summarized in Table 3. Table 3 demonstrates the mean hourly T_e profiles for each thermal microhabitat each month, along with the mean hourly T_b values for each month. From both Table 3 and Figure 2 it can be seen that Blanding's turtles readily exploit the thermal environment when the opportunity to obtain T_{set} is available to them.

It can also be seen that during the colder months that still allow a narrow window of time during the day to maintain T_bs within T_{set} (i.e. May and August) the most favourable thermal microhabitats which provide T_{set} range temperatures are the aerial basking option and at the surface of open water. During June and July the bog surface water also provides a narrow time period in which T_{set} temperatures are available to be exploited. The Ex values for September and October (0) are not surprising and simply verifies the fact that the environment constrains any possibility for turtles to obtain T_bs within T_{set}.

A one-way ANOVA comparing individuals' Ex values, revealed that month did not have a significant effect ($F = 1.0250$, $p = 0.3867$). The extent to which the turtles exploit the environment and the corresponding strategy does not change significantly across the active season. The months of September and October were not included in this analysis as the environment never provided the opportunity to attain T_{set} temperatures and thus Ex by definition was undefined for these months (interpreted as 'zero' exploitation).

Comparing Group Means

Turtles were grouped into the following groups to look for intra-species variation in temperature regulation strategies: males, non-gravid females, and gravid females. Certain categories of data were lacking in sample size, especially non-gravid females, while other individuals had incomplete data for certain months. Due to these 'holes' in the data set, the data used for statistical analyses was limited in size. The assumption of sphericity required to validate the use of a univariate repeated measure ANOVA approach was not met (Mauchly's Sphericity Test result yields $p = 0.0413$). Therefore a second approach using a MANOVA was used. The results of the MANOVA analysis revealed that month had a significant effect on T_bs ($F = 82.3352$, $p = <0.0001$). However, reproductive groups ($F = 1.4185$, $p = 0.2831$) and the interaction between the two terms ($F = 1.9209$, $p = 0.1034$) did not have a significant effect.

Discussion

This study supports the fact that Blanding's turtles' environment is highly challenging in the context of thermal quality. Throughout the entire active season the environment imposed thermal pressures on this population. Even when the environment reached its highest quality (during the month of July) active microhabitat selection was necessary to obtain optimal temperatures (T_{set}). Similar quantitative habitat quality values have been recorded in other studies of freshwater temperate turtles performed in similar environments at northern latitudes (Picard, 2008, and Edwards and Blouin-Demers, 2007); the thermally challenging nature of this populations range is, therefore, not surprising.

The d_e describing the thermal quality of the individual microhabitats available to the population of Blanding's turtles is a useful tool and reference when trying to predict the behaviour of Blanding's turtles during a specific time of the season. For example, in May, it appears that during day-time hours aerial basking provides the most ideal thermal habitat, while at night, turtles are more likely to favour the warmer surface waters. During the hotter months the mild surface waters provide the most ideal temperatures throughout the day, acting as a shelter from extreme heat during the day-time, and retaining the days warmth over-night. In October as temperatures begin to drop, the highest quality thermal environment shifts to the bottom of swamp, at 1m below surface. At this point it appears the turtles' strategy begins to shift to an overwintering strategy, remaining in this microhabitat for the majority of their time.

The overall pattern in thermoregulating behaviour across the active season seen with this population is very similar to the pattern observed by Sajwaj and Lang (2000) when they studied a population of Blanding's turtles found at similar latitude at the western extreme of Blanding's turtles' range. At the beginning of the season, during May, when the environment's thermal quality is actually lower than the quality in September Blanding's still manage to have a higher accuracy in thermoregulating and basking plays a pivotal role in achieving T_bs within T_{set}. This greater accuracy during a period when the thermal environment is of lesser quality could be the result of the increased reproductive energetic requirements of gravid females, and general energetic requirements of individuals who have just emerged from their dormant overwintering state. While this other study supports the idea that very geographically distant populations of Blanding's turtles behave similarly at similar latitudes, it would be beneficial to also look at another population at a more southern latitude of Blanding's turtles' range. Previous studies of other temperate freshwater turtles have noted that seasonal thermal strategies do vary across a latitudinal scale (Krawchuk and Brooks, 1998, and Grayson and Dorcas, 2004)

While Sajwaj and Lang (2000) make mention that Blanding's turtles' strategy seems to shift from a more thermoregulating strategy in the spring to a more thermoconforming strategy in the fall, they fail to provide further insight into the details of the turtles behaviour and habitat preferences. Our study shows that, despite the fact that the environment on average does not offer T_{set} temperatures during the month of October, and therefore by the definition of the exploitation index (Ex) our population does not *exploit* their thermal environment, the effectiveness index values seen in October do indicate that Blanding's turtles do in fact *select* a preferred microhabitat during October (the deeper waters 1 m below surface) and still maintain their T_bs higher than expected if the environment was used at random. During this time of year when the environment shifts towards colder temperatures, the deeper water within Blanding's turtles' habitat provides the most optimal thermal microhabitat consistently throughout the entire day. Sajwaj and Lang (2000) conducted their study throughout the winter months as well, and noted that their population of Blanding's turtles overwintered at depths of 1 m to 1.5 m; it appears that by October Blanding's turtles have selected their overwintering microhabitat and likely remain at these depths from this point onward throughout the winter.

When noting the effectiveness index, we can say that Blanding's turtles use the range of microhabitats in their entire environment in a non-random manner with respect to their thermal quality. It is not surprising to see that Blanding's turtles actively thermoregulate by selecting microhabitats of higher thermal quality as similar observations have been made for other freshwater temperate turtle studies (Picard, 2008; Edwards and Blouin-Demers, 2007; Sajwaj and Lang, 2000).

By definition the $d_e - d_b$ index is open ended and positive values do not have a strict limit to their magnitude. Because of this open ended characteristic, this index is difficult, if not impossible, to interpret by looking at individual values. This index therefore heavily relies on comparisons when interpreting results. Such comparisons may be done either from month to month for an individual study, or across species. Picard's 2008 study of musk turtles (*Sternotherus odoratus*), done within the same region, has revealed the highest effectiveness to be seen in May, with a decreasing trend from May until August. Other than a high effectiveness in May, our study demonstrates a different trend, with effectiveness increasing from June to August. This suggests that, though very close geographically speaking, these two species do not use the same thermoregulatory strategy and environmental factors other than the geographic location, may influence this difference. Such differences that may account for these differing strategies could be the fundamental difference in size of these two species, and the difference in habitat (though only about one kilometre apart, these two populations occupy very different aquatic environments).

By looking at the high values of Ex from May to August (average Ex = 80%), this suggests that Blanding's behaviours and microhabitat selection choices are highly influenced by the thermal quality of their environment. These values are much higher than previous values calculated for painted turtles (average Ex = 42%, Edwards and Blouin-Demers), and musk turtles (average Ex = 44.2%, Picard, 2008). Thus, Blanding's turtles demonstrate a much higher degree of exploitation of their thermal environment in comparison to other species in the same region (the painted turtle study site being less than 100 km from this study, and the musk turtle site located less than a kilometre away).

The findings of this study provide insight into the probable physical locations of the turtles at certain times of the day throughout the active season. For example, in May when considering that on average the only thermal microhabitat that provides T_{set} range is the aerial basking position between 11:00 and 18:00 and seeing that the population exploits this opportunity for 78% of its available time, one can say that there is a very high chance that Blanding's will be out of the water basking during these times of the day (with intermittent shuttling into cooler microhabitats if basking temperatures get too high). It should be noted that these observations are however monthly averages and daily weather variations will play a role in Blanding's thermoregulatory behaviour as well. For example, Sajwaj and Lang (2000) have shown that the turtles may be less likely to choose a basking position on an overcast day when surface water temperatures prove to be more favourable.

During the hottest time of the season the turtles remain in the water the majority of the time and will rarely venture onto mats of vegetation or land to bask. While basking was a key behaviour in May for optimising T_bs, the aerial basking position during the day-time of June and July often exceeds the upper bound of T_{set} becoming an unfavourable and possibly even harmful environment. Further support for the avoidance of aerial positioning was seen while tracking the turtles daily throughout the season in the field. During late June, July, and August turtles were rarely seen to be aerially basking and were usually in the water when they were located using radiotelemetry (see Annex II). The aqueous environment is an important thermal shelter for the turtles when their environment becomes too hot. This sheltering feature provides insight into the turtles' natural history and their highly aquatic nature, and has been noted amongst other highly aquatic species found in similar regions (Picard, 2008, and Grayson and Dorcas, 2004). Aquatic environments have previously been noted for their thermal refuge qualities at night, when terrestrial and aerial temperatures often drop below that of the aquatic medium (Dubois, Blouin-Demers, *et al*., 2009). It has been seen in this study that the aquatic medium not only provides a night-time refuge from thermal lows, but that it also provides key sheltering features from extreme temperatures during the day. This sheltering behaviour is modelled and demonstrated by other *Testudines* species found in much hotter climatic extremes (i.e. deserts), where it is necessary to avoid extreme heat by sheltering in burrows (Zimmerman *et al.*, 1994). Blanding's turtles' close tie to their aquatic environment during the hottest time of the season demonstrates a large dependence on the milder aquatic medium to maintain body temperatures not only within T_{set}, but more importantly, below fatal temperature levels. The thermal sheltering properties of the swamp from extreme heat provides insight into the life strategy of Blanding's turtles, a species already widely accepted as being highly aquatic.

Although inconclusive and impossible to state that differences in thermoregulatory behaviour do in fact exist between the different groups within this population of Blanding's turtles, there is some evidence to suggest that differences may still occur. As was seen in Fig. 3, a June profile of hourly T_bs, during the day-time hours gravid female temperatures were consistently higher then both other groups. The month of June was chosen because the largest differences in T_bs are expected to be seen in this month. Not only does the environment provide the turtles with a greater opportunity to maintain their T_bs within T_{set} (hours per day) but throughout this month gravid females were in the later stages of reproduction and eggs were laid towards the end of this month. Sajwaj and Lang (2000) have previously suggested potential causes for differences in behavioural thermoregulation within a species. They suggest that potential differences could be a result of either 1) female reproductive energetic needs or 2) male reproductive considerations (i.e. seeking out female mates, requiring more time in the water and less basking). Furthermore, Nutting and Graham's (1993) preliminary look at Blanding's turtles mean preferred temperatures in a laboratory setting suggest females do in fact maintain their T_b at higher values than males. Unfortunately Nutting and Graham's study is lacking in sample size so should only be considered with caution. The large error bars/standard error seen in Fig. 3 could be a result of uncontrollable environmental factors effecting hourly means. Such factors may include daily temperature variations throughout the month. Future studies should address intra-species differences by designing experiments in a controlled laboratory setting, eliminating such daily variances in environmental temperatures and solar radiation.

Overall the trends which have been described in this study are not surprising but instead support the importance of thermoregulation in Blanding's turtles' daily activities in a thermally challenging environment, and also demonstrate the large influence of thermal considerations when selecting microhabitats within a population's range. On a broader scale, Blanding's turtles' habitat or range selection should also be largely influenced by thermal qualities of the environment. In this respect, such an ideal thermal habitat for Blanding's thus provides an aquatic buffer zone with available T_{set} temperatures (which may not be possible in some cases of flowing water, etc.) coupled with readily available basking sites.

Broad-scale Implications

Blanding's turtles are listed by COSEWIC and 9 American states as either 'threatened' or 'endangered' across their range, with major contributing factors to this status originating from anthropogenic activities (i.e. road construction through or near Blanding's turtles' habitat, habitat destruction, habitat fragmentation, etc.) (Mockford, Herman, *et al.*, 2007). It is essential that ideal Blanding's turtle habitats be identified and subsequently protected by appropriate means (i.e. further expansion and creation of national or provincial parks, and additional legislation against destruction of key Blanding's habitats and populations, etc.) to advance conservational efforts. Due to the fact that this study supports a strong link between Blanding's turtles and their habitat selection, it is especially important to consider the thermal characteristics and quality of environments when attempting to identify suitable habitats for this species. An ideal habitat for Blanding's turtles should provide such characteristics as an aquatic buffer zone with highly preferable (i.e. T_{set}) temperatures during the hotter months coupled with readily available basking sites essential during the early and later part of the active season.

Acknowledgements

Although I spent the summer of 2009 with the same population of Blanding's turtles as in this study, using similar tracking and monitoring techniques, the actual collection of temperature data points were done in the previous season, 2008, and were made accessible to me for the completion of this study thanks to Catherine Millar. I would also like to thank Catherine for her help and mentoring both in the field and back in the lab. I would like to thank my supervisor, Dr. Gabriel Blouin-Demers for providing me with this great research opportunity, as well as St. Lawrence Islands National Park for providing many essential resources during the field season, including boats and a roof over our heads.

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Tables and Figures

Table 1. Abbreviations and definitions of quantitative indices of thermoregulation used in this study.

Symbol	Definition
T_b	Turtle body temperature, approximated by externally fixed temperature sensitive radiotransmitters.
T_e	Operative environmental temperature, the temperature of selected thermal microhabitats measured in the field, represents the equilibrium temperatures that would be attained by ectotherms in the given microhabitat.
T_{set}	Thermoregulatory set-point range, the preferred range of temperatures of Blanding's turtles when all other environmental factors are controlled for.
d_b[1]	Accuracy of body temperature, defined as the absolute value of the deviation of T_bs from either the upper or lower bound of T_{set}.
d_e[1]	The thermal quality of the habitat, defined as the absolute value of the deviation of T_es from either the upper or lower bound of T_{set}.
$d_e - d_b$[2]	Effectiveness of temperature regulation, defined as $d_b - d_e$, indicates the degree to which turtles depart from perfect thermoconformity
Ex[3]	Thermal exploitation index, the percentage of time T_bs fall within T_{set} as compared to the total amount of time T_{set} temperatures are available to the turtles.

[1] index introduced by Hertz, *et al.*, 1993
[2] index introduced by Blouin-Demers and Weatherhead, 2001
[3] index introduced by Christian and Weavers, 1996

Month	Time Period	d_b	d_e	$d_e - d_b$
May	Full Day	4.17 ± 2.59	7.71 ± 1.88	3.55
	Day time	3.71 ± 2.73	7.27 ± 1.84	3.56
	Night time	4.62 ± 2.51	8.16 ± 1.91	3.54
June	Full Day	2.36 ± 2.33	3.83 ± 2.27	1.47
	Day time	2.57 ± 2.45	3.97 ± 2.39	1.40
	Night time	2.15 ± 2.19	3.68 ± 2.13	1.54
July	Full Day	1.62 ± 1.66	3.42 ± 1.85	1.80
	Day time	1.86 ± 1.90	3.51 ± 2.10	1.65
	Night time	1.37 ± 1.37	3.33 ± 1.56	1.96
August	Full Day	2.34 ± 1.96	4.51 ± 1.77	2.18
	Day time	2.30 ± 2.03	4.53 ± 1.85	2.24
	Night time	2.38 ± 1.86	4.50 ± 1.67	2.12
September	Full Day	6.21 ± 2.97	6.90 ± 2.50	0.69
	Day time	6.18 ± 3.08	7.06 ± 2.60	0.88
	Night time	6.24 ± 2.88	6.73 ± 2.39	0.50
October	Full Day	9.96 ± 2.40	13.20 ± 3.27	3.21
	Day time	9.51 ± 2.82	12.70 ± 3.51	3.18
	Night time	10.40 ± 1.84	13.70 ± 3.02	3.24

Table 2. Monthly accuracy of body temperature (d_b ± 1 SE), thermal quality of the habitat (d_e ± 1 SE), and effectiveness of temperature regulation ($d_e - d_b$) indices calculated across an entire day, during the day (6h00-17h59) and during the night (18h00-5h59).

Month	Time set-point range possible (h)	Time set-point range exploited (h)	Ex (%)
May	7.3	5.7	78
June	11.7	10.5	90
July	12.9	10.6	82
August	9.4	6.5	69
September	0	0	0
October	0	0	0

Table 3. The values of mean number of hours T_{set} is available and T_{set} is exploited for each month used for calculating the thermal exploitation index (Ex).

Month/Habitat	Mean d_e		
	Full Day	Day-time	Night-time
May			
Copper model	7.86 ± 5.67	5.28 ± 4.96	10.35 ± 5.20
Bog surface	5.94 ± 3.37	5.35 ± 3.84	6.50 ± 2.75
1m below surface	9.79 ± 0.86	9.77 ± 0.84	9.80 ± 0.90
0.5m below surface	6.80 ± 2.22	7.05 ± 2.25	6.55 ± 2.17
Surface water	6.38 ± 2.26	6.37 ± 2.36	6.40 ± 2.18
Under bog	9.28 ± 1.29	9.59 ± 1.26	8.98 ± 1.25
June			
Copper model	6.03 ± 3.98	6.32 ± 4.45	5.73 ± 3.43
Bog surface	2.96 ± 2.49	2.92 ± 2.56	3.00 ± 2.42
1m below surface	6.08 ± 1.34	6.08 ± 1.35	6.08 ± 1.34
0.5m below surface	1.89 ± 2.16	2.11 ± 2.21	1.66 ± 2.09
Surface water	1.63 ± 2.10	1.76 ± 2.12	1.50 ± 2.07
Under bog	4.38 ± 1.95	4.63 ± 1.93	4.13 ± 1.94
July			
Copper model	5.70 ± 4.37	6.20 ± 5.01	5.19 ± 3.56
Bog surface	2.70 ± 1.77	2.39 ± 1.89	3.01 ± 1.58
1m below surface	5.19 ± 0.27	5.18 ± 0.28	5.19 ± 0.26
0.5m below surface	2.01 ± 1.03	2.09 ± 1.05	1.93 ± 1.02
Surface water	1.07 ± 1.12	1.16 ± 1.19	0.98 ± 1.05
Under bog	3.85 ± 0.76	4.03 ± 0.79	3.67 ± 0.69
August			
Copper model	6.48 ± 4.36	6.80 ± 4.65	6.16 ± 4.04
Bog surface	4.16 ± 2.01	3.77 ± 2.20	4.54 ± 1.72
1m below surface	5.82 ± 0.35	5.82 ± 0.35	5.83 ± 0.35
0.5m below surface	3.76 ± 0.91	3.80 ± 0.97	3.72 ± 0.85
Surface water	1.96 ± 1.68	1.88 ± 1.81	2.04 ± 1.53
Under bog	4.90 ± 1.24	5.11 ± 1.28	4.68 ± 1.17
September			
Copper model	8.14 ± 4.99	9.32 ± 5.27	6.96 ± 4.40
Bog surface	6.84 ± 2.74	6.48 ± 2.89	7.19 ± 2.53
1m below surface	7.14 ± 0.94	7.14 ± 0.94	7.14 ± 0.94
0.5m below surface	6.23 ± 2.16	6.38 ± 2.26	6.08 ± 2.05
Surface water	4.98 ± 2.86	4.82 ± 2.95	5.14 ± 2.76
Under bog	8.05 ± 2.12	8.22 ± 2.19	7.88 ± 2.03
October			
Copper model	14.50 ± 7.14	11.51 ± 7.74	17.47 ± 4.97
Bog surface	13.40 ± 2.82	13.20 ± 2.97	13.63 ± 2.65
1m below surface	11.20 ± 1.74	11.15 ± 1.73	11.21 ± 1.76
0.5m below surface	13.00 ± 3.31	13.19 ± 3.28	12.82 ± 3.34
Surface water	12.70 ± 3.54	12.65 ± 3.65	12.73 ± 3.43
Under bog	14.30 ± 2.33	14.50 ± 2.27	14.09 ± 2.37

Table 4. The mean quality of the environment (d_e ± 1 SE) for each thermal microhabitat throughout the season averaged over the entire day, during day-time hours (6h00-17h59), and during night-time hours (18h00-5h59).

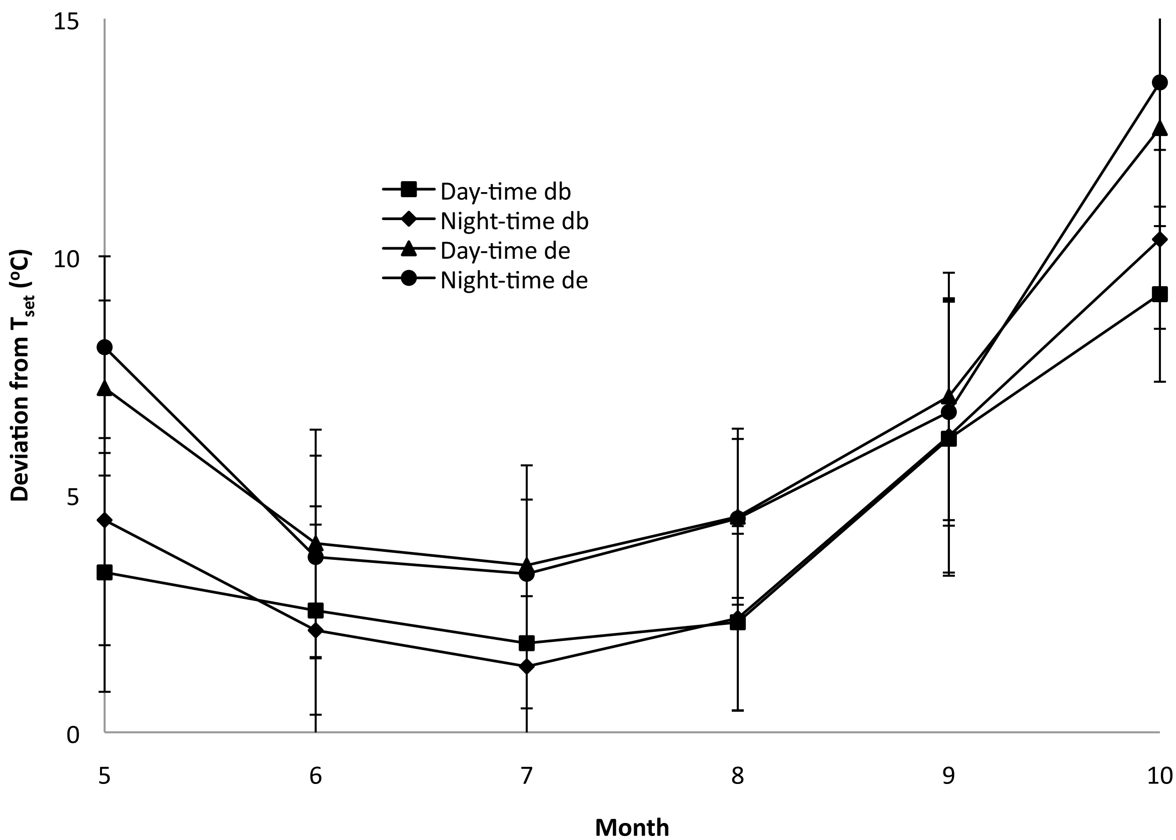

Figure 1. Comparing the mean day-time and night-time d_b (± 1 SE) and mean d_e values over all study months.

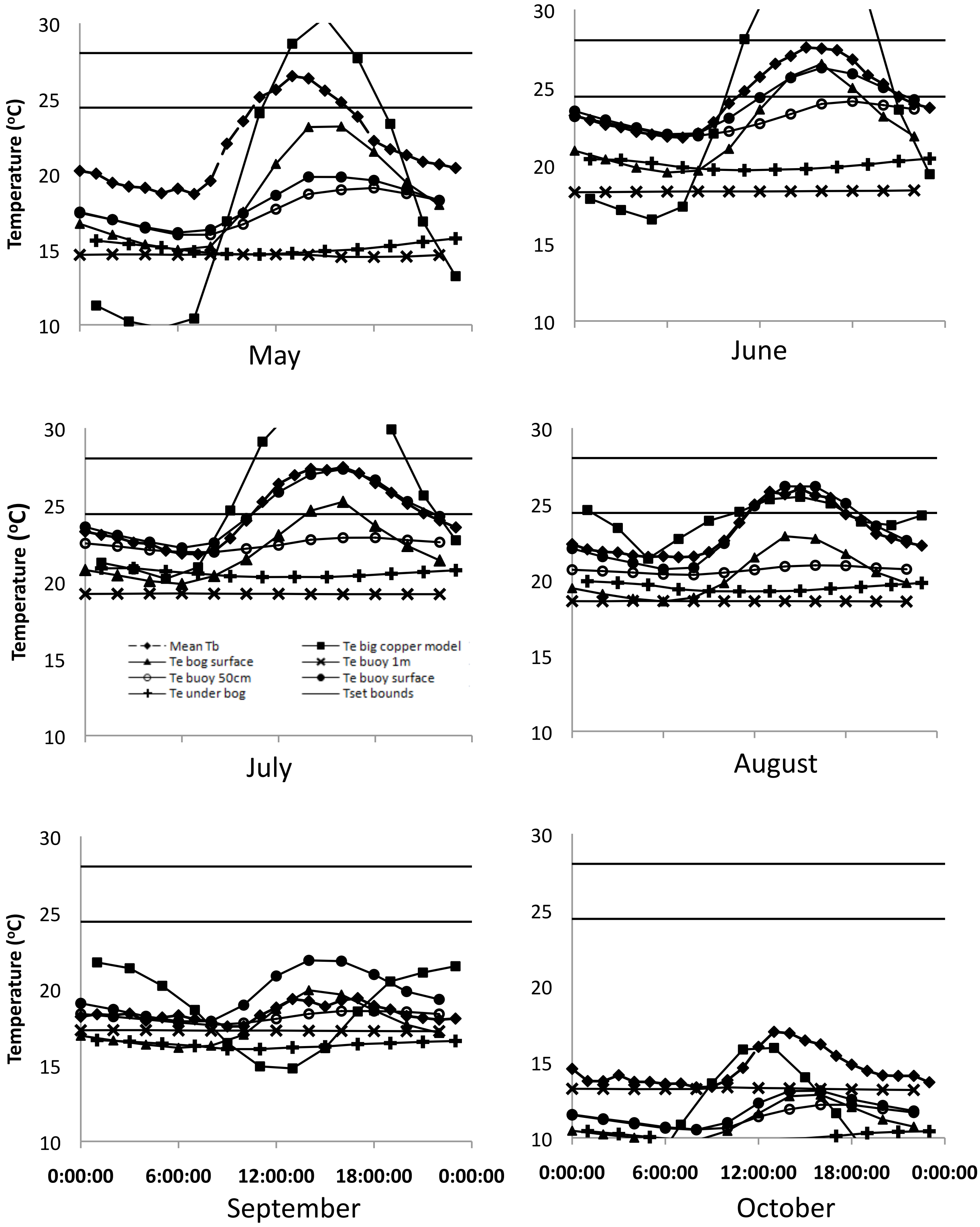

Figure 2. Mean hourly T_e values for each thermal microhabitat and the mean hourly T_b of all turtles (n = 22) plotted with the T_{set} range for each month of the study period.

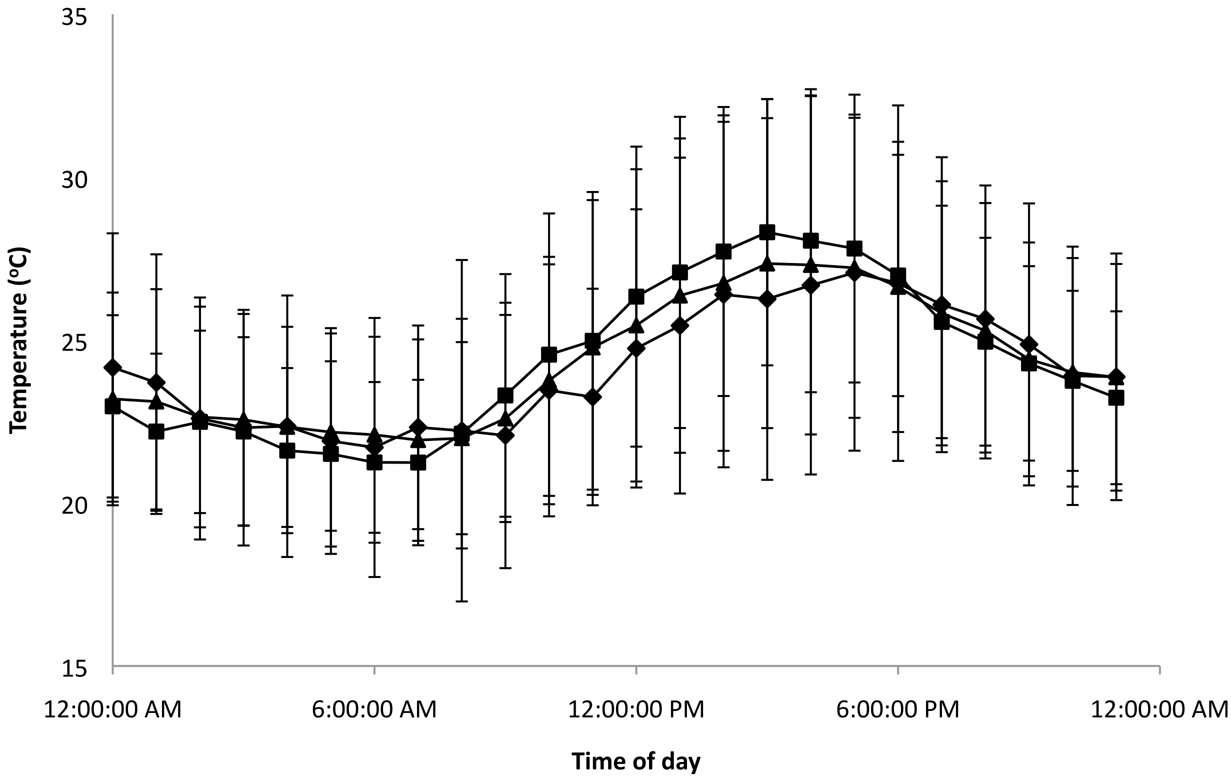

Figure 3. Mean hourly T_b values (± 1 SE) during the month of June for non-gravid females (diamond symbol, *n* = 3), gravid females (square symbol, *n* = 6), and for males (triangle symbol, *n* = 13).

Annex I

Data used to estimate, from the bounds of the central 50% of observed body temperatures (*Tb*), preferred temperature (*Tset*) of Blanding's turtles.

Species	Type of thermal gradient	n	MST[1] (°C)	25%[2] (°C)	75%[3] (°C)	Reference
Chelydra serpentina	Dry gradient	24	25±2.4	17.1	32.9	Williamson *et al.* 1989
Chelydra serpentina	Aquatic gradient	24	28±1.8	22.0	34.0	Williamson *et al.* 1989
Chelydra serpentina	Aquatic gradient	27	29.8±0.4	28.4	31.2	Knight *et al.* 1990
Chelydra serpentina	Aquatic gradient	10	28.1±0.18	27.7	28.5	Schuett and Gatten 1980
Clemmys guttata	Aquatic gradient	20	23.8±0.65	21.8	25.8	Graham and Hutchison 1979
Chrysemys picta	Dry gradient	15	23.3±0.59	21.8	24.8	Edwards and Blouin-Demers 2007
Chrysemys picta	Aquatic gradient	20	24.2±1.14	20.8	27.6	Graham and Hutchison 1979
Pseudemys nelsoni	Aquatic gradient	21	26.5±0.29	25.6	27.4	Nebeker and Bury 2000
Trachemys scripta	Dry gradient	10	24.6±0.17	24.2	25.0	Gatten 1974
Trachemys scripta	Dry gradient	10	29.1±0.22	28.6	29.6	Gatten 1974
Terrapene ornata	Dry gradient	10	29.8±0.07	29.7	29.9	Gatten 1974
Terrapene ornata	Dry gradient	10	28.3±0.2	27.9	28.7	Gatten 1974
Graptemys geographica	Dry gradient	23	NA	23.5	25.9	Ben Ezra *et al.* 2008
Graptemys geographica	Aquatic gradient	10	NA	22.5	31.8	Ben Ezra *et al.* 2008

[1] mean selected temperature
[2] 25% quartile of the central 50%
[3] 75% quartile of the central 50%

(Data table reproduced from Picard, 2008.)

Annex II

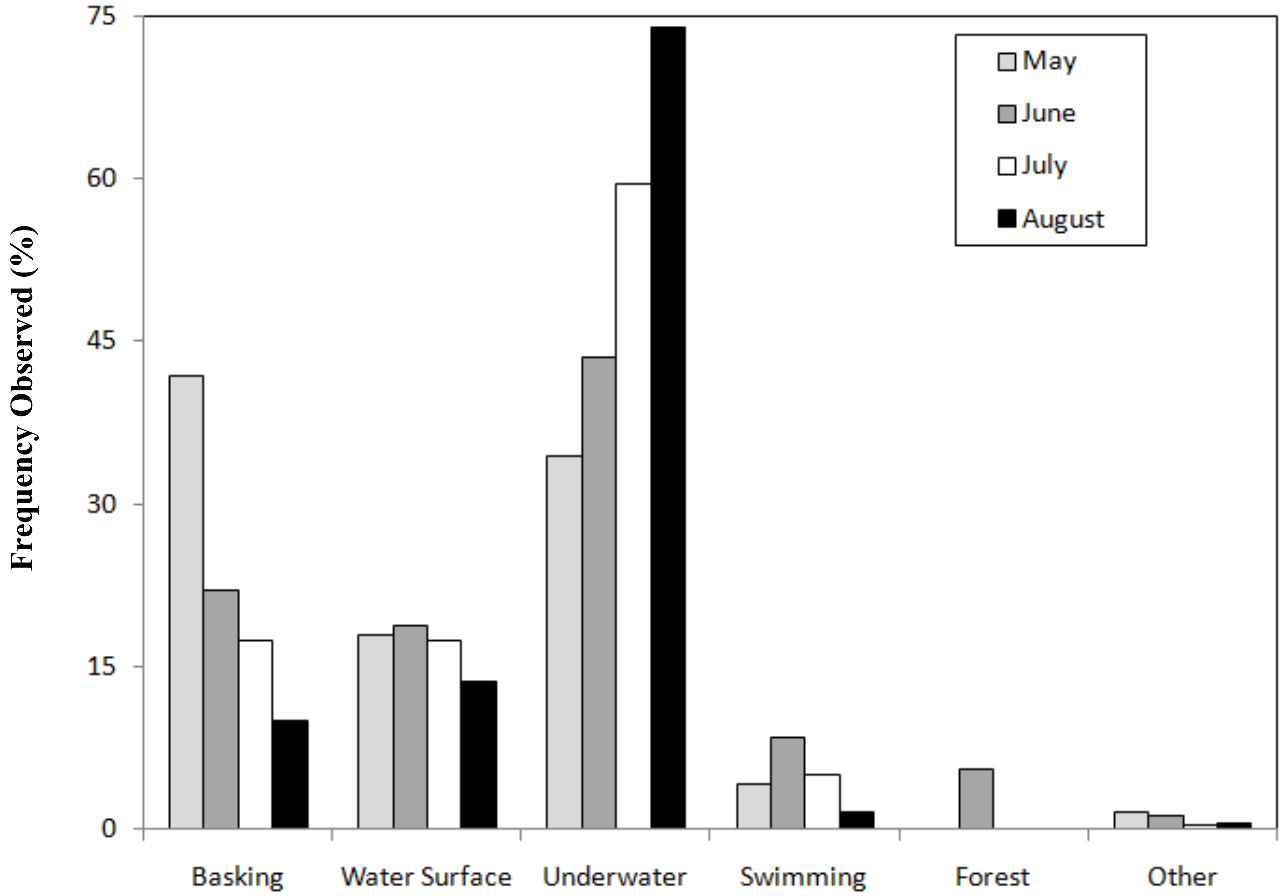

Figure 1.4. Frequency of observed turtle behaviour exhibited at relocation points (n = 1566) in May, June, July and August 2008 and 2009 on Grenadier Island, St. Lawrence Islands National Park, Ontario, Canada. Behaviours described as "other" include copulating(n =3), captured in hoop net (n = 6) or climbing a beaver lodge (n = 4).

(Figure adapted with permission from Millar, 2010)