# Does thermal quality of the environment affect habitat selection by musk turtles (*Sternotherus odoratus*)?

**by**

## Gabriel Picard

Thesis submitted to the Department of Biology in partial fulfillment of the requirements for the B.Sc. Honours degree, specialization Biology

University of Ottawa
Ottawa, Ontario

April 10, 2008

____________________________________

Supervisor's signature

# ABSTRACT

In ectotherms, variation in body temperature ($T_b$) greatly affects physiological performance and, ultimately, fitness. Therefore, reptiles behaviourally regulate $T_b$ by selectively choosing habitats of optimal temperature. In fact, this need to thermoregulate is thought to be the principal factor in habitat selection. The main goal of this study was to determine the link between patterns of thermoregulation and habitat selection by the musk turtle in a thermally challenging region where the link should be particularly strong. I expected habitat selection to be based on the fulfillment of thermoregulatory requirements, which can be accomplished by selecting thermally superior habitats. From early May to late August 2007, I located 22 musk turltes using temperature-sensitive radio-transmitters and collected daily $T_b$ profiles using automated radio-telemetry data loggers. In addition, temperature data loggers were placed at a variety of locations in the study area to measure the complete range of environmental operative temperatures ($T_e$) available to musks at all times. At the home range scale, the habitats with the highest thermal quality were the aquatic habitats with surface cover (i.e., lily pads, macrophytes, etc.) followed by shallow water, which also offered good opportunities to maintain $T_b$ within preferred range were. As expected, musk turtles used habitats non-randomly and had a strong preference for the thermally superior habitats with surface cover. This is consistent with the typical aquatic basking behaviour observed in musk turtles, suggesting that there is a strong link between the thermal quality of habitats and habitat selection.

# TABLE OF CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

# ACKNOWLEDGEMENTS

Special thanks to my supervisor Dr. Gabriel Blouin-Demers for the great research opportunity and everyone from the lab for their generosity in helping me with all my questions and many requests. Marie-Andrée Carrière, I am more than grateful for everything you have thought me. From catching turtles to driving boats, everything I learned during this project is the fruit of your immense patience. Véronique Juneau, your help was indispensable on the field. Thank you for your continuous tenacity, determination and good spirits. Thank you Marie Claude Michaud for your generous support throughout the whole year.

Funding for this research was provided by Parks Canada and by grants to Dr. Gabriel Blouin-Demers from the Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation, and the Ontario Innovation Trust.

# INTRODUCTION

All physiological processes depend on body temperature (Huey 1982). Therefore, in ectotherms such as reptiles, variation in the body temperature ($T_b$, Table 1) affects physiological performance and ultimately, fitness (Huey and Kingsolver 1989). Consequently, reptiles depend on behavioural thermoregulation to maintain $T_b$ in a certain range allowing achievement of maximal performance (Cowles and Bogert 1944, Huey and Kingsolver 1989). Inevitably, reptiles depend on the range of temperature provided by the physical environment, and as a result, behavioural regulation of $T_b$ can be realized by selectively choosing habitats of optimal temperature (Huey et al 1989). In fact, the obligation to maintain $T_b$ within an optimal range to maximize physiological performance seems to be the proximate factor in habitat selection (Huey 1991, Reinert 1993). Due to the tight link between thermoregulation and habitat selection, understanding this interaction is of primordial importance when studying threatened species in need of conservation efforts. My general goal was to determine the link between patterns of thermoregulation and habitat selection by the common musk turtle (*Sternotherus odoratus*), a species designated as Threatened in Canada, at the northern limit of its range.

The obligation of thermoregulation to maintain $T_b$ within an optimal range is of greater importance in most environmental extremes (Huey 1974, Shine and Madsen 1996). In north temperate regions for example, the task of thermoregulating can be particularly challenging due to the low average and high seasonal variability in environmental temperatures (Blouin-Demers and Weatherhead 2001). Due to the tight link between thermoregulation and habitat selection, we can assume that reptiles should take advantage of thermally favorable opportunities and select habitats that provide optimal thermal conditions to improve physiological performance and fitness (Huey et al 1989, Huey 1991). Evidence indicates that the link should be particularly tight for species living in thermally challenging environments (Blouin-Demers and Weatherhead 2002, Blouin-Demers and Nadeau 2005, Row and Blouin-Demers 2006b, Edwards and Blouin-Demers 2007). It is therefore beneficial for reptiles in thermally challenging environments to precisely select thermally superior habitats, thus minimizing costs in terms of investments in time and energy associated with thermoregulation. My objective was to determine if thermal quality affects habitat selection by musk turtles in a thermally challenging environment. The Thousand Islands ecosystem on the St. Lawrence River is located in a temperate region shared between the province of Ontario, Canada and the state of New York, U.S.A. I expected that habitat selection should be based on the fulfillment of thermoregulatory requirements, which can be accomplished by selecting thermally superior habitats.

To assess this, the first step was to quantify the thermal quality of habitats available to musk turtles in the study area. Musk turtles are highly aquatic and rarely go out of the water to perform “aerial basking” typical of most freshwater turtles and have instead been observed basking while floating at the surface of the water under or amongst aquatic vegetation (Ernst 1986). Therefore, I expected that aquatic habitats containing surface cover (aquatic vegetation such as lily pads or macrophytes for example) should be of higher thermal quality than other aquatic habitats deprived of such cover. More precisely, I expected that habitats with surface cover will be of higher thermal quality early in the season when the water is at its coolest. The difference between habitats with surface cover and the shallow water depths should be of less importance in the summer do to a more homogeneous distribution of water temperature, nevertheless should still be more important when compared with deep water. Thereafter, by comparing available $T_e$ to realized $T_b$, we expect to determine the species' thermoregulatory strategy. The second step was to determine if the thermoregulatory strategy is coherent with habitat use. In other words, do musk turtles use habitats non-randomly at the home range scale and select habitats with the highest thermal quality? More precisely, I tested the prediction that musk turtles should preferentially select aquatic habitats with surface cover, which I expected to offer the best opportunities for thermoregulation.

# METHODS

## *Study Area and Study Species*

From early May to late August 2007, I studied a population of musk turtles (*Sternotherus odoratus*), a species designated as Threatned in Canada (COSEWIC), at the northern extreme of their range on the St. Lawrence River in the Thousand Islands ecosystem. The study area covered a range of approximately 3.8 km by 1.1 km and was mostly located in the waters surrounding the north side of Grenedier Island, one of St. Lawrence Islands National Park's largest islands (Fig.1). Approximately 83% of the shoreline located in the study area is in its natural state.

## *Radio-telemetry and Data Collection*

Musk turtles were mostly captured at the beginning of the season either by hand while found floating or with a dip net when found buried or walking at the bottom of the water. Some individuals were also captured opportunistically later in the season when replacement was needed, mostly due to loss or damaged radio-transmitters. When captured, musk turtles were immediately brought to the lab for processing. All turtles were measured, weighted to the nearest 1g with a spring scale and sex was determined by examining the tail length and width. Marking was done by assigning each individual a unique combination of either holes or notches depending on the size of the marginal scutes. Holes were done with a hand held drill and notches with a triangular file.

In total, 22 musk turtles (13 females and 9 males) were fitted with temperature-sensitive radio-transmitters (Model SB-2T, 6.4g, battery life of 12 months at 20°C, Holohil Systems Inc., Carp, Ontario). To attach the transmitters, I tied them with steel fishing wire through holes drilled on the rear of the carapace. Sharp edges at the base of the transmitters were filed to prevent injuries to turtles. Marine silicone was used to cover wires and edges to facilitate adhesion and to prevent aquatic vegetation from snagging between the carapace and the transmitter. Turtles stayed in the lab overnight to allow the silicone to dry. The mass of transmitters (including wire) never exceeded 5% of the mass of the turtles. Transmitters were occasionally inspected during the study period and replaced or repaired when necessary to prevent them from falling off. All transmitters were recovered at the end of the study.

Turtles were located on average every two days from after being released to their point of capture to the end of the study, before reaching the deeper waters where they hibernate. Tracking was done using a telemetry receiver (AVM Instrument Co. Ltd., Colfax, California, U.S.A) and a directional antenna. Upon location, the individual’s location was recorded on a map, which I later retrieved from the Universal Transverse Mercator (UTM, datum NAD83) coordinates using ArcMAP 9.2 (ESRI 2000a). In addition, I noted each individual’s behaviour (basking, floating under surface cover, underwater, or burrowed) and habitat characteristics of its position (i.e. the percentage and type of surface cover).

### *Body Temperatures* ($T_b$)

The radio-transmitters that were fitted to musk turtles were chosen for their temperature-sensitive feature. In other words, the pulse rate that they emitted was proportional to the temperature. Due to the almost entirely aquatic behaviour of musk turtles, their small size, and the heat capacity of water, external temperature-sensitive transmitters are an appropriate tool in estimating $T_b$. Whenever a turtle was located, I measured the pulse rate by timing the duration of 10 pulses with a chronometer. $T_b$'s (°C, Table 1) were then derived from the pulse rates by fitting a polynomial equation to the calibration points (provided by the manufacturer) for each transmitter.

Daily $T_b$ profiles were also measured using automated radio-telemetry data loggers (SRX 400, Lotek Engineering Inc., Newmarket, Ontario). Two units were positioned at strategic locations in the study area to maximize the number of pulse rates recorded. The data loggers were programmed to scan for a new frequency every three minutes. The pulse rate, transmitter frequency, time and date were recorded in the internal memory of the data loggers once it located a transmitter within its range. Powered by marine deep-cycle 12 V batteries, our data loggers could operate for an average of seven days. Thus the data were weekly downloaded onto a desktop computer where they were then stored as datasheets. The transmission range depends on many factors (environmental, meteorological, transmitters, etc.). Musk turtles were mostly located in shallow waters of small bays or creeks; consequently, I could get a transmission range of approximately 120 metres. However, musk turtles used a relatively wide area and would frequently move out of the transmission range. For that reason, I was not able to record complete daily $T_b$ profiles for every individual and had to periodically relocate the data loggers where I could maximize the number of pulse rates recorded. $T_b$'s (°C) obtained with the data loggers were also derived from the pulse rates recorded by fitting a polynomial equation to the calibration points (provided by the manufacturer) for each transmitter.

### *Thermal Preference* ($T_{set}$)

Following the terminology introduced by Hertz et al (1993), $T_{set}$ (Table 1) represents the range of preferred body temperatures of the species. I did not measure $T_{set}$ myself, however, the diversity of values published for freshwater turtles demonstrate that the range of thermal preference seems to be a conserved trait. I reviewed the literature and combined all evidence of $T_{set}$ measured for temperate turtles, which had a sample size of ten individuals or greater. I estimated the 50% central of the observed $T_b$'s for each case and used the mean bounds of the central 50% (25% and 75%) of all estimates to determine an approximate $T_{set}$ for *S. odoratus.* (Hertz et al 1993, Christian and Weavers 1996, Blouin-Demers and Weatherhead 2001). See the annex for the compiled data utilized.

### *Environmental Operative Temperatures ($T_e$)*

Environmental operative temperatures ($T_e$, Table 1) present the complete range of available $T_b$'s an ectotherm can achieve in the field. A common method of measuring $T_e$'s, used widely in reptile studies, is done by placing a physical model, which mimics characteristics of the study organism, in different environments available in the field (Adolph 1990, Zimmerman et al 1994, Blouin Demers and Weatherhead 2001). These models, often proved to be complex and costly, can easily be replaced with simple electronic temperature data loggers, which can yield nearly identical results (Vitt and Sartorius 1999). Because of the small size and almost entirely aquatic behaviour of musk turtles, the later technique seemed to be simpler and as effective. Water has a very high temperature conductivity, therefore, I assumed that the $T_e$'s available to musk turtles in water was the same as water temperature. Consequently, $T_e$'s in water can easily be measured using simple temperature data loggers.

To record environmental operative temperatures ($T_e$), I placed temperature data loggers (Thermochron iButton DS1921; Dallas Semiconductor, Sunnyvale, California) coated with PlastiDip (Performix, Blaine, MN) at a variety of locations in the study area to try to represent the complete range of $T_e$'s available to musk turtles at all times. Data loggers were attached to a rope fixed with a floater and sunk at three different water depths (0.5m, 1m and 2m), all without any surface cover. In addition, a data logger was placed at the water surface under vegetation cover (lily pads and macrophytes) to mimic the aquatic basking of musk turtles (Ernst 1986). For better sampling, the four data logger's positions were replicated to have a total of two sets. This also provided security by having backup data in case one of the data loggers malfunctioned in the field. The two sets were placed surrounding locations which were thought to be the area where musk turtles were known to spend most of their time during the active season (Carrière 2007).

In total, the study site was composed of 61.8% deep-water habitat (>2m), 32.93% intermediate-water habitat, 4.24% shallow-habitat and 0.85% surface cover. The proportions varied during the study period due to the seasonal emergence of aquatic plants that composed the surface cover habitat, however this variation is negligible due to the large proportion of deep water within the study area. These proportions were used to weight $T_e$'s by habitat availability when necessary.

### *Accuracy of $T_b$ and Thermal Quality of Habitat*

Following the methods proposed by Hertz et al (1993), I measured the accuracy of $T_b$ and the thermal quality of each habitat. The accuracy of $T_b$ was measured as the mean of deviations of $T_b$ from $T_{set}$ ($d_b$, Table 1). If $T_b$ is above the preferred temperature range, $d_b$ was calculated as the difference between $T_b$ and the upper bound of $T_{set}$ and if $T_b$ is below $T_{set}$, $d_b$ was calculated using the lower bound. Ultimately, if $T_b$ is located within the range of preferred temperature, then a value of zero was attributed to $d_b$. The thermal quality of each habitat, the mean of deviations of $T_e$ from $T_{set}$ ($d_e$, Table 1), was calculated in the same way as for $d_b$.

### *Indices of Thermoregulation*

Following Blouin-Demers and Weatherhead (2001), I measured the effectiveness of thermoregulation by examining the magnitude of the difference between $d_e$ and $d_b$. If the measure obtained with the $d_e$ - $d_b$ (Table 1) index has a value equal to zero, then the animals are perfect thermoconformers, meaning that they can easily function under a wide range of body temperatures. A negative value represents animals that avoid habitats of high thermal quality and a positive value represent animals that thermoregulate.

The second thermoregulation index I chose to measure is the thermal exploitation index (Ex, Table 1) established by Christian and Weavers (1996). This quantifies the extent to which the reptiles make use of the thermal environments available to them. Ex is calculated by looking at the amount of time a reptile has its $T_b$ within $T_{set}$ divided by the amount of time that such behavior is possible (determined by the amount of time that $T_e$ is within $T_{set}$) in at least one habitat, expressed in percentage. Following the modifications done to this index by Brown and Weatherhead (2000), we also calculated the percentage of body temperatures that fell above and below $T_{set}$ when this could be achieved.

### *Home Ranges*

The home range for each individual tracked regularly throughout the whole active season was estimated using the Minimum Convex Polygon (MCP) method, which simply consists of drawing the smallest convex polygon that enclosed all recorded locations for one individual (Hayne 1949). Considering that musk turtles are highly aquatic, we excluded all land from the home range estimations. MCP's were calculated in ArcMap 9.2 (ESRI 2000a) using the Hawth's Analysis Tools extension (Beyer 2004).

MCP is one of the oldest, simplest, most widely used methods (Powell 2000) and has been recently demonstrated to represent an accurate home range estimate for reptiles (Row and Blouin-Demers 2006c), but it has its drawbacks. One major problem is that MCP's have the tendency to include extensive areas in the estimates that are never used by the animal. For example, a musk turtle's typical home range estimated with MCP's could include a variety of water depths including very deep water. A small specific fraction of this deep water could be used while traveling from one creek to the next, nevertheless the whole targeted area would certainly never entirely be used. Thus, by assuming that the individual uses the home range evenly or with the same intensity, patterns of selection within the home range are mistakenly ignored (Powell 2000).

To examine habitat use or habitat selection within the home range, I used the non-parametric method of Kernel density estimators. Kernels are considered to be the best estimators available due to their capacity to accurately quantify the intensity of use by calculating a density estimate (Worton 1989, Seaman and Powell 1996). These density estimates designate the area where individuals are the most likely to be found and therefore, represent the home range utilization distribution (Powell 2000). Like any other home range estimator, Kernels also have their drawbacks. The major drawback is the difficult task of setting up the numerous parameters associated with the calculation of kernels, especially selecting a suitable smoothing factor (h), which can greatly affect the size and shape of the home range (Worton 1989, Seaman and Powell 1996). The most widely used method in choosing h, the least-squares cross-validation (LSCV), has proved to be accurate in most cases. It does however, overestimate the dimensions of the home range of amphibians and reptiles, animals with high site fidelity and may use the same location for a long time, leading to autocorrelated telemetry data (Row and Blouin-Demers 2006c). Therefore, I followed the method proposed by Row and Blouin-Demers (2006c), which consisted of combining the MCP and kernel methods to accurately quantify the intensity of use by reptiles. Using the Animal Movement extension for ArcView 2.0 (ESRI 2000b, Hooge and Eichenlaub 2000), I adjusted the smoothing factor (h) for each individual until the area of the 95% kernel (excluding land) was of similar size as the MCP calculated. To allow habitat selection comparison at two different usage intensities, I also calculated the 50% kernel. This permits us to obtain accurate index for home range size using the MCP method while examining the areas used more intensely within the home range without overestimating the dimensions.

### *Macrohabitat Characterization and Selection*

I characterized macrohabitat using high-resolution digital aerial orthoimagery from New York State GIS Clearinghouse (2006). The orthoimagery was produced in

2003 at a 0.6m pixel resolution in color infrared, and projected in NAD83 UTM datum zone 18. In addition, I used a nautical chart layer (NAD83, 1:25000 scale) from Fisheries and Oceans Canada to classify depth into three habitat categories; shallow water (<1 m), intermediate water (1-2 m), deep water (>2 m). Water depths obtained from the nautical chart layer were cross-referenced to turtle telemetry locations where depth had been measured in the field to determine accuracy. In addition, I used photographs taken at the end of each month at every locations where musk turtles were located cross-referenced with hand drawn estimates to create a surface cover layer for each month (May to August). For the purpose of this study, I defined surface cover as sparse (i.e. open reeds) and dense (i.e. matted marshes, cattails) aquatic emergent vegetation that is present throughout the entire study season combined with seasonally emergent aquatic vegetation (i.e. lily pads). The area of surface cover was deducted from the depth layers in order to obtain four independent habitat layers. These four habitat categories are in accordance with the four sets of locations chosen to represent the range of operative environmental temperatures ($T_e$) available to all individuals. All habitat layers were created in ArcMap 9.2 (ESRI 2000a).

To determine habitat selection at the macrohabitat scale, I compared habitat use within the home range by each individual to its availability. To quantify habitat use and availability, I determined the proportion of surface cover (SCOVER), shallow water (SHALLOW), intermediate (INTER) and deep water (DEEP) in the 95% and 50% kernels. The proportions of these four habitat types sum to one, thus creating nonindependence. Therefore, following Aitchinson (1986), log-ratio transformation was used to remove this linear dependency. I utilized a "use versus availability" compositional analysis to examine which habitat was preferred by musk turtles in respect to the two different intensity levels (Aebischer et al 1993). The compositional analysis tests the null hypothesis that habitats are used in a random manner. If habitat use is found to be significantly non-random, following the methods of Aebischer (1993), a matrix was created to establish the rank of preference of each habitat. Pairwise comparisons were done to determine if the differences between the ranks were significant.

### *Statistical Analyses*

The compositional analysis was conducted using Resource Selection For Windows (Leban 1999). All other statistical analyses were conducted on JMP version 5.0.1 (SAS Institute 2002) and R (R Development Core Team 2004). All assumptions of normality and homogeneity of variance were met and verified by examining box-plots. I reported all means ± one standard error and accepted significance of tests at $\propto = 0.05$.

## Results

From May to August 2007, a total of 29406 body temperature ($T_b$) measurements from the 22 musk turtles (13 females and 9 males) were recorded. This sum includes 429 measurements that were recorded manually, the rest were recorded with the automated data loggers. These observations were condensed to 10725 hourly mean $T_b$ values, which were used as the basis for all necessary analyses.

### *Thermal Preference*

In total, 14 thermal preference measurements of 7 different turtles were used to estimate $T_{set}$ for *Sternotherus odoratus* (see annex for data). Averaged for all studies, the mean 75 and 25% quartiles of the distribution of selected $T_b$ were 28.02 ± 0.78 and 24.4 ± 0.98°C, respectively.

### *Thermal Quality of Habitats*

Due to technical difficulties experienced in the field, we do not have $T_e$ measurements for the month of May. As a result, all analyses including $T_e$ measurements will use data from June, July and August only. A total of 8344 $T_e$ measurements were collected from 8 locations. These were condensed to 4401 measurements representing the 4 respective habitats. Mean monthly *T*e increased during the study period reaching the highest temperature in August, however, mean $T_e$ never reached $T_{set}$ in any month (Fig. 2), suggesting that the habitat of musk turtles in the Thousand Islands ecosystem is thermally challenging. The deep water (>2m) habitat was the coolest and less variable throughout the day (Fig. 2) and had the lowest mean monthly $T_e$ throughout the whole study period (Table 2). In fact, the lowest bound of $T_{set}$ (24.4°C) was reached only once in this particular habitat (representing 0.05% of observations), suggesting that deep habitats could serve as a refuge from high temperatures. The surface cover habitat provided the highest values of $T_e$ in every month.

The habitat with the highest thermal quality (lowest $d_e$), by comparing the mean $d_e$ for the whole study period, was the habitat with surface cover (3.21 ± 0.43). Deep water had the lowest thermal quality (5.16 ± 3.07). I used the mean monthly $d_e$ and the percentage where $T_e$ was within the range of $T_{set}$ ($d_e = 0$) to quantify the thermal quality of each habitat by month. Mean monthly $d_e$ values ranged from 1.5 ± 0.07 for the shallow habitat in August to 8.0 ± 0.07 for the deep habitat in June (Table 2). In general, the thermal quality (low $d_e$) of habitats increased during the study period. The surface cover habitat had the highest quality in June and July but the lowest in August. In fact, $d_e = 0$ in June could practically only be reached in the habitat with surface cover (18.9% compared to near 0% for the other habitats). In July, however, surface cover habitats were closely followed by shallow habitats in terms of thermal quality, and were surpassed in August ($d_e = 0$ for 37.1% of time in shallow habitats).

### *Patterns of Body Temperature*

A repeated measures two-way ANOVA indicated that $T_b$ varied significantly between months ($F=37.61$, $p<0.0001$) and sex ($F=4.94$, $p=0.0314$). However, the interaction term was not significant. The significant $T_b$ difference observed between sexes is only 1.6°C (a mean of 23.77 ± 0.55°C for males and 25.37 ± 0.48°C for females). This difference, when looked at on a performance curve, does not change performance due to the typically flat plateau of such curves (Ben Ezra et al 2008). Therefore, we could assume that the statistically significant difference in body temperatures between sexes is not biologically significant. However, when plotting the monthly mean $T_b$ for males and females separately, I observed that compared to other months, the most important difference seems to be in May ($\Delta$=2.86°C), when gravid females are carrying their eggs (Fig. 3). This suggests that there is a possibility of an effect of sex; nevertheless, due to my relatively low sample size and the unsatisfactory amount of $T_b$ measurements for the month of May, I pooled the data for both sexes for all further analyses. Mean monthly $T_b$ was the lowest in May (20.69 ± 0.54°C) and reached a peak in August (26.6 ± 0.48°C). However, a Tukey-Kramer HSD test revealed that mean monthly $T_b$ in August was not different from June and July.

The distribution of mean hourly $T_e$ was compared to the distribution of mean hourly $T_b$ using a two-sample Kolmogorov-Smirnov test and was found to be significantly different ($D = 0.6251$, $p < 0.0001$). In fact, for all observations, $T_b$ fell within the range of $T_{set}$ 47.4% of the time while $T_e$ were located within this range for only 10.7% of the time (Fig. 4). The distribution indicates that musk turtles avoided low temperature extremes and maintained body temperatures above the mean $T_e$. The distribution of mean hourly $T_e$ was weighted by the habitat availability. In this way more importance is given to temperatures of the deep habitat (61.8% of the total area) where the lowest temperatures were found. The observed pattern indicates that musk turtles avoided this habitat and selected habitats with less availability but with higher thermal quality.

Monthly plots of mean hourly $T_b$, maximum hourly $T_e$ and minimum hourly $T_e$ showed that musk turtles were as warm as they could get during the night for all three months (Fig. 5). In June, musk turtles were as warm as their environments permitted throughout the whole day, suggesting that the habitats with the highest temperatures were selected. However, in July and August, the warmest environments were avoided during the day. Furthermore, hourly mean $T_b$ of musk turtles generally fell within the range of $T_{set}$ throughout the whole day (Fig. 5).

### *Indices of Thermoregulation*

The mean $d_b$, according to the mean calculated for all individuals during the study period, was 1.91 ± 0.18 and the mean $d_e$ (weighted by habitat availability) for all four habitats was 4.5 ± 0.46. Therefore, the average value of $d_e$-$d_b$ (effectiveness of thermoregulation index) for all individuals was 2.59 ± 0.18. This demonstrates that musk turtles are on average 2.59°C closer to $T_{set}$ than what is randomly available. In the same way, I calculated the mean monthly $d_e$-$d_b$ and the mean hourly $d_e$-$d_b$ for all individuals (Fig. 6). The difference between $d_e$ and $d_b$ was greatest early in the season and decreased throughout the active season resulting in higher thermoregulation effectiveness in June than July and August. In June, musk turtles were on average 6.56°C closer to $T_{set}$ than what is available, compared to 1.1°C in August (Fig. 6). Additionally, the pattern observed when looking at the mean hourly $d_e$-$d_b$ suggests that musk turtles thermoregulated more effectively during the night than during the day (Fig. 7).

After averaging the Ex values for all individuals, the proportion of $T_b$ within $T_{set}$ when it was possible was 44.2 ± 2.56%. Consequently, the proportion of $T_b$ above $T_{set}$

was 41.4 ± 2.14% and the proportion of $T_b$ below $T_{set}$ was 14.3 ± 0.51%. A one-way ANOVA indicated that the proportions of Ex did not differ between months (Fig. 7, F=1.134, p=0.3293). This pattern indicates that throughout the active season, musk turtles chose habitats that permitted them to maintain $T_b$ equal or above $T_{set}$ more often than below.

*Home Range and Macrohabitat selection*

Habitat data was collected for 22 (13 females and 9 males) individuals who were tracked regularly throughout the whole active season. The home range size differed greatly from one individual to the other, ranging from (0.622 ha) to (22.11 ha) with a mean of (6.63 ± 1.1) but did not significantly differ with sex ($t_{20}$= 1.519, p = 0.14). In both kernel intensities, musk turtles selected the shallow water, intermediate water and surface cover habitats more than what was available and deep water less than was available (Fig. 8). Habitat was used non-randomly at both the 95% kernel ($\chi^2_3 = 50.08$, $p < 0.0001$) and the 50% kernel ($\chi^2_3 = 86.63$, $p < 0.0001$) for all individuals. The same habitat preference trend was observed at both intensity levels (Table 3). The ranking from most to least preferred is SCOVER > SHALLOW > INTER > DEEP. For both kernel densities, all pairs are significantly different (see Table 3 for t-test values and p-values).

## DISCUSSION

### *Thermal Quality and Patterns of Thermoregulation*

The musk turtles in the study area were exposed to an environment that was thermally challenging throughout most of the active season. In fact, mean monthly $T_e$ never reached the bounds of $T_{set}$ and mean hourly $T_e$ only reached the bounds of $T_{set}$ in habitats with surface cover, and only for a few hours during the afternoon. The environment was especially challenging in June, where $T_{set}$ could only be reached in habitats with surface cover. As a result, habitats with surface cover provided superior thermoregulation opportunities earlier in the active season, by having $T_e$'s falling within $T_{set}$ 18.9% of observations compared to 0% for the other habitats. Early active season (late May-June) is considered a critical time for turtles coming out of hibernation and especially for pre-nesting females needing great energetic requirements (Krawchuk and Brooks 1998), therefore I assume that the thermal quality of surface cover habitats at that time would be very important for musk turtles in the St. Lawrence River. This, however, changed as the season progressed and the water got warmer. Nevertheless, the majority of the habitat within the home range (deep water) never reached preferred temperatures. In July, the habitats with surface cover were of similar thermal quality to habitats in shallow waters deprived of such cover and in August, the difference in thermal quality between all habitats was minor (Table 2). Despite this, the highest percentages of $T_e$'s falling within $T_{set}$ were observed in habitats with surface cover and shallow water. Therefore as expected, the habitats that provided optimal thermal conditions early in the active season when the water was at its coolest were the regions of the river with surface cover.

However, it became less evident which habitat was thermally superior later in the season when the water temperature was more homogenous between habitats. Our quantification of the thermal quality of the habitat reflects similar challenging thermal conditions found in previous reptilian studies in Ontario (Blouin-Demers and Weatherhead 2002, Row and Blouin-Demers 2006b, Edwards and Blouin-Demers 2007).

Despite the evidence of poor environmental thermal quality, musk turtles were able to closely maintain their $T_b$ within the preferred range throughout the whole study period (Fig.5), indicating that they are effective thermoregulators. The daily $T_b$ profile for the month of June indicates that musk turtles were as warm as the environment permitted them to be throughout the whole day. The profile for July and August followed a comparable trend by keeping a relatively similar and constant $T_b$ throughout the whole day. However, unlike June, musk turtles thermoregulated more carefully at night by keeping mean hourly $T_b$ at the maximal temperatures available and avoided those extremes during the day (Fig. 5).

Compared to the thermoregulation indices ($d_e - d_b$ and Ex) quantified for other snakes and lizards, musk turtles can be categorized as moderate thermoregulators (Blouin-Demers and Nadeau 2005). To my knowledge, only one other study has applied quantitative indices of thermoregulation to describe the thermal ecology of a turtle species (Edwards and Blouin-Demers 2007). Compared to the painted turtle (*Chrysemys picta*) population studied by Edwards and Blouin-Demers (2007), which is also located in the temperate region of Ontario, musk turtles displayed very similar index values. Musk turtles had a mean effectiveness of thermoregulation value of 2.59 and exploited the thermal environment for 44.2% of the time, where values calculated for painted turtles were 2.4 and 42% respectively (Edwards and Blouin-Demers 2007). Both of these species can be found living in the same habitats and thus, are exposed to the same thermal environments (Ernst 1994). However, both species seem to utilize different basking strategies in the field. Musk turtles are mostly found basking under water (“aquatic basking”) and painted turtles above water (“aerial basking”) (Ernst 1994). I did not record any observations of “aerial basking” by musk turtles during the study period, whereas Edwards and Blouin-Demers (2007) observed painted turtles basking out of water more than twice as much as under water. As such, my findings of the thermoregulatory behaviour of musk turtkes compared to painted turtles suggests that both basking strategies are equally effective and permit the exploitation of the thermal environment to the same extent.

### *Habitat Selection*

As expected, the present study indicates that at the home range scale, musk turtles used habitats non-randomly and had a strong preference for thermally superior habitats. Musk turtles living near the south shore of Grenadier Island in the St. Lawrence River strongly preferred aquatic habitats composed of floating or submerged aquatic vegetation, such as lily pads (*Nymphaea odorata* and *Nuphar variegata*), cattails (*Typha* sp.), and macrophytes, that serve as surface cover. These habitats were mostly found in small bays near shoreline with shallow water and very slow current, therefore could explain why habitats with shallow water closely followed surface cover in terms of habitat preference. On the other hand, despite being the dominant habitat within the study area, deep waters were clearly avoided during the active season. The fact that musk turtles clearly preferred aquatic habitats with surface cover and of shallower depths over intermediate and deep water depths provides evidence that there is a strong link between the thermal quality of habitats and habitat selection. The physical factors influencing heat exchange are evidently very complex, however for the simplicity of things, I assume that floating vegetation such as lily pads provide great thermoregulation opportunities because it absorbs sunlight and heats the water directly underneath, thus creating thermally superior habitats.

In thermally challenging conditions such as the temperate environment of Ontario, the link between thermoregulation and habitat selection has been determined to be very strong (Blouin-Demers and Weatherhead 2002, Row and Blouin-Demers 2006b). However, thermoregulatory requirements are certainly not an exclusive factor contributing to habitat selection. Other studies have shown that reptiles tend to select habitats based on other factors than thermoregulation, such as foraging requirements (Reinert 1993, Compton et al 2002) and predator avoidance (Webb and Withing 2005, Downes 2001). Musk turtles have been described as omnivorous generalists, searching for food at the bottom of the water by probing their head into the soft substrate (Mahmoud 1968, Ernst 1986) and feeding mostly on algae, leeches, various mollusks and insects (Ford and Moll 2004). The shallow waters in our study area, by having slow current favoring accumulation of decaying organic matter, provided great foraging opportunities for musk turtles. Having said that, since the dietary components of musk turtles are not limited to shallow waters and are mostly found throughout the entire study area, foraging requirements does not seem to be a driving factor for the selection of habitats with surface cover and shallow water during my study period. Ford and Moll

(2004) have shown that foraging patterns of a musk turtle population in Missouri differed between sex and seasons, therefore, if the choice of diet would influence habitat selection, a shift in habitat preference could be expected between seasons. Since our study did not cover the entire active period of musk turtles in temperate regions (post to pre-hibernation) and that I did not quantify food consumed, formal exclusion of the fact that seasonal change in foraging requirements might be an important factor driving habitat selection was not possible. As for predator avoidance, musk turtles are very cryptic and are rarely observed out in the open (Ernst 1986). Upon location, the tracked individuals were mostly found burrowed in the substrate or floating amongst or under vegetation, and in either case, were rarely completely revealed. This suggests that surface cover habitat does provide good hiding opportunities but musk turtles also buried themselves at areas without any aquatic vegetation, possibly in order to conceal themselves from predators. Due to the fact that two musk turtles were found dead, however were presumably killed while nesting, and that I did not quantify the predation pressure in the different habitats, I cannot formally exclude predator avoidance as a driving factor in habitat selection by musk turtles.

Quantification of habitat selection at a finer spatial scale would give us a more complete picture and would be an important step in determining if factors other than thermoregulatory requirements are affecting habitat selection by musk turtles (Orians and Wittenburger 1991, Rettie and Messier 2000, Compton et al 2002). For example, Compton, Rhymer and McCollough (2002) examined the habitat selection by wood turtles (*Clemmys insculpta*) and determined that selection differed between the two scales investigated (micro- and macrohabitat). At the home range scale (macrohabitat), wood turtles selected moderately forested areas near bodies of water, potentially rich in food, and selected nonforested locations that provided good basking opportunities within these activity areas (microhabitat). This between-scale conflict in preferred habitats suggests that wood turtles selected forest edges in order to adjust to the trade-off between the thermoregulatory and foraging requirements (Compton et al 2002). In a similar fashion, the selection of shallow water habitats with abundant plant surface cover by musk turtles in the study area could also suggest a trade-off between thermoregulation and feeding or even between thermoregulation and hiding from predators.

### *Conservation Implications*

Musk turtles have a remarkably vast geographical range and can be found as far south as Florida and as far west as Wisconsin and Texas (Reynolds and Seidel 1982). This study has been done at the northern limit of their range in Ontario Canada, where one single study (Edmonds and Brooks 1996) limits the amount of ecological knowledge accessible for recovery planning and management efforts. Therefore in this study, I present the first in-depth quantitative study of the thermal ecology of the musk turtle, providing critical information on the habitat selection of the species at the home range scale.

Factors brought up to explain the recent global decline of reptile populations are diverse (i.e. invasive species, pollution, diseases, harvesting, etc, Gibbons et al 2000). However, reptiles are particularly vulnerable to habitat lost and degradation and therefore are considered to be the primary factors driving their decline (Gibbons et al 2000). Consequently, due to the strong link observed between thermoregulation and habitat selection, understanding this thermal relationship is therefore an essential conservation tool for the identification and protection of critical habitats needed for survival. The present study underlines the importance of protecting natural shoreline habitats used by musk turtles in the study area, in Ontario Canada, where the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has listed the species under a threatened status. Natural shorelines, compared to developed shorelines, possess more emergent and aquatic vegetation (Radomski and Goeman 2001), which is associated with musk turtles and crucial to their aquatic behaviour. Accordingly, this study provides fundamental information to Parks Canada, who have an obligatory mandate to protect critical habitats of the species as part of their recovery plan.

### *Conclusion*

In summary, my results support the hypothesis that the thermal quality of the environment is strongly linked to habitat selection by reptiles living in a thermally challenging environment. The present findings demonstrate that aquatic vegetation is an important structural component affecting habitat selection by musk turtles in the St. Lawrence River, Ontario. Habitats with aquatic vegetation such as lily pads and macrophytes were of highest thermal quality within the activity range of musk turtles during our study period. Preferential selection of these habitats is consistent with the prediction that these thermally superior habitats provide optimal thermoregulating opportunities, especially when the water is very cool. This also explains the typical aquatic basking behaviour of musk turtles, which consists of floating under or amongst aquatic vegetation. Similar quantitative studies looking at habitat selection in relation to thermal ecology in other parts of the species range would be needed in order to compare whether the relationship is as strong in less thermally challenging environments where factors other than thermoregulation would presumably be driving habitat selection.

Table 1. Definitions of the various symbols and indices used in the quantification of thermoregulation.

| Symbol | Definition |
|---|---|
| $T_b$ | The body temperatures of the study animals. |
| $T_e$ | The operative environmental temperatures: the equilibrium body temperatures that animals would experience at a specific location. |
| $T_{set}$ | The range of preferred body temperatures of an animal. Typically measured by the bounds of the central 50% of the distribution of body temperatures selected in a laboratory thermal gradient. |
| $d_b$ | A measure of the accuracy of body temperature (Hertz et al 1993). Measured by the absolute value of the deviations of field $T_b$s from $T_{set}$. |
| $d_e$ | A measure of the thermal quality of the habitat (Hertz et al 1993). Measured by the absolute value of the deviations of field $T_e$s from $T_{set}$. |
| $d_e - d_b$ | Index of the effectiveness of thermoregulation proposed by Blouin-Demers and Weatherhead (2001). |
| Ex | Exploitation of the thermal environment index: calculated as the time in which an animal's $T_b$s are within $T_{set}$ divided by the time available for the animal to have its $T_b$ within $T_{set}$ (Christian and Weavers 1996). |

Table 2. Monthly mean (± 1 SE), maximum and minimum operative environmental temperatures ($T_e$) recorded in the four main habitats available to musk turtles in the St. Lawrence River, Ontario, Canada. Monthly mean (± 1 SE), maximum and the percentage of $T_e$ falling within the range of $T_{set}$ ($d_e = 0$).

| Habitat | $T_e$ | | | $d_e$ | | |
|---|---|---|---|---|---|---|
| | Mean | Maximum | Minimum | Mean | Maximum | %=0 |
| June | | | | | | |
| Shallow (<1m) | 18.94±0.09 | 25.5 | 13 | 5.5±0.09 | 11.4 | 0.8 |
| 1-2m | 17.40±0.07 | 21 | 12 | 6.7±0.07 | 12.4 | 0.0 |
| Deep (>2m) | 16.44±0.07 | 19 | 11.5 | 8.0±0.07 | 12.9 | 0.0 |
| Surface Cover | 21.62±0.12 | 30 | 13.5 | 3.2±0.10 | 10.9 | 18.9 |
| July | | | | | | |
| Shallow (<1m) | 22.11±0.08 | 28 | 17.5 | 2.5±0.07 | 6.9 | 17.1 |
| 1-2m | 20.44±0.06 | 25 | 17.5 | 4.0±0.06 | 6.9 | 0.9 |
| Deep (>2m) | 19.57±0.05 | 22.5 | 17 | 4.8±0.05 | 7.4 | 0.0 |
| Surface Cover | 23.56±0.16 | 37.5 | 15.5 | 2.7±0.08 | 9.5 | 19.9 |
| August | | | | | | |
| Shallow (<1m) | 23.44±0.09 | 28.5 | 17 | 1.5±0.07 | 7.4 | 37.1 |
| 1-2m | 22.73±0.04 | 25.5 | 19 | 1.7±0.04 | 5.4 | 9.1 |
| Deep (>2m) | 22.14±0.03 | 25 | 20.5 | 2.3±0.03 | 3.9 | 0.1 |
| Surface Cover | 23.15±0.19 | 38.5 | 13.5 | 3.3±0.11 | 10.9 | 21.2 |

Table 3. Matrices of t-values and associated p-values comparing between-pairs of habitat types in the 50% and 95% kernel for musk turtles (n = 23) in the St. Lawrence River, Ontario, Canada. Preference rankings are in order of most (1) to least (4) preferred.

| Habitat Type | Value | SCOVER | SHALLOW | INTER | DEEP | Rank |
|---|---|---|---|---|---|---|
| 50% Kernel | | | | | | |
| SCOVER | t-value | | 8.6306 | 5.3572 | 30.0513 | 1 |
| | p-value | | <0.0001* | <0.0001* | <0.0001* | |
| SHALLOW | t-value | | | 2.1051 | 27.1176 | 2 |
| | p-value | | | 0.0469* | <0.0001* | |
| INTER | t-value | | | | 17.8647 | 3 |
| | p-value | | | | <0.0001* | |
| DEEP | t-value | | | | | 4 |
| | p-value | | | | | |
| 95% Kernel | | | | | | |
| SCOVER | t-value | | 5.5034 | 9.7149 | 12.8717 | 1 |
| | p-value | | <0.0001* | <0.0001* | <0.0001* | |
| SHALLOW | t-value | | | 2.6883 | 11.8223 | 2 |
| | p-value | | | 0.0134* | <0.0001* | |
| INTER | t-value | | | | 12.4602 | 3 |
| | p-value | | | | <0.0001* | |
| DEEP | t-value | | | | | 4 |
| | p-value | | | | | |

* denotes significant difference

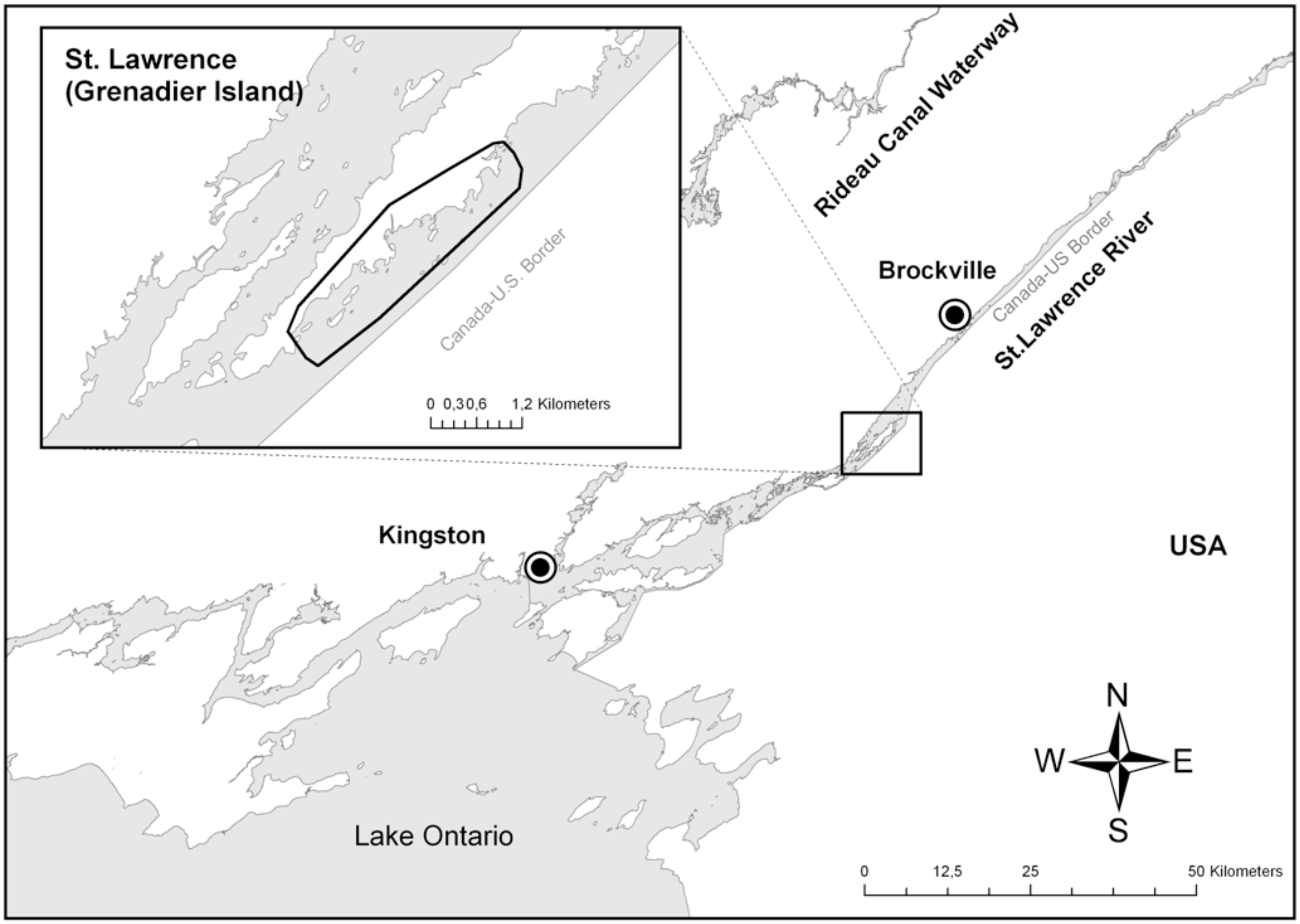

**Figure 1.** Grenadier Island located in the St. Lawrence River, Ontario, Canada. The bold polygon in the enlarged region represents the study area.

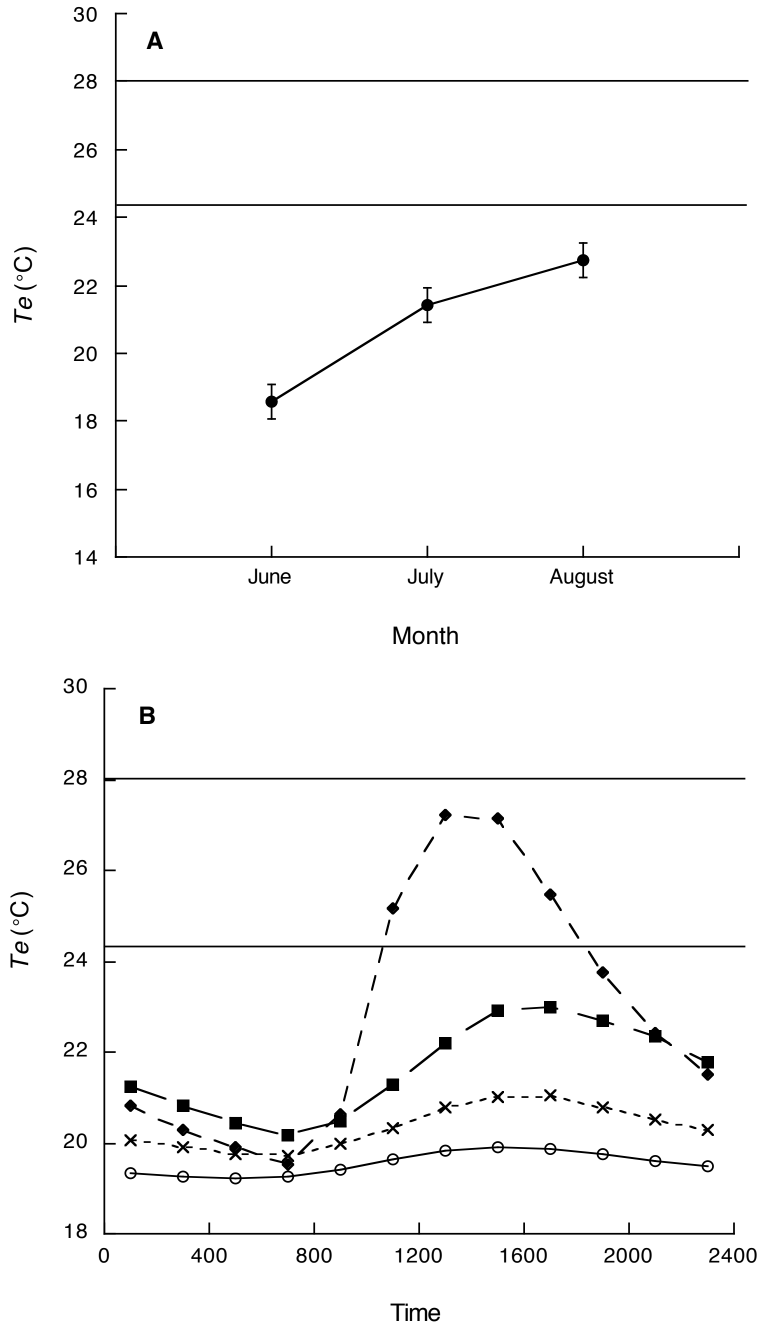

**Figure 2**. (A) Mean operative environmental temperatures ($T_e$ ± 1 SE) for the month of June, July and August, and (B) mean operative environmental temperatures for each hour of the day in deep water (open circles), intermediate water (x symbols), shallow water (closed squares) and under surface cover (closed lozenges). The range of preferred body temperatures (*T*set) estimated for musk turtles is represented by the horizontal lines.

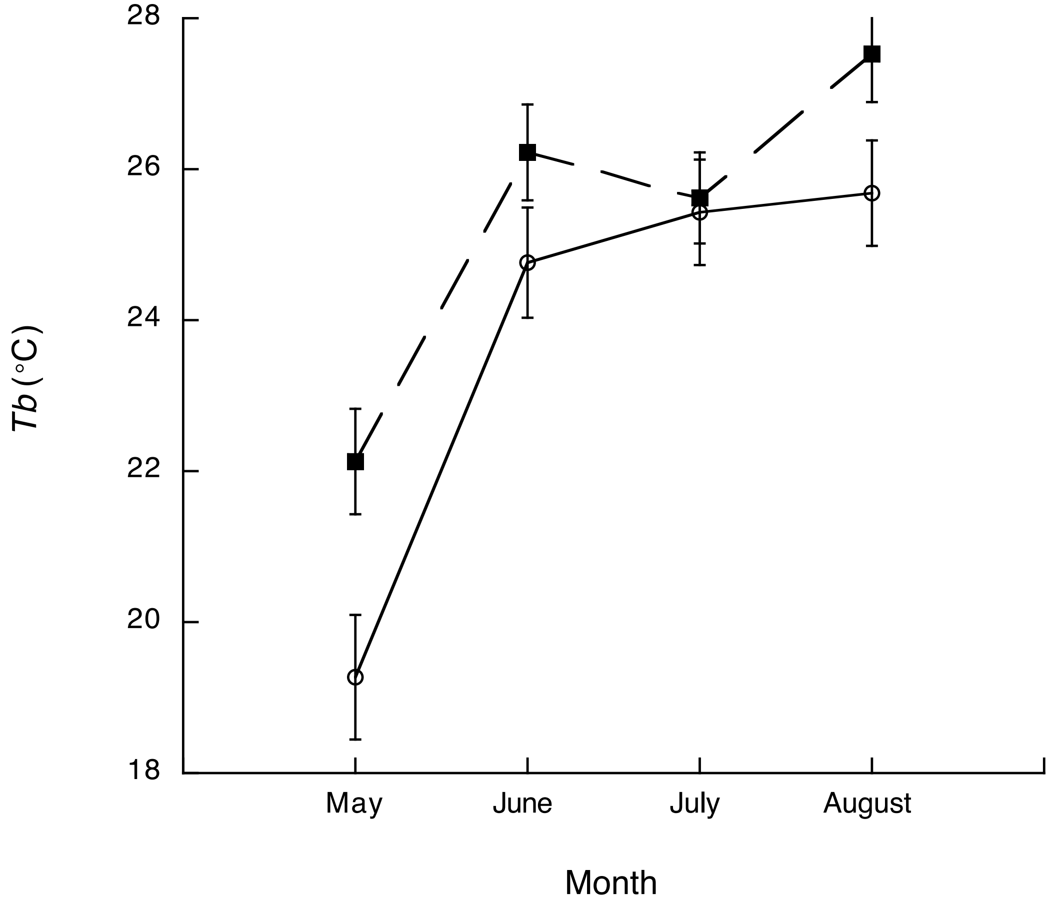

**Figure 3.** Mean (± SE) monthly body temperatures (*Tb*) of male (empty circles) and female (filled squares) musk turtles in the St. Lawrence River, Ontario, Canada.

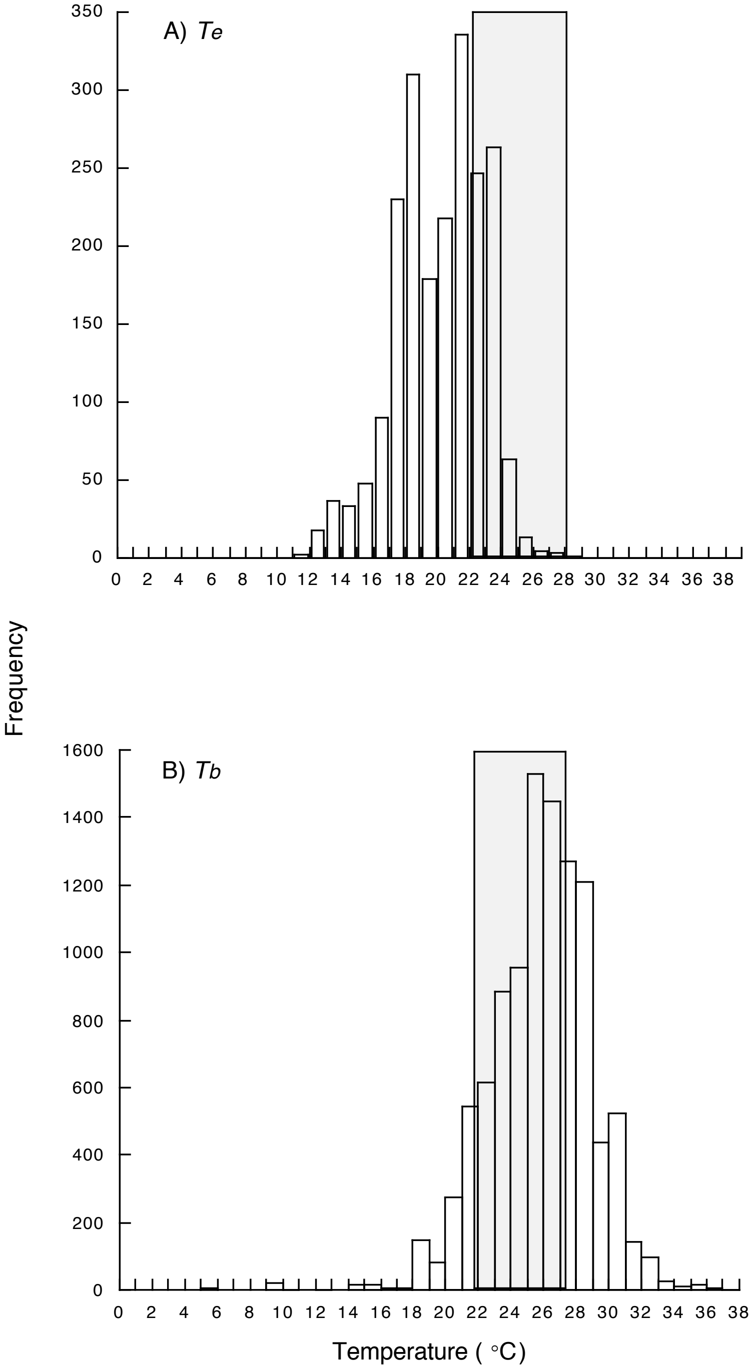

**Figure 4.** Frequency distribution of (A) hourly mean operative environmental temperatures (*T*$_e$) weighted by the habitat availability, and (B) hourly mean body temperatures of 22 musk turtles in the St. Lawrence River, Ontario, Canada. The range of preferred body temperatures (*T*set) estimated for musk turtles is represented by the shaded region. The data includes measurements from June, July and August.

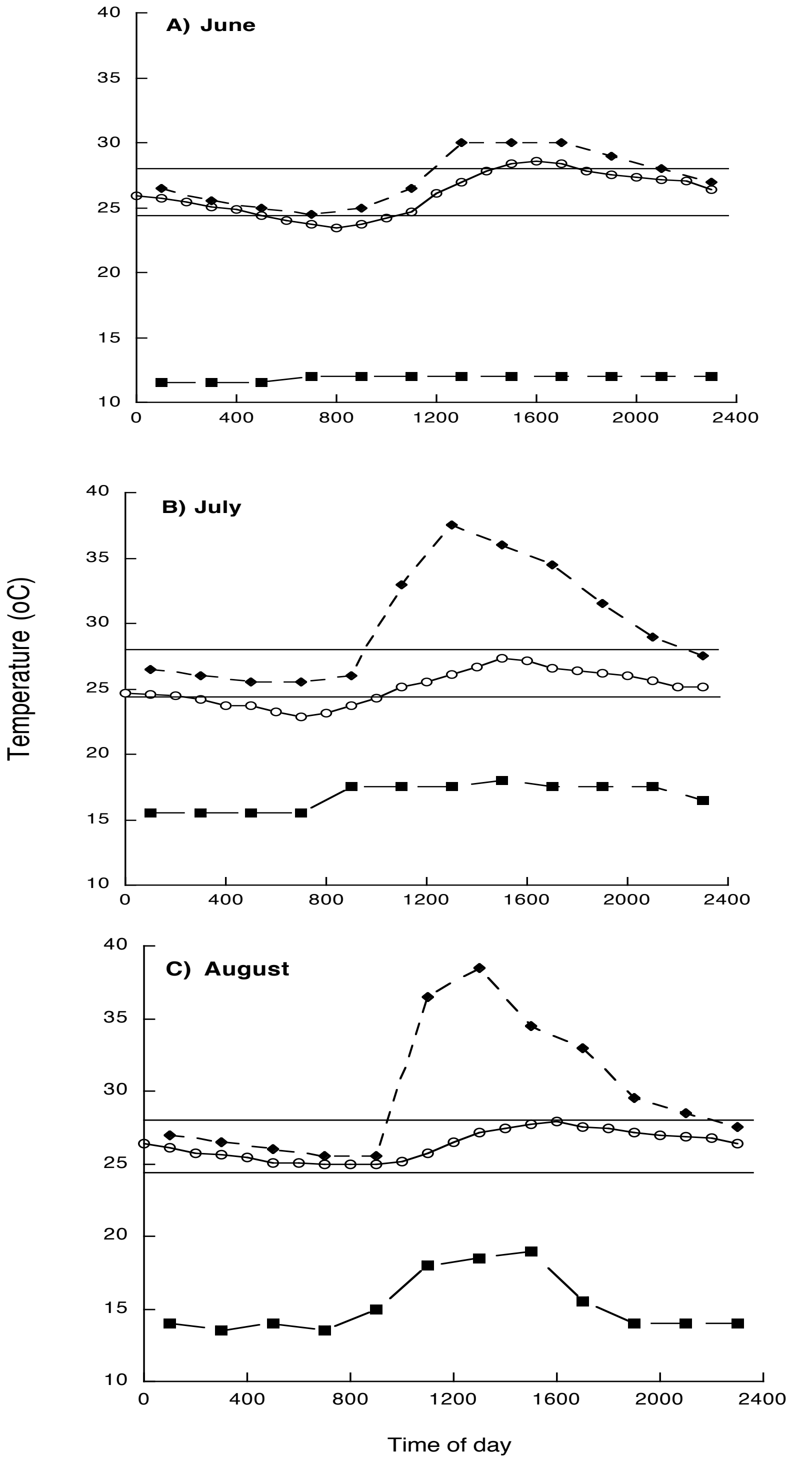

**Figure 5.** Hourly mean body temperatures (*T*b; empty circles) of Musk turtles and hourly mean maximum (*T*e; lozenges) and minimum (*T*e; squares) operative environmental temperatures (A) for June, (B) for July and (C) for August. The range of preferred body temperatures (*T*set) estimated for Musk turtles is represented by the horizontal solid lines.

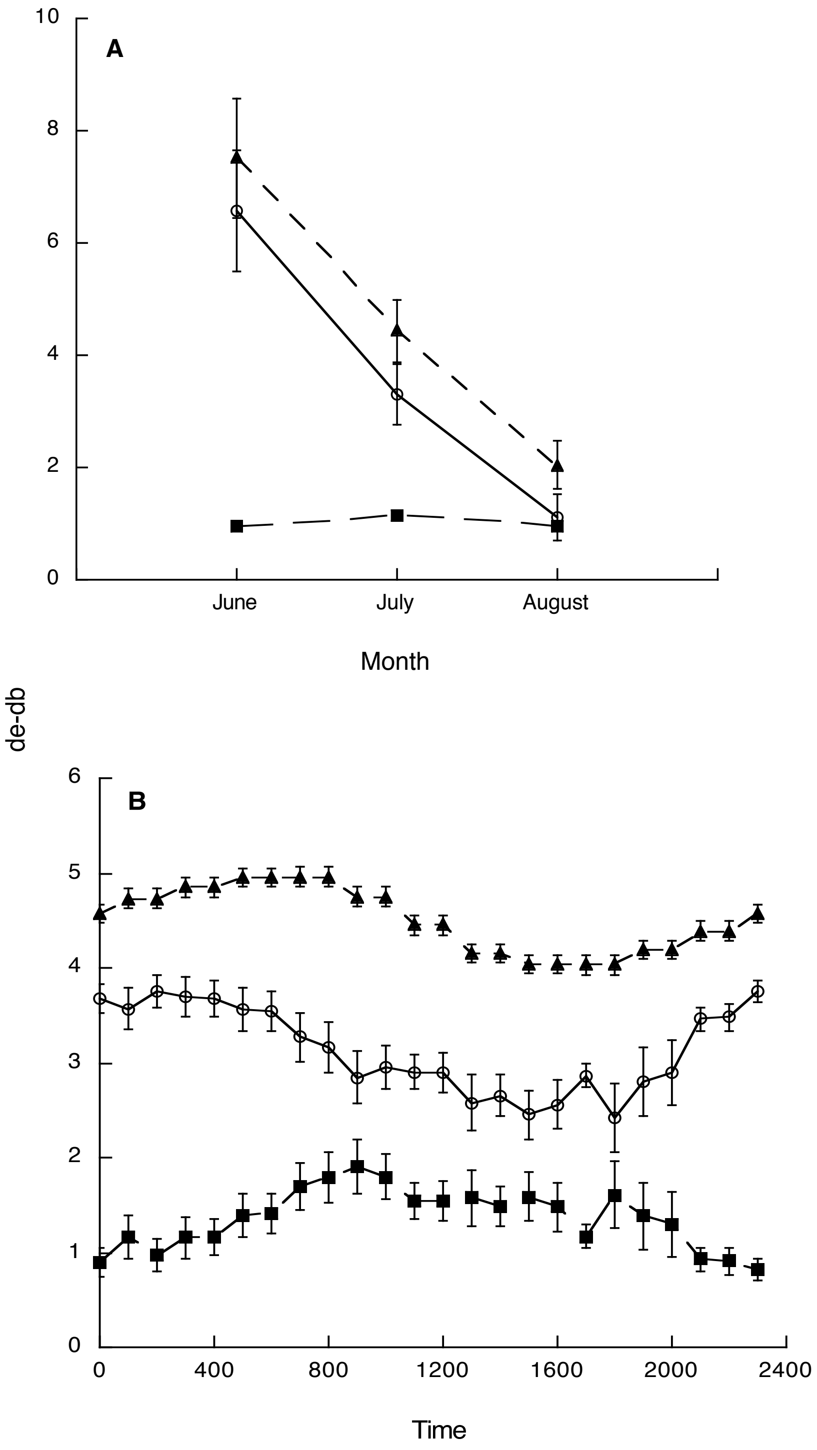

**Figure 6.** Monthly (A) and hourly (B) mean (± 1 SE) deviations of field $T_b$s from $T_{set}$ ($d_b$, filled squares), deviations of field $T_e$s from $T_{set}$ ($d_e$, filled triangles), and thermoregulation effectiveness index ($d_e$- $d_b$) for musk turtles in the St. Lawrence River, Ontario, Canada.

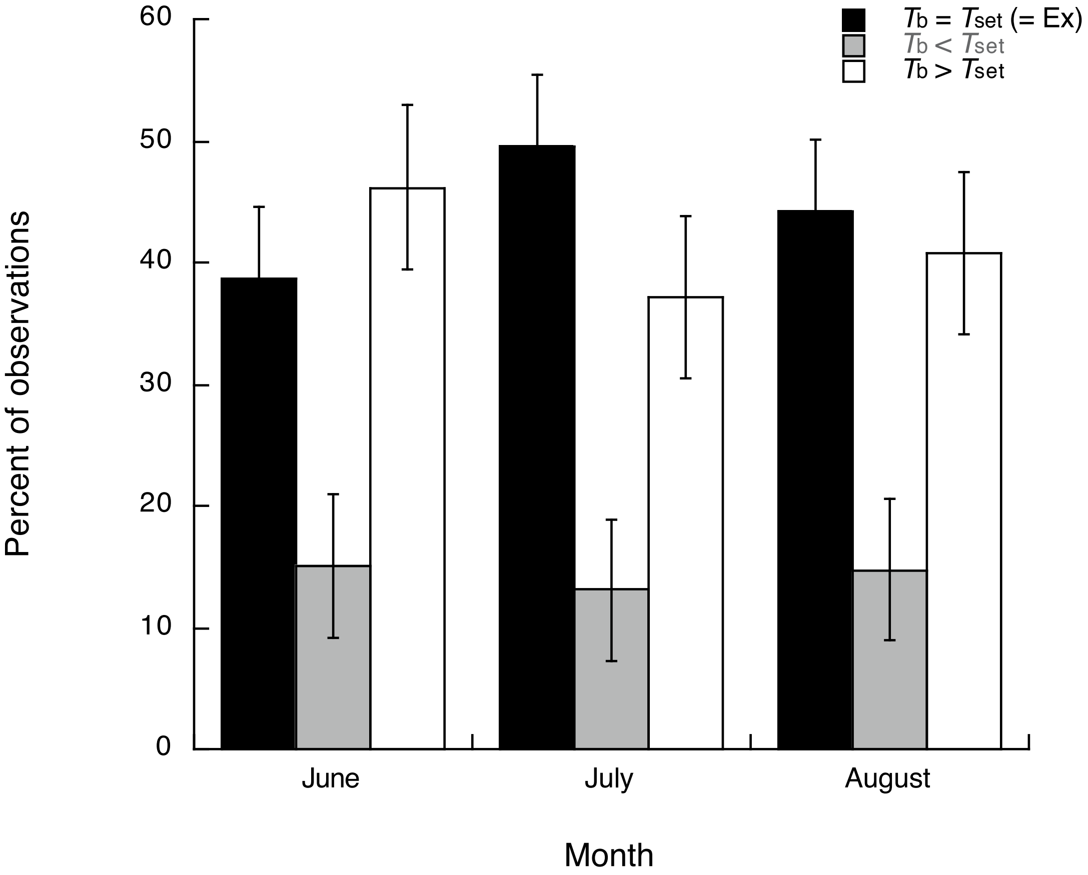

**Figure 7**. Mean percentage (± 1 SE) of the modified exploitation of the thermal environment index (Ex) for all musk turtles (n = 22) in the St. Lawrence River, Ontario, Canada.

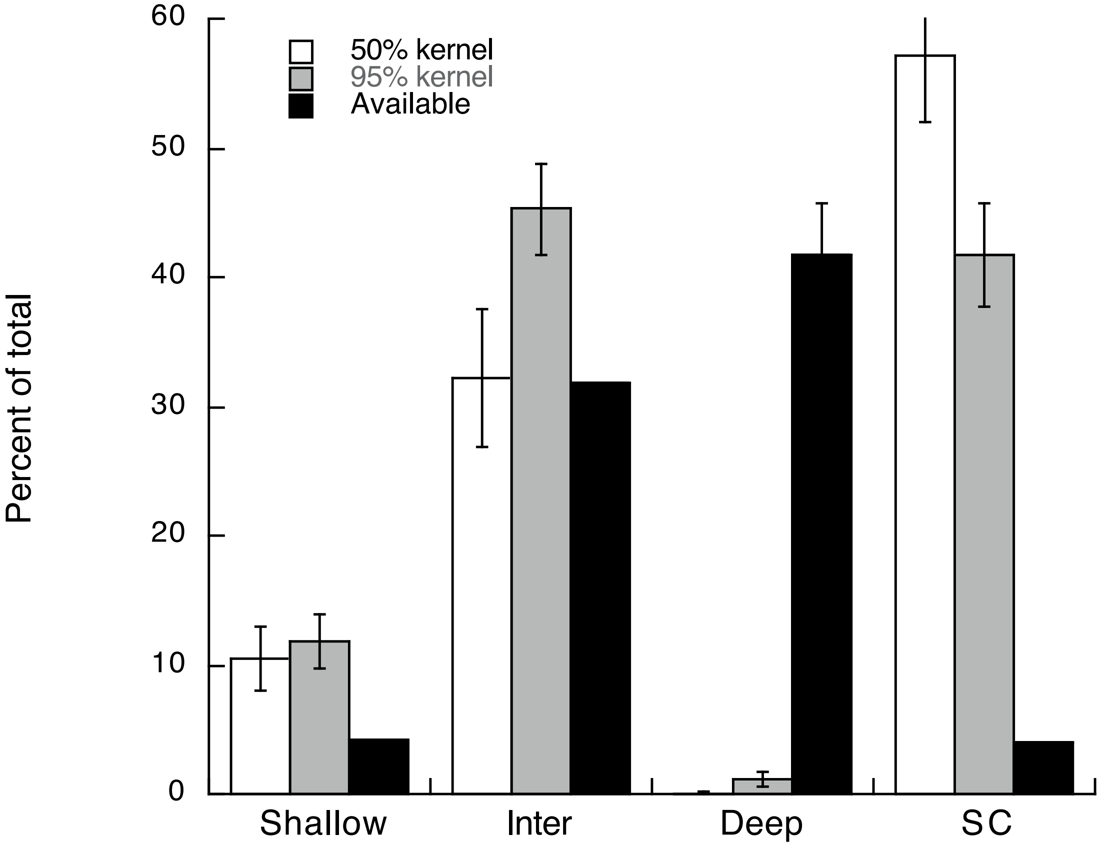

**Figure 8**. Mean percentage (± 1 SE) of the four habitat types within the 50% and 95% kernel home ranges and the available habitat for all musk turtles (n = 22) in the St. Lawrence River, Ontario, Canada.

# ANNEX

Data used to estimate, from the bounds of the central 50% of observed body temperatures ($T_b$), preferred temperature ($T_{set}$) of musk 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%

## CITED LITERATURE

Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by 2 *Sceloporus* lizards. Ecology **71**:315-327.

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology **74**:1313-1325.

Aitchinson, J. 1986. The statistical analysis of compostional data. Chapman and Hall, London, England.

Ben-Ezra E., Bulté, G. and Blouin-Demers, G. 2008. Are locomotor performances co-adapted to preferred basking temperature in the northern map turtle (*Graptemys geographica*)? Journal of Herpetology. *In press.*

Blouin-Demers, G., and P. Nadeau. 2005. The cost-benefit model of thermoregulation does not predict lizard thermoregulatory behaviour. Ecology **86**: 560-566.

Blouin-Demers, G., and P. J. Weatherhead. 2001. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology **82**: 3025-3043.

Blouin-Demers, G., and P. J. Weatherhead. 2002. Habitat-specific behavioural thermoregulation by black rat snakes (*Elaphe obsoleta obsoleta*). Oikos **97**: 59-68.

Beyer, H. L. 2004. Hawth's Analysis Tools for ARCGIS. *In* www.spatialecology.com/htools.

Brown, G. P., and P. J. Weatherhead. 2000. Thermal ecology of northern water snakes, *Nerodia sipedon*: population patterns and variation in relation to sexual size dimorphism. Ecological Monographs **70**: 311-330.

Carrière M. A. 2007. Movement patterns and habitat selection of common map turtles (*Graptemys geographica*) in St. Lawrence Islands National Park, Ontario, Canada. Unpubl. MSc thesis. University of Ottawa, Ottawa, Ontario, Canada.

Christian, K. A., and B. W. Weavers. 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. Ecological Monographs **66**: 139-157.

Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): An application of paired logistic regression. Ecology **83**: 833- 843.

Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bulletin of the American Museum of Natural History **83**: 265-296.

Downes, S. 2001. Trading heat and food for safety: costs of predator avoidance in a lizard: Ecology **82**: 2870–2881.

Edmonds, J. H., and R. J. Brooks. 1996. Demography, sex ratio, and sexual size dimorphism in a northern population of common musk turtles (*Sternotherus odoratus*). Canadian Journal of Zoology **74**: 918-925.

Edwards, A. L. and Blouin-Demers, G. 2007. Thermoregulation as a function of thermal quality in a northern population of painted turtles, *Chrysemys picta*. Canadian Journal of Zoology **85**: 526-535.

Ernst, C. H. 1986. Ecology of the turtle, *Sternotherus odoratus*, in southeastern Pennsylvania. Journal of Herpetology **20**: 341-352.

Ernst, C. H., J. E. Lovich, and R. W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C. 578 p.

ESRI. 2000a. ArcMAP 9.2. *in* Envrionmental Systems Research Institute, Redlands, California.

ESRI. 2000b. ArcView 3.2. *in* Environmental Systems Research Institute, Redlands, California.

Ford, D. K. and D. Moll. 2004. Sexual and seasonal variation in foraging patterns in the common musk turtle, *Sternotherus odoratus*, in southwestern Missouri. Journal of Herpetology, **38**: 296-301.

Gatten R. 1974. Effect of nutritional status on the preferred body temperature of turtles *Pseudemys scripta* and *Terrapene ornata.* Copeia **4**: 912-917.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, T. M. Greene, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. BioScience **50**: 653-666.

Graham, T. and Hutchinson, V. 1979. Effect of temperature and photoperiod acclimatization on thermal preferences of selected freshwater turtles. Copeia. **1**: 165-169.

Hayne, D. W. 1949. Calculation of size of home range. Journal of Mammalogy. **30**: 1-18.

Hertz, P. E., R. B. Huey, and R. D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms - the fallacy of the inappropriate question. American Naturalist **142**: 796-818.

Hooge, P. N., and B. Eichenlaub. 2000. Animal movement extension to ArcView 2.0. *in*. Alaska Science Center - Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.

Huey, R. B. 1974. Behavioral Thermoregulation in Lizards: Importance of Associated Costs Science. **184**: 1001-1003

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist **137**: S91-S115.

Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pages 25- 91 *in* C. Gans and F. H. Pough, editors. Biology of the Reptilia. Academic Press, New York.

Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends in Ecology and Evolution **4**: 131-135.

Huey, R. B., C. R. Peterson, S. J. Arnold, and W. P. Porter. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. Ecology **70**: 931-944.

Knight, T. W., J. A. Layfield & R. J. Brooks, 1990. Nutritional status and mean selected temperature of hatchling snapping turtles (*Chelydra serpentina*): Is there a thermophilic response to feeding? Copeia, **1990**: 1067-1072.

Krawchuk, M. J and Brooks, R. J. 1998. Basking behavior as a measure of reproductive cost and energy allocation in the painted turtle, *Chrysemys picta.* Herpetologica **54**: 112-121.

Leban, F. A. 1999. Resource Selection for Windows. *in* U. o. Idahoe, editor., Moscow, Idaho, USA.

Mahmoud, I. Y. 1968. Feeding behavior in kinosternid turtles of Oklahoma. Southwestern Naturalist, **14**: 31-66.

Nebeker, A. V., and Bury, R. B. 2000. Temperature Selection by Hatchling and Yearling Florida Red-bellied Turtles (*Pseudemys nelsoni*) in Thermal Gradients. Journal of Herpetology. **34**: 465-469.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist **137**: S29-S49.

Powell, R. A. 2000. Animal Home Ranges and Territories and Home Range Estimators. Pages 65-110 *in* L. Boitani and T. Fuller, editors. Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York.

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radomski, P., and T. J. Goeman. 2001. Consequences of human lakeshore development on emergent and floating-leaf vegetation abundance. North American Journal of Fisheries Management **21**: 46-61.

Reinert, H. K. 1993. Habitat selection in snakes. Pages 201-240 *in* R. A. Seigel and J. T. Collins, editors. Snakes: Ecology and Behavior. The Blackburn Press, Caldwell.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography **23**: 466-478.

Reynolds, S. L., and M. E. Seidel. 1982. *Sternotherus odoratus*. *in* C. H. Ernst, editor. Catalogue of American amphibians and reptiles. American Society of Ichtyologists and Herpetologists, New York.

Row, J. R., and G. Blouin-Demers. 2006a. Thermal quality influences effectiveness of thermoregulation, habitat use, and behaviour in milk snakes. Ecophysiology **148**: 1-11.

Row, J. R., and G. Blouin-Demers. 2006b. Thermal quality influences habitat selection at multiple scales in milksnakes. Écoscience **4**: 443-450.

Row, J. R., and G. Blouin-Demers. 2006c. Kernels are not accurate estimators of home-range size for herpetofauna. Copeia **4**: 797-802.

SAS Institute. 2002. JMP 5.0.1 Statistical Analysis Systems. *in*, Cary, North Carolina.

Schuett, G. W., and Gatten, R. E.. 1980. Thermal preference in snapping turtles (*Chelydra serpentina*). Copeia **1980**: 149-152.

Shine, R., and T. Madsen. 1996. Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. Physiological Zoology **69**: 252-269.

Vitt, L. J. and Sartorius, S. S. 1999. HOBOs, Tidbits and lizard models: the utility of electronic devices in field studies of ectotherm thermoregulation. Functional Ecology **13**: 670-674.

Webb, J. K. and Whiting, M. J. 2005. Why don't small snakes bask? Juvenile broad-headed snakes trade thermal benefits for safety. Oikos. **110**: 515-522

Williamson, L. U., Spotila, J. R., and Standora, E. A. 1989. Growth, selected temperature and CTM of young snapping turtles, *Chelydra serpentina.* J. Therm. Biol. **14**: 33-39.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology. **70**: 164-168.

Zimmerman, L.C., M.P. O'Connor, S.J. Bulova, J.R. Spotila, S.J. Kemp and C.J.Salice. 1994. Thermal ecology of desert tortoises in the eastern Mojave Desert: seasonal patterns of operative and body temperatures and microhabitat utilization**.** Herpetological Monographs. **8**: 45-59.