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Do boating and basking mix? The effect of basking disturbances by motorboats on the body temperature and energy budget of the northern map turtle

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ABSTRACT

1. Basking is the primary mechanism used by many freshwater turtles to maintain their body temperature (T_b) in a range that maximizes physiological performance. Basking turtles are easily disturbed by motorboats, but the consequences of the increasingly popular use of motorboats on turtles is largely unknown.

2. In this work, predictive models built from field and laboratory data were used to assess the effects of the frequency of basking disturbance by motorboats on T_b and metabolic rate (MR) of female northern map turtles (*Graptemys geographica*), a species of conservation concern.

3. Simulations revealed that the effects of boat disturbance vary seasonally. In early May, a conservative estimate of the disturbance rate (0.15 per hour) resulted in a 0.34°C decrease in mean daily T_b, which translated to a 7.8% reduction in mean MR. In June, July and August, owing to warmer lake temperatures, the effect of disturbance was less marked and the observed disturbance rates (0.32, 0.96 and 1.23 per hour, respectively) reduced the mean MR of an adult female by 2.1%, 0.5%, and 0.4 %, respectively.

4. Reduction in MR decreases the rate of energy assimilation, which could translate into sublethal effects on turtles, such as reduced growth and reproductive output.

5. Motorboat usage is increasing in many areas and is probably affecting other species of freshwater turtles that use aerial basking. This study offers important insights on the implications of disturbances for species that bask.

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KEY WORDS: recreation; physiology; behaviour; modelling; reptiles; lake

INTRODUCTION

Human activities can interfere with many critical aspects of wildlife behaviour (Candolin and Wong, 2012). For example, anthropogenic noises can interfere with acoustic communication, therefore affecting mating and territorial behaviour in some species (Slabbekoorn and Ripmeester, 2008;

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Kaiser and Hammers, 2009; Hanna *et al.*, 2011). Human disturbance can trigger anti-predatory behaviour such as flight responses, increasing energy used for locomotion and causing disruption of important activities, such as foraging and parental care (Riddington *et al.*, 1996; Galicia and Baldassarre, 1997; Duchesne *et al.*, 2000; Verhulst *et al.*, 2001). Chronic human disturbance may ultimately affect individual fitness and lead to population declines (Frid and Dill, 2002).

Thermoregulation is a particularly important behaviour for ectotherms. Indeed, temperature influences nearly all aspects of their physiology and behaviour, including food intake and digestion (Kepenis and McManus, 1974; Parmenter, 1981; Avery *et al.*, 1993), growth (Brander, 1995; Kellar and De Nardo, 1995), metabolic rate (Gillooly *et al.*, 2001), locomotion (Stevenson, 1985; Damme *et al.*, 1991; Careau, 2014), immune function (Mondal and Rai, 2001), mating (Gayou, 1984), and reproductive output (Zuffi *et al.*, 1999; Rollinson and Brooks, 2007). Body temperature (T_b) is one of the key determinants of the fitness of ectotherms (Angilletta, 2002), and most ectotherms rely largely on behaviour to regulate their T_b (Tanaka *et al.*, 2000; Ouedraogo *et al.*, 2004; Ward, 2010). Behavioural thermoregulation is especially important for reptiles living in temperate regions where environmental temperatures are frequently far from physiologically optimal (Blouin-Demers and Nadeau, 2005). Thus, temperate reptiles tend to allocate an important part of their time budget to behavioural thermoregulation to decrease the duration and extent to which their T_b is outside their optimal range for performance (Row and Blouin-Demers, 2006; Dubois *et al.*, 2009; Picard *et al.*, 2011). Consequently, chronic interference with thermoregulatory behaviour has the potential to decrease the performance, and ultimately the fitness, of temperate reptiles.

The costs of interfering with behavioural thermoregulation may be particularly severe in freshwater turtles. The main thermoregulatory mechanism of many freshwater turtles is basking outside the water (atmospheric or aerial basking). This behaviour is essential for many turtles to achieve their physiologically optimal T_b (Bulté and Blouin-Demers, 2010a). Basking turtles are generally easily startled into the water (Moore and Seigel, 2006), and entering the water causes their T_b to drop rapidly (Spray and May, 1972). The energy budget of temperate freshwater turtles appears to be more limited by temperature-dependent food processing rates, rather than by food availability (Congdon, 1989), because freshwater turtles typically inhabit highly productive habitats and have long digestive turnover times (Parmenter, 1981). Therefore, interruption of basking behaviour appears to affect the energy budget of turtles adversely through its effect on T_b, thereby potentially causing sublethal adverse effects.

Boats are likely to be an important trigger of basking disturbance for freshwater turtles. In particular, motorboats have a high probability of disturbing basking turtles because of their high speed, noise, wake, and prevalence (Asplund, 2000). In Canada alone, 4.3 million recreational motorboats were registered in 2012 (NMMA, 2012) while in the United States that number was 12.5 million (NMMA, 2010). The frequency of basking disturbance by motorboats has been quantified for the yellow-blotched map turtle (*Graptemys flavimaculata*). Moore and Seigel (2006) found that when a motorboat passed a group of basking yellow-blotched map turtles throughout the year, the probability of at least one turtle entering the water was 57%, and on average 69% of the basking turtles entered the water. In addition, at least 13% of the disturbed turtles failed to return to basking that day. Given the ubiquity of boats on many bodies of water, the relative wariness of basking turtles to boats, and the energetic importance of basking behaviour for freshwater turtles, it is important to quantify the thermal and energetic costs that boat disturbance imposes on freshwater turtles. To our knowledge, the only study looking at the physiological consequences of basking disturbances in turtles was conducted by Selman *et al.* (2013) who found that higher rates of basking disturbance were associated with increased stress (heterophil/lymphocyte levels) and decreased body condition in yellow-blotched sawback turtles (*Graptemys flavimaculata*), suggesting that there may be energetic consequences of basking disturbance.

The objective of the present study was to quantify the thermal and energetic costs of basking disturbance for female northern map turtles (*Graptemys geographica*), a species of special concern in Canada (COSEWIC, 2012), at the northern limit of their range. The large size of female map turtles makes them more constrained than males by temperature (Bulté and Blouin-Demers, 2010b) and northern populations are more constrained by lower environmental temperatures than populations further south. The northern map turtle is a medium-sized freshwater turtle that inhabits large lakes and rivers where motorboats are common. In addition, the range of the northern map turtle coincides with highly populated areas of Canada and the USA. Thus, the northern map turtle is commonly exposed to boat disturbance throughout much of its range. The energetic importance of basking behaviour in juvenile northern map turtles has been demonstrated in a previous study. Bulté and Blouin-Demers (2010a) found that basking behaviour increased the standard metabolic rate (SMR) of juvenile northern map turtles by 17–30%, and that their basking behaviour is essential for managing energy assimilation. Juvenile northern map turtles were also found to spend 46% of daylight hours basking, highlighting the importance of basking time in this species (Bulté and Blouin-Demers, 2010a).

To assess the thermal and energetic consequences of motorboat disturbance on the northern map turtle, a simulation was developed to predict the body temperature of an average adult female map turtle under a range of frequencies of boat disturbance and at four times during the active season. The thermal and energetic effects of disturbance frequency were then quantified for each time period by comparing the T_b and metabolic rate (calculated from T_b) of a disturbed turtle with those of an undisturbed turtle. The study brought together elements of behaviour and physiological ecology to address a pressing conservation problem (Cooke *et al.*, 2014), and provides resource managers and conservation practitioners with information needed to ensure that disturbance to basking turtles arising from boating is minimized.

METHODS

Predictive heating and cooling equations

Field and laboratory data were collected at the Queen's University Biological Station on Lake Opinicon (44.5671°N, 76.3239°W) in Ontario, Canada. The simulation required the development of equations to predict the T_b of turtles while basking and when submerged. The equations predict changes in T_b based on the T_b of the turtle and the temperature of the turtle's surroundings, and assume that the derivative of the rate of change in T_b is constant across all differences in body temperature and water temperature when submerged, and constant across all differences in body temperature and air temperature when basking. To develop these equations, rates of heating in air and rates of cooling in water were measured for six female turtles (wild-caught from Lake Opinicon) ranging in mass from 1367–1976 g. Rates of change in T_b were measured using a K-type thermocouple inserted into the turtle's cloaca. The cloacal temperature was recorded every minute using a HOBO (U12-014) temperature data logger. To measure rates of heating, the turtles were first cooled below air temperature in an outdoor holding tank filled with circulating lake water. They were then placed in a plastic mesh cage (only slightly larger than the turtle to restrain movement) on an east-facing dock on Lake Opinicon to measure heating rates while basking. After approximately 2 h, the turtles were placed in an indoor water tank (80 L capacity) where they were unable to crawl out of the water, but where they could breathe, with a continuous flow of lake and well water. Turtles were left in the tanks for approximately 1 h to measure cooling rates while submerged. In addition, the water temperature (T_w) in the tank was measured at the beginning of submergence using an alcohol thermometer, and data on air temperature were collected from the Queen's University Biological Station weather station where it was measured every quarter of an hour. This process was repeated on 11 days with air temperatures ranging between 16.1°C and 23.2°C, and with water temperatures ranging between 12.5°C and 22.2°C, which are within the range of temperatures commonly experienced by turtles in Lake Opinicon (Bulté and Blouin-Demers, 2010a).

To determine rates of change in T_b of a turtle submerged in water, for every cooling experimental trial the mean rate of change in T_b was determined between every consecutive temperature measurement. When submerged, turtles experience convective cooling, so their rate of change in T_b is proportional to the difference between the temperature of the surrounding water (T_w) and their T_b (Dzialowski and O'Connor, 2001). Thus, the mean rate of change (dT_b/dt) was regressed against T_b–T_w to obtain an equation predicting dT_b/dt as a function of T_b–T_w when submerged in water (Figure 1):

$$\text{submerged}: \quad \frac{dT_b}{dt} = c_1\left(T_{b_{[t]}} - T_{w_{[t]}}\right) \qquad (1)$$

where c_1 was found to be 0.0591 and the regression fitted the data with $R^2 = 0.86$. Note that the constant c_1 is equivalent to the mean thermal time constant (a constant often used to compare rates of heating and cooling) of the turtles multiplied by the mean surface area of the turtles (Dzialowski and O'Connor, 2001).

To determine rates of change in T_b of a basking turtle, the mean rate of change in T_b was determined between every consecutive temperature measurement taken from basking turtles. When basking, turtles experience more than just convective heating and cooling; however, the rate of change is probably still well explained by the surrounding temperature (T_{air}). Thus, dT_b/dt was regressed against T_b and T_{air} to obtain an equation predicting dT_b/dt as a function of T_b and T_{air} when basking (Figure 1):

$$\text{basking}: \quad \frac{dT_b}{dt} = -c_2 T_{b_{[t]}} + c_3 T_{air_{[t]}} \qquad (2)$$

where c_2 and c_3 are constants. The value of c_2 and c_3 were found to be 0.00624 and 0.0149, respectively. The regression fitted the data with an $R^2 = 0.66$.

The rate of change in T_b across a one-unit time interval (from t–1 to t) can also be expressed as:

$$\frac{dT_b}{dt} = T_{b_{[t]}} - T_{b_{[t-1]}} \qquad (3)$$

substituting Equation (1) into Equation (3) yields an equation that can be used to estimate the T_b of a female northern map turtle in water given the turtle's body temperature one time step (a minute) earlier and given the water temperature:

$$\text{submerged}: \quad T_{b_{[t]}} = \left(T_{w_{[t]}} + \frac{T_{b_{[t-1]}}}{c_1}\right)\left(\frac{c_1}{1+c_1}\right) \qquad (4)$$

Substituting Equation (2) into Equation (3) results in an equation that can be used to estimate the T_b of a female northern map turtle in air given the turtle's body temperature one time step earlier and given the air temperature:

$$\text{basking}: \quad T_{b_{[t]}} = \left(c_2 T_{air_{[t]}} + T_{b_{[t-1]}}\right)\left(\frac{1}{1-c_3}\right) \qquad (5)$$

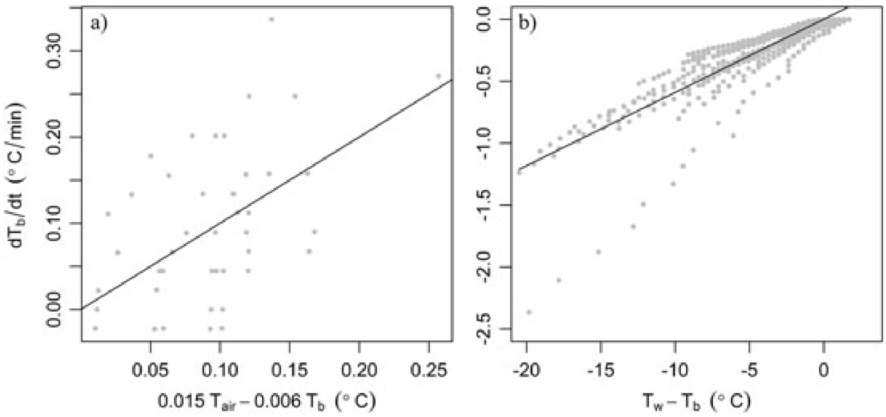

Figure 1. Models fitted to the rate of change in body temperature (dT_b/dt) of (a) a basking adult female northern map turtle (*Graptemys geographica*) as a function of air temperature (T_{air}) and body temperature (T_b) and (b) a submerged adult female northern map turtle as a function of water temperature (T_w) and T_b.

Field measurements of basking behaviour and responses to disturbance

The simulation integrated direct measurements of basking behaviour and responses to disturbance. These observations were made between April and August 2014. In April and May 2014, 92 mature female northern map turtles were captured from Lake Opinicon while snorkelling at hibernation sites. To allow the recognition of individual turtles on the time-lapse pictures (see below), unique identification numbers were painted on the carapace of each individual. The turtles were released at their site of collection within 24 h of their capture.

Time-lapse cameras were placed at natural basking sites to measure how long it takes for undisturbed and for disturbed turtles to resume basking after entering the water. One camera was installed at each of five basking sites and set to take a picture every minute between 7:00 and 19:00 from mid-May until basking ceased at each of the sites at the end of July to early August. A disturbance was defined as an event causing at least half of the basking turtles in the field of view to leave the basking site within one minute. Instances where only one turtle was present at a basking site were excluded. In addition, experimental disturbances were carried out using a 5.8 m aluminum jon boat with a 25 hp motor (Table 1). Disturbances involved approaching the basking site at 15–20 km h^{-1} until half the turtles at the site entered the water. The boat was then immediately turned around, leaving the area at the same speed. The approach distance was typically 15–25 m before turtles entered the water. For each disturbance (including the experimental disturbances) captured by the cameras, the time it took for every numbered individual in the field of view to resume basking at the same location was recorded, with the set of times referred to as r_{dist}. Because turtles also interrupt basking for reasons other than disturbances, the time lapse pictures were also used to record how long it took for seemingly undisturbed numbered turtles to resume basking after entering the water (r_{undist}). Turtles entering the water were considered undisturbed if other basking turtles present at the site did not cease basking when the focal turtle did. Instances where turtles did not return to basking during the same day were excluded from the data set because turtles could have resumed basking at other basking sites not under camera surveillance. The total sample size of r_{dist} is much larger than that of experimental disturbances because it includes disturbances not caused by researchers (Table 1), and the sample mean of r_{dist} (mean = 24.3 min, SD = 56.3) was less than that of the mean time to return following experimental disturbance (mean = 29.1 min, SD = 37.1). Therefore, the distribution of r_{dist} was used as a conservative estimate of the time to return to basking following motorboat disturbances. There was no significant difference in r_{dist} (ANOVA: $P = 0.884$, $F_{3,\ 127} = 0.218$) and r_{undist} (ANOVA: $P = 0.878$, $F_{2,\ 143} = 0.1302$) between months, thus a single distribution was fitted to r_{dist} and a single distribution was fitted to r_{undist}. To estimate actual disturbance frequencies in Lake Opinicon, the number of non-experimental disturbances for numbered turtles was tallied on time lapse photographs and divided by the sum of the hours spent basking by numbered turtles (Table 2).

Table 1. Time (in minutes) for individual northern map turtles (*Graptemys geographica*) from Lake Opinicon, Ontario, Canada to return to basking when not disturbed, when experimentally disturbed with a motorboat, or when disturbed by unknown causes (all instances where at least half the turtles basking entered the water)

	No disturbance	Experimental disturbances	All disturbances
Mean	14	29	24
Median	2	6	8
Max	184	200	200
Min	0	2	1
Sample size	146	13	131
SD	34	56	37

Simulating the effects of disturbance on body temperature for each activity period

The T_b of a mature female map turtle was simulated under different frequencies of boat disturbance and for different activity periods. Each simulation trial calculated the T_b of a turtle every minute for 24 h (incorporating time not spent basking) for a given activity period and level of disturbance (Figure 2). In the simulation trials, disturbance frequency was varied from 0 to 15 disturbances per hour. The activity periods considered were: (1) emergence from hibernation (1–5 May); (2) early-nesting (1–5

Table 2. Observed frequencies of water entry per individual per hour while basking, for northern map turtles (*Graptemys geographica*) from Lake Opinicon, Ontario, Canada, caused by a disturbance or no disturbance. Frequencies were calculated for different times of year centred on the four activity periods of interest in this study

	9–20 May	21 May–20 June	21 June–20 July	21 July–2 Aug
Disturbance	0.15	0.32	0.96	1.23
No disturbance	0.37	0.36	0.59	0.76

June); (3) late-nesting (1–5 July); and (4) post-nesting (1–5 August). For a given activity period, the quarter hourly weather variables used in the simulation (water temperature and air temperature) were taken from the Queen's University Biological Station weather station and were averaged over the 5 days of that activity period and over 2 years (2005–2006). Data from 2005–2006 were used because water temperature was monitored at several sites in Lake Opinicon during those years (Bulté and Blouin-Demers, 2010b). Because environmental temperatures were used in the simulation to recreate the water and air temperatures available to the simulated turtle, it is inconsequential that the years that the temperature data were collected were different from the year in which the basking observations were made. The number of potential basking hours in a day also varied with the activity period. For each activity period, the potential basking hours were determined from the mean times at which basking was observed to start and to end in time lapse photographs (Table 3).

In the simulation iterations, at each time step (1 min) the turtle could either be basking or submerged and its T_b was calculated based on Equation (4) or Equation (5), depending on which behaviour was exhibited. Each simulation trial began at the mean time at which basking was observed to begin for the given activity period (Table 3), and with the simulated turtle basking. The simulation trial ended after 24 h. In each simulation trial, the turtle could cease basking for only three reasons: (1) because the mean time at which turtles were observed to cease basking for the day for the given activity period was reached (Table 3); (2) because the turtle's T_b exceeded the voluntary maximum (see below); or (3) because the turtle was disturbed**.** It was assumed that other behaviour requiring the cessation of basking, such as feeding and reproduction, were infrequent enough to be excluded from the simulation. When the mean time that basking ceased for the day of the given activity period was reached, the simulated turtle returned to the water for the rest of the day. The upper voluntary maximum for northern map turtles is 27.8 to 32.5°C (Bulté and Blouin-Demers, 2010b). It has been argued that the upper voluntary maximum represents the

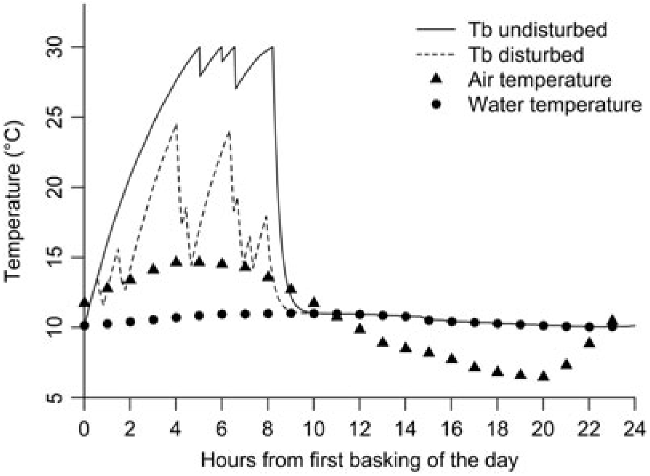

Figure 2. Examples of two simulation trials predicting body temperature (T_b) of female northern map turtles (*Graptemys geographica*) from Lake Opinicon, Ontario, Canada. One trial shows predicted T_b of a turtle never disturbed (solid line) and the other trial shows predicted T_b of a turtle disturbed at a frequency of 1 disturbance per hour (dashed line), during the 1–5 May activity period. Also shown is the air temperature and water temperature used to predict body temperature (T_b).

Table 3. Times of day that basking began and ceased by female northern map turtles (*Graptemys geographica*) from Lake Opinicon, Ontario, Canada, during different times of year

	1–5 May		1–5 June		1–5 July		1–5 August	
	start	finish	start	finish	start	finish	start	finish
Mean	9:20	17:35	8:47	17:41	10:25	15:10	10:41	15:46
Median	9:30	18:00	8:30	18:30	10:30	15:30	10:30	16:30
Max	14:30	21:30	12:30	22:30	14:30	18:30	15:30	20:30
Min	6:30	12:30	5:30	10:30	8:30	10:30	4:30	5:30
SD (min)	2.3	2.8	1.7	2.5	1.5	2.1	2.4	3.3
Sample size	13	13	58	62	29	29	32	32

optimal temperature for energy acquisition, and thus represents the temperature that a turtle aims to maintain (Dubois *et al.*, 2008). Thus, when the T_b of the simulated turtle rose above 30°C, the turtle became submerged during the next time step and resumed basking after X_1 min, where X_1 was selected randomly from the distribution of r_{undist} (Table 1). When the simulated turtle entered the water because of a disturbance, it resumed basking after X_2 min, where X_2 was selected randomly from the distribution of r_{dist}. If the turtle's T_b reached 30°C at the same time as it was disturbed, it resumed basking after X_2 min.

For a given activity period and level of disturbance, 1000 trials were performed and the mean value of T_b was calculated over the 24 h period of the simulation. The effects of disturbance on T_b, were calculated using the difference between the mean daily T_b of a turtle that was never disturbed from basking and the mean daily T_b of a turtle that was disturbed with a given frequency. All statistics and simulations were run in R version 3.2.1.

Metabolic rate

To calculate the effects of disturbance on the energy budget of turtles, effects on T_b were transformed to effects on SMR. To accomplish this, T_b at every time step in a simulation trial was transformed to SMR using an equation fitted to open-flow respirometry results collected by Bulté and Blouin-Demers (2008) : $\log_{10}\text{VO}_2 = -2.23 + 0.872 \times \log_{10}M + 0.055 \times T_b (\text{R}^2 = 0.83)$.

A turtle mass of 1500 g was assumed, approximately the mean mass of adult female map turtles in Lake Opinicon (Bulté and Blouin-Demers, unpublished data). The percentage reduction in mean SMR with disturbance was then calculated with the following equation:

$$\%\text{reduction in SMR} = \frac{\text{Mean SMR}_{\text{undisturbed}} - \text{Mean SMR}_{\text{disturbed}}}{\text{Mean SMR}_{\text{undisturbed}}} * 100$$

RESULTS

The consequences of basking disturbances by motorboats varied markedly by activity period (Figure 3). Differences in body temperature caused by disturbance and ensuing reductions in SMR were more marked earlier in the active season, and disturbance approached its maximum effect on T_b and SMR at lower frequencies earlier in the active season.

The estimated boat disturbance frequency experienced by map turtles at the basking sites monitored in Lake Opinicon increased as the activity season progressed: from 0.15 disturbances per hour in early May to 1.23 disturbances per hour at the end of July (Table 2). The number of entries into the water when turtles were undisturbed also increased as the activity season progressed: from 0.37 entries per hour in early May to 0.76 entries per hour at the end of July (Table 2).

For the 1–5 May activity period, frequencies of 0.05, 0.15 (that observed at monitored basking sites), 1.00, and 5.00 disturbances per hour caused a turtle to experience a mean decrease in daily T_b of 0.11°C, 0.34°C, 1.9°C, and 4.0°C, respectively, compared with undisturbed turtles (Figure 3). These differences in body temperature translate to a mean reduction in SMR of 2.7%, 7.8%, 39.2%, and 62.7%, respectively. The general trends were similar in the first five days of June, July, and August, but the effect of

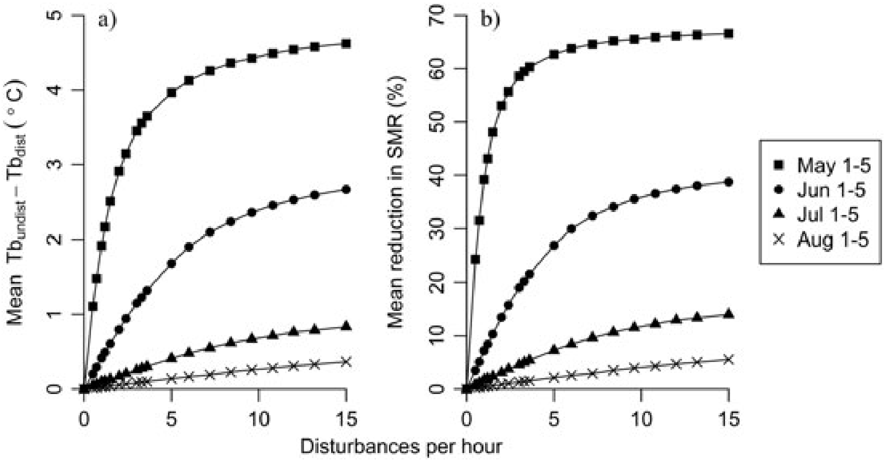

Figure 3. Simulation results of (a) the reduction in daily mean body temperature (T_b) of adult female northern map turtles (*Graptemys geographica*) from Lake Opinicon, Ontario, Canada with disturbances in basking at varying frequencies, and (b) daily mean percentage reduction in standard metabolic rate (SMR) due to basking disturbances at various frequencies for a 1500 g female northern map turtle. Results are shown for different activity periods: emergence from hibernation and pre-nesting (1–5 May), early-nesting (1–5 June), late-nesting (1–5 July), and post-nesting (1–5 August).

disturbance became progressively weaker with each consecutive month (Figure 3).

DISCUSSION

Energetic consequences of disturbance

The goal of the study was to quantify the thermal and energetic effects of basking disturbance by motorboats on adult female northern map turtles. The results showed that basking disturbance can decrease the mean daily T_b experienced by turtles, and consequently their mean SMR. The simulation showed that the adverse effects of motorboat disturbance on turtle T_b are more pronounced at the beginning of the active season (early May), and limited throughout the rest of the active season. This more pronounced effect in May is favourable in mitigating the effects of disturbance on turtle energetics because boat traffic is lower in early May than in June, July, and August. The adverse effect on energetics in the early active season may nonetheless be biologically significant. Indeed, at the disturbance frequencies observed at monitored basking sites, the simulation indicated that turtles in early May experience a reduction in mean body temperature of 0.34°C and in SMR of 7.8%.

It is important to note that the estimate of disturbance frequency based on the time-lapse photos are likely to have underestimated the real frequencies of disturbances of map turtles in Lake Opinicon for several reasons. (1) It was assumed that a turtle basking alone and then entering the water was undisturbed (since there were no other turtles present to indicate a disturbance as multiple turtles entering the water at the same time), which is unlikely always to be the case. (2) It was assumed that basking disturbances were constant throughout the day, but disturbance frequencies are likely to be higher during warmer parts of the day when disturbances have a larger effect on T_b. (3) The basking sites monitored were not within the primary boat channel of Lake Opinicon. Lake Opinicon is part of the Rideau Canal waterway. The mean number of boats entering Lake Opinicon from the Chaffey's lock station varied from 9.9 boats per day in May to 70 boats per day in July between 2004 and 2006 (Parks Canada, unpublished data). Provided that the locks are operated for 8 hours per day on average, the hourly boat traffic in the Rideau Canal ranged from 1.23 boats per hour to 8.75 boats per hour and reached 15 boats per hour in July. In May, boat traffic exceeded 1.75 boats per hour on 25% of the days and reached 4 boats per hour. In addition, motorboat traffic is increasing (NMMA,

2012) and there are water bodies within the northern map turtle range with much more boat traffic than Lake Opinicon. For example, the St Lawrence River Thousand Islands National Park, which is inhabited by northern map turtles, receives approximately 1000 motorboats every May and nearly 6000 motorboats every July (Bulté *et al.*, 2010). This is why the simulation was also run at higher disturbance frequencies than those observed at the study location.

Standard metabolic rate was used to estimate the effects of the change in T_b on the energetics of map turtles. Net energy retention (NER) is the amount of energy available for growth and reproduction. Standard metabolic rate is argued to be a proxy for NER for freshwater turtles because the processes required for energy assimilation are dependent on metabolic rate; both SMR and NER increase exponentially with T_b and the Q_{10} of NER is generally higher than that of metabolic rate (Dubois *et al.*, 2008). Thus, SMR is a conservative estimate of the effect of T_b on NER. If this is correct, a change in SMR caused by disturbance would translate to a corresponding change in NER. A reduction in NER may have consequences on individual fitness and on population growth. Painted turtles (*Chrysemys picta*) allocate approximately half of the energy required for a clutch before hybernation, and the other half following their emergence during May and early June (Congdon and Tinkle, 1982). Map turtles probably allocate energy to follicular development at similar times of the year. Although some of the energy allocated to follicles in the spring may be from stored lipids, map turtles almost certainly depend on energy inputs as well. Basking in the spring is likely to be important for increasing food processing rates so that energy can be allocated to eggs, and to increase the rates of physiological processes vital to follicular development. Thus, the large reduction in NER caused by basking disturbances in May could result in decreased clutch size, clutch frequency, and clutch survivorship.

Basking has been demonstrated to be important to the reproduction of female turtles. Exposure to low temperature during the pre-nesting period prevented follicle development beyond initial stages in female soft-shelled turtles (*Lissemys punctata*) (Sarkar *et al.*, 1996) and prevented ovulation in painted turtles (Ganzhorn and Licht, 1983). There is also evidence of carry-over effects of maternal basking opportunities on offspring condition in reptiles. For example, in a scincid lizard (*Niveoscincus ocellatus*), females that were allowed to bask gave birth earlier, and their offspring were in better condition and grew faster, than females that were not permitted to bask (Wapstra, 2000). It would be of interest to model the effects of disturbance in autumn in future studies, as temperature again becomes important to follicular development during this period. For instance, autumn temperature was found to affect clutch frequency of painted turtles (Rollinson and Brooks, 2007). In addition, Selman *et al.* (2013) found basking disturbances to result in reduced body condition.

Juvenile and male northern map turtles would probably be less affected by basking disturbances than mature females because they are smaller and thus warm at a faster rate when basking (Dzialowski and O'Connor, 2001). However, reductions in NER that were to be allocated to growth could be detrimental to juvenile turtles, as predation risk decreases with increasing size. Reduction in NER in male map turtles may also affect sperm production.

Simulation assumptions

The variation unexplained by the submerged T_b model (Equation (4), Figure 1) was probably due to lag time between T_b and T_w measurements, and variation in turtle body size. Variation unexplained by the basking model (Equation (5), Figure 1) probably resulted from radiation not being incorporated into the predictive equation. It was also assumed that evaporative heat loss did not affect the overall daily temperature profile of a turtle because there was no evidence of relatively greater heat loss when turtles would experience evaporative heat loss (when they were first experimentally removed from water to basking locations). In addition, as the basking model (Equation (5) Figure 1) was based on a turtle placed to bask on a wooden dock, the simulation best represents turtles basking on logs that would experience similar rates of conduction from the substrate on which they are situated.

In the simulation, a turtle entered the water undisturbed only if its T_b exceeded the voluntary maximum, or if the end of potential basking time for a day was reached. Other reasons for entering the water could be to allocate time to other activities, such as feeding or reproduction. Entering the water to participate in such activities was incorporated to some extent in the simulation because turtles that entered the water undisturbed could participate in different activities for X_2 amount of time, but only when the upper voluntary maximum was reached. Feeding and reproduction are not likely to take up a large portion of potential basking time. Northern map turtles inhabit highly productive habitats. For example, in Lake Opinicon, the mean population densities of the main prey items of map turtles – zebra mussels (*Dreissena polymorpha*) and trap-door snails (*Viviparus georgianus*) – are 2592 and 35 m^{-2}, respectively (Bulté *et al.*, 2008). Moreover, freshwater turtles have long digestive turnover times that can be reduced by increasing T_b (Parmenter, 1981; Congdon, 1989). Thus, foraging probably takes up only a small proportion of a map turtle's time budget, as they are likely to be more constrained by basking time than by foraging time.

It should be noted that the potential basking hours did not encompass all the daylight hours, so there was potential time for other activities that may require daylight, such as foraging, before and after the potential basking hours (Table 1). Later in the season, time spent submerged by simulated turtles that experienced no disturbances increased, leaving more time for other activities.

The simulation also assumed that a turtle completely entered the water to cool when it reached its upper voluntary maximum rather than using other behaviour, such as putting a limb into the water, a cooling mechanism that was observed in the time-lapse photographs. Having turtles that use only full submergence as a cooling mechanism in the simulation renders the results more conservative because, in this simulation, turtles could not be disturbed when they were completely submerged. The absence of underwater disturbances is also an assumption that renders the simulation more conservative, if boats can indeed disturb turtles under water and delay their emergence to bask.

Implications for conservation

The results of this study indicate that human disturbance of thermoregulation has thermal consequences that could translate into sublethal adverse effects on turtles, such as reduced growth and reduced reproductive output. The northern map turtle is listed as a species of special concern in Canada (COSEWIC, 2012) and approximately 51% of the world's freshwater turtles are threatened with extinction (Böhm *et al.*, 2013). As basking behaviour is common in freshwater turtles (Obbard and Brooks, 1979; Sarkar *et al.*, 1996; Cadi and Joly, 2003; Moore and Seigel, 2006; Selman and Qualls, 2011), basking disturbance probably affects many turtle species in a manner similar to the northern map turtle, especially those species inhabiting temperate regions and areas with high boat traffic. Management strategies to prevent the adverse effects of basking disturbance could include restricting boat use near important basking areas during the periods of the year conducive to basking behaviour (i.e. when the air is warmer than the water), and especially during key times for energy assimilation such as during egg development. Such a strategy would require the a priori identification of important basking areas and of areas subjected to high disturbance rates. Once disturbance rates at a location are quantified, the corresponding thermal and metabolic effects can be estimated using the simulation results in Figure 3, assuming map turtles at other locations behave similarly to those at the monitored basking sites and are of similar size. In North America, recreational boaters are largely unrestricted with regard to areas they can reach within a water body. Moreover, recreational power boating is extremely widespread. Therefore, the identification of important basking areas and subsequent regulation of boat traffic in these areas may be impractical on a large geographical scale.

If effective, outreach programmes informing boat owners of the impacts boats have on local wildlife, particularly on basking turtles, would be a more cost-efficient way to obtain a positive conservation outcome on a larger scale. Developing strategies to minimize boat disturbance to turtles could be accomplished more efficiently by first answering some key questions: What is the minimum passage distance to prevent disturbance? Does the responsiveness of turtles to boats vary with seasons? What areas are experiencing boat traffic that could translate to substantial declines in energy assimilation? Do turtles respond differently to different types of boats (e.g. canoe vs. motor boat) and to different types of approaches (e.g. slow vs fast)? Are turtles responding to boat noise or movement? We trust that the work described here will stimulate additional studies on this issue, helping to address the research questions identified above, and thus help to conserve turtle populations.

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