# Habitat-specific behavioural thermoregulation by black rat snakes (*Elaphe obsoleta obsoleta*)

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Thermoregulation is thought to be the most important factor influencing habitat selection by terrestrial ectotherms, at least in temperate climates. The cost-benefit model of thermoregulation predicts that ectotherms should invest more in thermoregulation when the costs of doing so are low (when the thermal quality of the habitat is high). However, the extent to which ectotherms vary their thermoregulatory behaviour according to the thermal quality of habitats is currently unknown. We studied the relationship between habitat use and thermoregulation in 53 black rat snakes using temperature-sensitive radio-transmitters. Among the habitats available to black rat snakes, edges had the highest thermal quality, retreat sites and forest were intermediate, and open habitats had the lowest thermal quality. Black rat snakes experienced more favourable body temperatures while in barns (retreat sites) than in edges, and in edges than in forest. During the day, the effectiveness and the extent of thermoregulation by the snakes were equal in barns and forest, but much lower in edges. In fact, black rat snakes selected thermally favourable microhabitats less than their availability while in edges. Therefore, more favourable body temperatures were not necessarily achieved in thermally superior habitats by increased thermoregulation, but simply because favourable temperatures were encountered more often in those habitats. This result is contrary to the central prediction of the cost-benefit model of thermoregulation and we suggest that this model should be modified to put more emphasis on other costs of thermoregulation, such as increased predation risk or lost foraging opportunities.

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Because all physiological processes are temperature dependent, variation in the body temperature  $(T_b)$  of ectotherms affects their physiology (Christian and Tracy 1981, Hertz et al. 1982, Arnold and Bennett 1984). Therefore, virtually all aspects of reptile ecology are affected by  $T_b$  variation and  $T_b$  ultimately has an impact on fitness (Huey and Kingsolver 1989). Variation in  $T_b$  will increase in importance to ectotherms at higher latitudes as the difficulty of achieving appropriate  $T_b$  increases (Shine and Madsen 1996). In terrestrial ectotherms,  $T_b$  regulation is achieved behaviourally by adjusting habitat selection and timing of activity (Huey et al. 1989, Grant 1990). The discovery of behavioural thermoregulation (Cowles and Bogert 1944) has led to the tenet that thermoregulation is the single most important proximate factor influencing habitat selection by terrestrial squamates (Reinert 1993). One expectation arising from this perspective is that squamates should preferentially use thermally superior habitats, particularly when thermal demands are high (e.g. dur-

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ing gestation or digestion). Direct evidence in support of this expectation is limited (Reinert 1984a, b, Shine and Madsen 1996), but results presented by Blouin-Demers and Weatherhead (2001a, b, c) suggest that thermoregulation plays an important role in habitat selection by black rat snakes (*Elaphe obsoleta obsoleta* (Say)).

A second, and less obvious question that arises from the view that snakes vary habitat use, at least in part to help regulate their  $T_b$ , is whether snakes thermoregulate differently when in different habitats. For instance, while in thermally superior habitats snakes may thermoregulate precisely because doing so is easy. While snakes are in thermally inferior habitats they may become thermoconformers because it is too expensive in time or energy to attempt to regulate  $T_b$  behaviourally (Withers and Campbell 1985). Alternatively, snakes may invest equally in thermoregulation in all habitats, and achieve more favourable  $T_b$ s in the thermally superior habitat simply because those temperatures are encountered more often. We are unaware of any study that has investigated how the same individuals of an ectothermic species thermoregulate in habitats differing in thermal quality. Our general goal in this paper is to investigate this issue in black rat snakes.

Previously we demonstrated that black rat snakes prefer habitat edges, such as the boundaries between forest and open habitats, including ponds, wetlands, and rock outcrops (Blouin-Demers and Weatherhead 2001a). These analyses confirmed the results of previous studies that had shown that rat snakes prefer edges in human-modified landscapes (Weatherhead and Charland 1985, Durner and Gates 1993). We also showed that gravid female black rat snakes used edges more than non-gravid females and males. We hypothesised that gravid female black rat snakes prefer edges because of the superior thermoregulatory opportunities (Blouin-Demers and Weatherhead 2001a). We ruled out foraging and predator avoidance as potential reasons that gravid females might be attracted to edges, because female black rat snakes do not feed while gravid and retreat sites were as numerous in forest as in edges. We provided more direct support for our hypothesis that edges are used for thermoregulation by showing that gravid females maintained higher  $T_b$ s by thermoregulating more carefully than either males or non-gravid females (Blouin-Demers and Weatherhead 2001b). Finally, we demonstrated experimentally that, when digesting a large meal, male and female rat snakes went to edges and thermoregulated more carefully (Blouin-Demers and Weatherhead 2001c).

While our previous studies are consistent with our assertion that edges are used for thermoregulation, thus far we have not demonstrated empirically that edges are of higher thermal quality than other habitats available to black rat snakes. Also, if edges are preferred because they offer better opportunities for thermoregulation, then snakes should have  $T_b$ s closer to their preferred body temperature range  $(T_{set})$  while in edges than while in other habitats, independent of their reproductive status. Our first objective here was to confirm that edges are thermally superior habitats and to test the prediction that black rat snakes achieve preferred body temperatures more while in edges.

If snakes maintain  $T_b$ s closer to their  $T_{set}$  while in edge habitat, they could do so in two ways. Snakes could either invest equally in thermoregulation in all habitats but realise higher  $T_b$ s in edges because edges are thermally superior, or alternatively, they could invest more in thermoregulation while in edges than while in other habitats. The latter prediction is consistent with Huey and Slatkin's (1976) cost-benefit model of thermoregulation, which predicts that lizards should invest more in thermoregulation when the costs of thermoregulating are low. While the cost-benefit model of thermoregulation has received support from a number of studies on lizards, few attempts have been made to apply it to snakes. Therefore, our final objective was to test the prediction that black rat snakes invest more in thermoregulation while in thermally superior habitats.

# Materials and methods

## Study area, study animals, and radio-telemetry

We conducted this study from 1997 to 1999 at the Queen's University Biological Station on the shore of Lake Opinicon, approximately 40 km north of Kingston (Ontario, Canada). The study area was approximately 9.5 km by 2.5 km and was mostly covered by second-growth deciduous forest. Black rat snakes were captured both at communal hibernacula during spring emergence (Blouin-Demers et al. 2000a) and opportunistically during the remainder of the active season (Prior et al. 2001). From all the individuals captured, we selected a subset for surgical implantation of temperature-sensitive radio-transmitters (Model SI-2T, Holohil Systems Inc., Carp, Ontario). Our choice of study animals was dictated by size and sex. Snakes had to be large enough to bear the transmitter (maximum ratio of transmitter mass: body mass = 0.025) and we aimed at tracking equal numbers of males, non-gravid females, and gravid females. Implantation was done under isoflurane anaesthesia (Blouin-Demers et al. 2000b). Transmitters weighed 8.6 g with a battery life of 20 months at 20°C. Prior to implantation we verified the calibration curves relating radio-transmitter pulse rate to temperature supplied by the manufacturer for each transmitter. Snakes were released three days following surgery and thereafter were located every second day using a radio-receiver (TRX-2000S, Wildlife Materials Inc., Carbondale, Illinois). All locations of snakes were categorised in general habitat categories (see below) and recorded using a Global Positioning System unit (Pathfinder, Trimble Navigation Ltd, Sunnyvale, California) with sub-meter accuracy in the field.

We positioned two automated radio-telemetry data loggers (SRX 400, Lotek Engineering Inc., Newmarket, Ontario) in the study area to record  $T_b$ s of black rat snakes every 10 min throughout the day each year. Because the snakes regularly moved out of range of the data loggers, it was not possible to obtain complete  $T_b$  profiles for each individual. From May 1997 to November 1999 we followed 17 males and 36 females for periods ranging from 1 to 30 months. Twenty-three snakes (nine males and 14 females) were followed in multiple years and therefore we have data for 79 "snake years" (25 "male years" and 54 "female years").

## Thermal quality of habitats

We constructed physical models of black rat snakes using 40 cm-long pieces of copper pipe painted black to measure operative environmental temperatures  $(T_e s)$ available to rat snakes in different habitats in the study area. We confirmed that the models accurately predicted the  $T_{h}$  of black rat snakes using carcasses of rat snakes freshly killed on the road (Blouin-Demers and Weatherhead 2001b). We attempted to measure  $T_e$ s in all microhabitats available to black rat snakes within each habitat type. While it would be practically impossible to measure every nuance in the thermal quality of microhabitats within a given habitat, we assumed that, with the exception of edges, thermal heterogeneity in microhabitats is much greater among than within habitat types. Therefore, we deployed the models in four to eight of the most common microhabitats in each of the different habitats and left them in place for several weeks. In positioning the models in microhabitats, we were sensitive to the natural history of black rat snakes and placed the models in microhabitats that were available to the snakes. The models were always placed on the ground, except in forest where they were also positioned in tree branches. We used multiple regression to build predictive equations of the mean model temperature in all microhabitats within the different habitats based on climatic data collected hourly at the Queen's University Biological Station. We used these equations to generate mean  $T_e$ s for each habitat each hour for the duration of the study (Blouin-Demers and Weatherhead 2001b).

Our aim was to measure  $T_e$ s in all the habitats available to black rat snakes. We placed model snakes in forests, rock outcrops and fields, but excluded open water because rat snakes are terrestrial. We also excluded wetlands because in our study area most wetlands are heavily vegetated with sedges and cattails. Thus, from a black rat snake's perspective, wetlands are structurally similar to fields, so we considered  $T_e$ s for wetlands to be the same as for fields. There were also a number of retreat sites (rock piles, crevices in rock outcrops, large logs, old barns, old machinery, snags) that were used by all snakes and that could not be adequately classified in any of the above categories. Therefore, we also placed models in two representative and commonly used retreat sites (under flat rocks on rock outcrops and in barns) to measure the  $T_e$ s available to black rat snakes in retreats.

To quantify the thermal quality of the different habitats, we used the thermal quality index  $(d_e)$  introduced by Hertz et al. (1993). For a given habitat,  $d_e$  is the mean of the deviations of  $T_{es}$  from  $T_{set}$ . If  $T_e$  is below the preferred  $T_b$  range,  $d_e$  is the difference between the lower bound of  $T_{set}$  and  $T_e$  and if  $T_e$  is above the preferred  $T_b$  range,  $d_e$  is the difference between  $T_e$  and the upper bound of  $T_{set}$ . Because reproductive status does not affect  $T_{set}$  in black rat snakes, we used  $T_{set} =$ 26.5°C-29.8°C based on data for 41 fasted individuals assessed in a laboratory thermal gradient (Blouin-Demers and Weatherhead 2001b).

We defined an edge as extending 15 m on each side of the boundary between forest and any open habitat (Blouin-Demers and Weatherhead 2001a). We assumed that snakes had access to both sides of the boundary at no cost because shuttling between the open habitat and forest involves very short movements.  $T_e$ s in forests in our study area rarely exceed the upper bound of  $T_{set}$ and thus provide a permanent refuge against high temperatures (Blouin-Demers and Weatherhead 2001b). Therefore, in determining the thermal quality of edges we were only interested in instances where the lower bound of  $T_{set}$  could not be reached on either side of the boundary, because overheating was never a concern in the forest. Hence, we defined  $d_e$  for edges as the smallest deviation of  $T_e$  from the lower bound of  $T_{set}$  in either the forest or the open habitat.

## Thermoregulation in different habitats

The first method we used to investigate whether black rat snakes experienced more favourable  $T_b$ s while in edges than while in other habitats was simply to calculate their mean  $T_b$  in the different habitats. More refined methods used to quantify thermoregulation require the determination of the "accuracy" of  $T_b$ , or the extent to which an ectotherm experiences  $T_b$ s within its  $T_{set}$ . Following Hertz et al. (1993), we used  $d_b$  as such an index. Similar to  $d_e$ ,  $d_b$  is defined as the mean of the deviations of  $T_b$ s from  $T_{set}$ . These data were used to test the prediction that black rat snakes realise more favourable  $T_b$ s while in edges than while in other habitats.

Using  $d_e$  and  $d_b$ , Hertz et al. (1993) designed an index of thermoregulation effectiveness (E) defined as E =

 $1 - (\overline{d_h}/\overline{d_e})$ . E is problematic because it is not defined if the thermal environment is perfect, it cannot be interpreted without considering the magnitude of  $d_a$ and  $d_b$ , and it can give spurious quantifications of the thermal ecology of a species because it uses a ratio (Blouin-Demers and Weatherhead 2001b). Blouin-Demers and Weatherhead (2001b) recommended that  $d_e - d_b$  be used instead of E, which we do here. Potential values of  $d_e - d_b$  are open-ended, with negative numbers arising when animals use thermally favourable habitats less than their availability, 0 representing perfect thermoconformity, and positive numbers representing animals that thermoregulate to some extent. The magnitude of the difference is a measure of how much an animal departs from thermoconformity, and thus is an index of the effectiveness of thermoregulation. Finally, to get a complete picture of the thermoregulatory behaviour of rat snakes, we also used an index of thermal exploitation (Ex) introduced by Christian and Weavers (1996). Ex is defined as the percentage of  $T_b$ s that fall within  $T_{set}$  only during periods in which  $T_e$ s indicate that the lower bound of  $T_{set}$  could have been reached. We calculated the different thermoregulation indices separately for each habitat to compare black rat snake thermoregulation while in these different habitats. We also calculated the indices separately for day (600 h-1800 h) and night (1800 h-600 h) because black rat snakes thermoregulate differently during those periods (Blouin-Demers and Weatherhead 2001b) and tend to be most active during the day.

In calculating indices of thermoregulation for black rat snakes, we wanted to determine the effectiveness of thermoregulation  $(d_e - d_b)$  in each habitat and the extent to which black rat snakes exploited the thermal opportunities (Ex) offered by each habitat, relative to the thermal opportunities available in each habitat. Thus, for this analysis we quantified thermoregulation within a given habitat regardless of thermal opportunities that might have been available in other habitats, and we used  $T_e$  or  $d_e$  values for that habitat only. For example, while calculating  $d_e$  –  $d_b$  in forest, we only considered the  $d_e$  values of models in the forest. These calculations quantify how much the  $T_b$ s of snakes deviate from their  $T_{set}$  or how much time the snakes spend with  $T_b$ s within  $T_{set}$ compared to the  $T_b$  deviations or time with  $T_b$  within  $T_{set}$  they would experience if they used the habitat randomly (the average deviations of  $T_{es}$  from  $T_{set}$  or the average time with  $T_e$  within  $T_{set}$  in the habitat). Therefore, these calculations determine how selective the snakes were about microhabitats within a habitat. These data were used to test the prediction that black rat snakes thermoregulate more carefully while in habitats of higher thermal quality.

Because the monitoring interval for  $T_b$ s (monitored almost continuously on the data loggers) and the

monitoring interval for determining the habitat in which the snake was located (monitored at relocation every 48 h) were different, not every  $T_b$  measurement recorded could be assigned to a given habitat with certainty. Therefore, we only included in our analyses  $T_b$  measurements for snakes that had not changed habitats while the  $T_b$ s were recorded. However, we excluded data collected during intervals in which a snake had changed locations but not habitats, but would have had to cross a different habitat to get to its new location.

## Statistical analyses

Because gravid females use edges more, and thermoregulate more than males and non-gravid females (Blouin-Demers and Weatherhead 2001a, b), we entered reproductive status and habitat as factors in two-way analyses of variance (ANOVA) to control statistically for the potential confounding effect of differential habitat use and thermoregulation by gravid females. Series of  $T_b$ s recorded from a single individual are not statistically independent. Therefore, all analyses were performed on data  $(T_b, d_e - d_b, or$ Ex) averaged for each individual over each active season. Some females changed reproductive status from one year to the next (gravid vs non-gravid), so we considered  $T_b$ s measured for an individual in different years to be independent. Tracking periods for individual snakes varied and we did not have complete  $T_b$  data for each individual. Therefore, it was not practical here to use repeated measure analyses on individuals.

We performed all analyses using JMP Version 3.2 (SAS Institute 1997) on a Macintosh desktop computer. We inspected box plots to determine if the assumptions of normality and homogeneity of variance were upheld. We detected no significant violations of these assumptions. We accepted significance of statistical tests at  $\alpha = 0.05$ . We report all means  $\pm$  one standard error unless otherwise indicated.

## Results

During the three active seasons of the study (1 May to 30 September of 1997 to 1999), we recorded 130 669  $T_b$ s from the 53 individuals we followed. For analysis we reduced these readings to 29 722 hourly mean  $T_b$ s. Of these hourly mean  $T_b$ s, the habitat occupied by the snake was known for 19 884 (66.9%) of the one-hour intervals. Of these hourly mean  $T_b$ s in known habitats, 11 764 (59.2%) were recorded during the day (600 h–1800 h) and 8120 (40.8%) during the night.



Fig. 1. Mean operative environmental temperatures ( $T_e$ s averaged over the whole active season) for each hour of the day in forest, open habitats (mean of operative environmental temperatures in fields/wetlands and rock outcrops), and retreat sites (mean of operative environmental temperatures in barns and under flat rocks on rock outcrops) in eastern Ontario. The horizontal lines represent the preferred body temperature range ( $T_{set}$ ) of black rat snakes in eastern Ontario.

# Thermal quality of habitats

For each hour of the entire active season we calculated a mean  $T_e$  for each habitat available to black rat snakes.  $T_e$  measurements in each habitat indicated that, on average,  $T_e$  did not reach the lower bound of  $T_{set}$  in any of the shaded habitats (forest, barn, under flat rocks) during the course of the day (Fig. 1). Forests had the lowest mean  $T_e$  (Table 1) and were the coolest habitat for most of the day. In all exposed habitats (rock outcrops and field/wetland),  $T_e$  exceeded the upper bound of  $T_{set}$  daily from 900 h to 1830 h on average (Fig. 1). The two retreat sites in which we measured  $T_es$ (barn and under flat rocks) were buffered from daily climatic variation. Retreat sites tended to be warmer than other habitats during the night and cooler during the day.

We used the mean  $d_e$  calculated for the entire active season to measure the average thermal quality of the habitats available to black rat snakes. Mean  $d_e$ s were highest for open habitats (field/wetlands and rock out-

crops), intermediate for forests, and lowest for the two retreat sites (barns and under flat rocks) and for the three types of edges (Table 1). On average, open habitats were too cold at night and too warm during the day, forests were never too warm but often too cold, and retreat sites were buffered from the daily variations in  $T_e$  but were slightly too cold. However, because we have assumed that edge habitats allowed simultaneous access to the high  $T_e$ s of the open habitat and low  $T_e$ s of the forest during the daytime, snakes in edges would have the potential to maintain  $T_b$ s very close to  $T_{set}$ . We also calculated the proportion of time that  $d_e$ equalled zero in each habitat (Table 1). Values of  $d_e = 0$ occurred three to five times more often in the three edge habitats than in other habitats. Overall these results indicate that, from a thermoregulatory perspective, habitat edges are superior to all other habitats. Edges were followed in thermal quality by retreat sites, then by forest, and finally by the open habitats.

#### **Body temperatures**

For the analyses of the thermoregulatory behaviour of black rat snakes while in different habitats, we grouped the different edge types and eliminated the habitats for which we had fewer than 100 hourly mean  $T_b$ s recorded. This produced three habitat categories: (1) inside barns, (2) edge habitats, and (3) forest. By reducing the number of habitat classes, we increased the power and meaningfulness of the ANOVAs. Black rat snakes were warmer during the day than at night in all three habitats, and during both day and night their mean  $T_b$ s were below the lower bound of  $T_{set}$ , except in barns during the day (Fig. 2). Black rat snakes experienced smaller mean  $d_b$ s during the day than during the night in edges and forest (as one would expect based on their mean  $T_{h}$ s). In barns, however,  $d_{h}$ s were lower at night than during the day. This occurred because, during the day in barns, black rat snakes sometimes maintained  $T_b$ s that were actually above  $T_{set}$ , which happened rarely in edges and almost never in forest.

Table 1. Mean  $\pm 1$  SE, maximum, and minimum operative temperatures recorded in each habitat available to black rat snakes. Mean  $\pm 1$  SE, maximum, and percent equal to zero deviations of operative temperatures from the preferred body temperature range of black rat snakes in each habitat in Ontario. Values for mean  $T_e$  and mean  $d_e$  are from Blouin-Demers and Weatherhead (2001b).

Habitat	$T_e$			$d_e$		
	mean	max	min	mean	max	% = 0
Forest	17.5 + 0.06	34.5	-2.7	9.2 + 0.06	29.2	6.2
Field/wetland	20.8 + 0.13	59.1	-7.9	12.0 + 0.07	34.4	4.6
Rock outcrop	25.9 + 0.13	63.6	-5.6	9.5 + 0.07	33.8	8.0
Barn	20.4 + 0.04	34.3	7.1	6.2 + 0.04	19.4	6.3
Under flat rock	21.5 + 0.05	35.6	3.1	5.5 + 0.04	23.4	12.5
Edge forest-field/wetland		_	_	7.5 + 0.06	29.2	29.5
Edge forest-rock outcrop	_	_	_	5.6 + 0.06	29.2	40.7
Edge forest-water body	-	-	-	$7.0 \pm 0.06$	29.2	32.7



Fig. 2. Least square mean (corrected for reproductive status) body temperatures  $(T_b s)$  (A), deviations of body temperatures from the preferred body temperature range  $(d_b s)$  (B), and percentages of deviations of body temperatures from the preferred body temperature range  $(d_b s)$  equal to zero (C) in barns, edge habitats, and forest during the day and during the night for radio-tracked black rat snakes in eastern Ontario. Means with the same letters are deemed not significantly different based on Tukey-Kramer HSD tests.

The percentage of time that  $T_{bs}$  were within  $T_{set}$  (i.e.  $d_{bs} = 0$ ) was higher during the day than at night in edges and forest, but equal in barns, again because some  $T_{bs}$  were actually above  $T_{set}$  in barns during the day (Fig. 2).

We used two-way ANOVAs (with reproductive status included as a control variable because gravid females have been shown to thermoregulate more carefully and to use edges more than males and non-gravid females: Blouin-Demers and Weatherhead 2001a, b) to test whether the  $T_b$ s,  $d_b$ s, and the percentage of  $d_b$ s = 0 of black rat snakes differed while they were in barns, edges, and forest during the day and at night. Black rat snakes maintained significantly different  $T_b$ s in the three habitats both during the day ( $F_{(2,163)} = 7.231$ , p = 0.001) and at night ( $F_{(2,93)} = 7.872$ , p < 0.001).

Tukey-Kramer HSD tests indicated that, during the day, rat snakes were significantly warmer in barns than in edges and significantly warmer in edges than in forest. At night, black rat snakes were significantly warmer in barns than in other habitats, but their  $T_b$ s were not significantly different in edges and forest (Fig. 2).

ANOVA also indicated that deviations of black rat snake  $T_{b}$ s from  $T_{set}$  (i.e.  $d_{b}$ s) were significantly different in the three habitats during the day ( $F_{(2,163)} = 5.849$ , p = 0.004) and at night ( $F_{(2,93)} = 7.486$ , p = 0.001). Tukey-Kramer HSD tests indicated that, during both day and night, deviations from preferred body temperatures were significantly smaller in barns than in the other two habitats and smaller, but not significantly so, in edges relative to forest (Fig. 2).

The proportion of time black rat snakes spent with  $T_b$ s within  $T_{set}$  ( $d_b = 0$ ) differed significantly in the three habitats during the day ( $F_{(2,163)} = 3.784$ , p = 0.025) and at night ( $F_{(2,93)} = 8.592$ , p < 0.001). Tukey-Kramer HSD tests revealed that the only significant pairwise difference during the day was that black rat snakes spent more time with  $T_b$ s within  $T_{set}$  in barns than in forest. At night, black rat snakes spent significantly more time with  $T_b$ s within  $T_{set}$  while in barns than in edges and forest (Fig. 2). Collectively these results indicate that, from a purely thermoregulatory perspective, black rat snakes should have spent their time in barns because this was the habitat in which they experienced  $T_b$ s closest to their  $T_{set}$ .

## Effectiveness of thermoregulation

We used a two-way ANOVA (with reproductive status included as a control variable) to test whether indices of thermoregulation effectiveness  $(d_e - d_b)$  differed while the snakes were in barns, edges, and forest during the day and at night. Black rat snakes had higher indices of thermoregulation effectiveness at night than during the day in all habitats.

Thermoregulatory effectiveness of black rat snakes  $(d_e - d_h)$  differed significantly by habitat during the day  $(F_{(2,163)} = 31.581, p < 0.001)$  but not at night  $(F_{(2,93)} =$ 0.055, p = 0.95). Tukey-Kramer HSD tests indicated that black rat snakes thermoregulated significantly less effectively while in edges than while in barns and forest during the day (Fig. 3). This indicates that, while in edges, snakes did not always use the thermally superior microhabitats that were available. For example, rat snakes could have been spending more time in the shade on the forest side of the edge rather than being in the open habitat (field/wetland or rock outcrop), where  $T_{e}$ s within  $T_{set}$  were available. While in edges, the deviations of  $T_b$ s from  $T_{set}$  ( $d_b$ s) that black rat snakes experienced were actually larger than the average deviations of  $T_e$ s from  $T_{set}$  ( $d_e$ s) indicated by the models in

edges. In contrast, while rat snakes were in barns and forest their mean  $d_b$ s were larger than the mean  $d_e$  for the habitat. Thus, while black rat snakes used microhabitats selectively while in barns and forest (the microhabitats they used had a mean thermal quality above the average for the habitat), at least from a thermal perspective they were not selective in edges (the microhabitats used had a mean thermal quality below the mean of edges).

## Thermal exploitation

Of the 19884 hourly mean  $T_b$ s recorded from black rat snakes in known habitats,  $T_e$  values indicated that snakes could have achieved  $T_b$ s within  $T_{set}$  in the habitat in which they were located 4865 times (4523 hourly mean  $T_b$ s during the day and 342 hourly mean  $T_b$ s during the night). Again, black rat snakes tended to have higher indices of thermal exploitation at night than during the day in all habitats.

A two-way ANOVA (controlling for the reproductive status of individuals) testing for differences between habitats in the extent to which black rat snakes exploited thermal opportunities (Ex) revealed significant interactions between reproductive group and habitat during the day (reproductive group × habitat  $F_{(4,139)} =$ 2.757, p = 0.030) and at night (reproductive group  $\times$ habitat  $F_{(4,37)} = 3.024$ , p = 0.030). Separate one-way ANOVAs for each reproductive group indicated that, during the day, the extent to which black rat snakes exploited thermal opportunities (Ex) differed by habitat for males  $(F_{(2,42)} = 6.562, p = 0.003)$  and non-gravid females  $(F_{(2,60)} = 7.306, p = 0.001)$ , but not for gravid females ( $F_{(2,37)} = 0.396$ , p = 0.676). Tukey-Kramer HSD tests showed that male black rat snakes exploited their thermal opportunities significantly more while in barns than while in edges and forest. However, non-gravid female black rat snakes exploited their thermal oppor-



Fig. 3. Least square mean (corrected for reproductive status) thermoregulation effectiveness index  $(d_e - d_b)$  calculated in relation to the thermal opportunities offered by each separate habitat in barns, edge habitats, and forest during the day and during the night for radio-tracked black rat snakes in eastern Ontario. Means with the same letters are deemed not significantly different based on Tukey-Kramer HSD tests.



Fig. 4. Least square mean (corrected for reproductive status) thermal exploitation index (Ex) calculated in relation to the thermal opportunities offered by each separate habitat (index calculated separately for males (M), non-gravid females (NGF), and gravid females (GF)) in barns, edge habitats, and forest during the day and during the night for radio-tracked black rat snakes in eastern Ontario. Means with the same letters are deemed not significantly different based on Tukey-Kramer HSD tests.

tunities significantly less while in edges than while in barns and forest (Fig. 4). At night, the extent to which black rat snakes exploited thermal opportunities (*Ex*) differed by habitat for non-gravid females ( $F_{(2,17)} =$ 4.489, p = 0.027), but not for males ( $F_{(2,10)} = 1.105$ , p = 0.368) or gravid females ( $F_{(2,10)} = 1.583$ , p = 0.253). Post-hoc tests indicated that non-gravid females exploited their thermal opportunities less while in edges than while in barns and forest (Fig. 4). However, the results of the analysis during the night should be interpreted cautiously because they are based on only 342 hourly mean  $T_b$ s.

## Discussion

For black rat snakes, the environment in eastern Ontario is thermally challenging. Only open habitats that could receive full solar radiation throughout the day (fields/wetlands and rock outcrops) provided  $T_{es}$  that, on average, rose above the lower bound of  $T_{set}$  during the course of the day. The most common terrestrial habitat in the study area is forest (48%, Blouin-Demers and Weatherhead 2001a), and this was the coolest of all the habitats available to black rat snakes.  $T_{es}$  in the forest were above the lower bound of  $T_{set}$  in only  $\approx 7\%$ of the observations. Thus, despite being a forest species, a rat snake in Ontario usually has to use habitats other than forests or has to use forest edges to be able to achieve  $T_bs$  within its  $T_{set}$ .

Given the strong preference for edges by black rat snakes (Blouin-Demers and Weatherhead 2001a), we had hypothesised that edges should be of higher thermal quality than the other habitats in the study area. We confirmed that edges were the habitats with the highest thermal quality. Edges were followed in thermal quality by retreat sites and forest and then by open habitats. Edges had among the lowest mean  $d_e$ s of all the habitats and had the highest proportions of  $d_e$ s equal to 0. The thermal quality of edges is conferred by their location at the interface of the coolest habitat (forests) that is always shaded and the warmest habitats (open habitats: fields/wetlands and rock outcrops) that receive full solar radiation. This result is a consequence of our assumption that snakes in edges always have access both to a refuge from high temperatures (forest) and to the warmest possible habitats (open habitats). This assumption seems reasonable because there is almost no travel time involved in shuttling between these two habitats. Thus, edges provide the best opportunities for behavioural thermoregulation of all the habitats in the study area.

The different thermoregulation metrics revealed consistent differences in how black rat snakes thermoregulated in the different habitats. Black rat snakes tended to maintain higher  $T_b$ s and tended to have  $T_b$ s closer to, or more often within,  $T_{set}$  while in barns than while in edges and while in edges than while in forest. Overall, these results indicate that black rat snakes experienced more favourable  $T_b$ s while in barns than while in edges and while in edges than while in forest. Therefore, our prediction that snakes should experience more favourable  $T_b$ s in edges than in other habitats was only partially supported. However, it should be noted that in the snakes' natural state, barns would not be available and black rat snakes would experience the most favourable  $T_b$ s in natural retreats such as under flat rocks on rock outcrops (which have almost the same thermal characteristics as barns, but are even more favourable from a thermoregulation perspective: Table 1 and Blouin-Demers and Weatherhead 2001b) and while in edges. In fact, natural retreats such as under flat rocks on rock outcrops are most often situated in edges because it is rarely possible for a snake to be more than 15 m away from the forest while on a rock outcrop given the relatively small size of the rock outcrops in our study area. Thus, among the natural habitats, black rat snakes do experience more favourable  $T_b$ s while in edges.

When we considered the thermoregulation effectiveness of black rat snakes with regard to the thermal opportunities offered by each specific habitat, we found little difference between habitats at night. During the day, however, black rat snakes thermoregulated much less effectively while in edges than while in barns and forest. In fact, our calculations of thermoregulation effectiveness in edges during the day showed that black rat snakes actually used thermally favourable microhabitats less than had they used microhabitats in proportion to their availability (negative  $d_e - d_b$ ). The differences between habitats were more variable for thermal exploitation (*Ex*) in relation to the thermal

opportunities offered by each habitat, partly due to significant interactions between habitat and reproductive status. The trend was for all black rat snakes to exploit thermal opportunities more while in barns and less while in edges during the day. At night there was no consistent trend and small sample sizes made the validity of the comparisons questionable. Overall these results indicated that the snakes did not necessarily achieve more favourable  $T_b$ s in the thermally superior habitats by thermoregulating more in those habitats. In fact, while in edges, the snakes appeared to invest less in thermoregulation but nonetheless benefited from the high thermal quality of edges. In contrast, while in forest during the day, black rat snakes thermoregulated more but realised lower  $T_b$ s than while in edges. Even a small thermoregulatory effort in a habitat of high thermal quality can produce higher  $T_b$ s than a large thermoregulatory effort in a habitat of low thermal quality. Therefore, our prediction that black rat snakes should invest more in thermoregulation while in thermally superior habitats was not supported.

It is possible that black rat snakes do not actively thermoregulate, but may simply be thermoconformers that favour edges for reasons other than thermoregulation and, therefore, their increased  $T_b$ s in edges relative to forest is simply a by-product of their habitat preference. For example, black rat snakes could be attracted to edges for foraging (Weatherhead and Charland 1985, Durner and Gates 1993). Under this scenario, black rat snakes would tend to have higher  $T_b$ s in edges than in the forest simply because the  $T_e$ s in edges are higher. Two lines of evidence suggest that black rat snakes' preferential use of edges is thermally based, and that the higher  $T_b$ s recorded in edge habitats relative to forest are not just attained passively. First, rat snakes increase thermoregulation following feeding both in the laboratory and in the field, and when they are fed in the field the snakes increase their use of edges (Blouin-Demers and Weatherhead 2001c). Second, gravid females thermoregulate more carefully than males and nongravid females in the field, and also use edges more than males and non-gravid females (Blouin-Demers and Weatherhead 2001a, b).

There are at least three possible explanations for the lack of agreement we documented between thermal quality and the extent of thermoregulation. First, it is possible that our assumption that black rat snakes in edges have access to both sides of the boundary at no cost is wrong and that the unsuspected costs actually decrease the thermal quality of edges below that of retreats such as barns. However, even if our assumption is wrong, it would not explain why thermoregulatory effort was less in edges than in the forest, because the thermal quality of edges cannot be lower than the thermal quality of forest; it can only be equal or superior given that edges are half forest and therefore give access to forest and to open habitat. Second, other costs of thermoregulation (besides time) could be at play and could differ between the habitats. For example, predation risk could be lower in retreats than in edges and therefore the costs associated with thermoregulating in edges may be higher than the costs of thermoregulation in barns. A higher predation risk in edges would be consistent with our observations that snakes in edges had not moved between relocations 45% of the time and they were concealed for 70% of the relocations (Blouin-Demers and Weatherhead 2001a). Alternatively, snakes in edges may be foraging as well as thermoregulating, changing the priority associated with thermoregulation. Also, perhaps black rat snakes invest more in thermoregulation in barns and forest than in edges because the thermal heterogeneity is less in the former habitats than in the latter. It may be easier for black rat snakes to evaluate their thermal options in a habitat of low thermal heterogeneity than in a habitat of high thermal heterogeneity because not as much sampling is required in the former. Finally, black rat snakes may prefer edges even if they normally do not invest a lot in thermoregulation because if the need for increased thermoregulation arises (e.g. after feeding, Blouin-Demers and Weatherhead 2001c), then it will be easy to achieve higher body temperatures. Third, the cost-benefit model of thermoregulation (Huey and Slatkin 1976) was designed for lizards and most lizard species are believed to attempt to maximize net energy gain. Thus, it is possible that black rat snakes differ from lizards in not trying to maximize net energy gain.

In the cost-benefit model of thermoregulation (Huey and Slatkin 1976), the cost of thermoregulation is believed to increase monotonically with the magnitude of the difference between the  $T_b$  to be achieved and  $T_e$ s (for field-active ectotherms the  $T_b$  to be achieved is  $T_{set}$ ). Thus, as  $T_e$ s are further from  $T_{set}$  (denoted by high  $d_e$ s, indicative of low thermal quality), the cost of thermoregulation increases. The central prediction of this model relating the cost of thermoregulation to the extent of thermoregulation is that "For all reasonable forms for c (cost curve) and b (benefit curve), we would predict that a lower value of k (increased thermoregulation) would be optimal in the habitat with the lower cost (higher thermal quality)" (Huey and Slatkin 1976, p. 371). Black rat snakes in Ontario experience very challenging thermal conditions and we had therefore expected that they should be particularly sensitive to the thermal quality of habitats. Thus, if black rat snakes are trying to maximize net energy gain, they should have thermoregulated more in habitats of high thermal quality because the cost of thermoconformity is high when the thermal quality of the environment is generally low (the  $T_b$ s experienced by a thermoconformer are far from  $T_{set}$ ). The mismatch we observed between thermoregulation in a habitat and the thermal quality of the habitat is contrary to the central prediction of the cost-benefit model of thermoregulation.

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Although it seems reasonable to assume that the optimal amount of thermoregulation for an ectotherm is determined by some trade-off between costs and benefits, our results suggest that the main cost of thermoregulation identified in the original model is insufficient to explain the extent of thermoregulation in black rat snakes. Huey and Slatkin (1976) had recognised that other factors expected to influence the extent of thermoregulation, such as foraging requirements and predation risk, affect the shape of the cost and benefit curves. However, it seems that these factors affect the shape of the cost and benefit curves more than differences in the thermal quality of habitats for black rat snakes. Two research needs are suggested. First, the cost-benefit model needs to be modified, building on the qualitative arguments made by Huey and Slatkin (1976), so that the influence of predation risk and foraging on thermoregulation are incorporated quantitatively. Second, and probably more challenging, will be to design field studies (both correlational and experimental) to test the predictions made by a model that is ecologically more complex than its predecessor.

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