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A test of the thermal coadaptation hypothesis with black rat snakes (*Elaphe obsoleta*) and northern water snakes (*Nerodia sipedon*)

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Abstract

1. The thermal coadaptation hypothesis predicts that (1) ectotherms experiencing a narrow range of body temperatures in the wild will evolve to perform well over a narrow range of body temperatures and that (2) the optimal temperature for performance will be equal to the preferred body temperature of the species.
2. We tested the predictions of the thermal coadaptation hypothesis with black rat snakes (*Elaphe obsoleta*) and northern water snakes (*Nerodia sipedon*) because black rat snakes experience lower and more variable body temperatures than northern water snakes at our study site.
3. We measured swimming speed, tongue-flicking speed, and striking speed in black rat snakes, and swimming speed and tongue-flicking speed in northern water snakes.
4. Adult water snakes generally had narrower performance breadths and higher optimum performance temperatures than adult black rat snakes.
5. Performance breadths were the same for swimming, tongue flicking, and striking within adult black rat snakes, but performance optima for these behaviours differed significantly. Performance breadths differed and performance optima were the same for swimming and tongue flicking within adult northern water snakes.
6. The relative swimming performance of neonates of the two species was similar in breadth to that of adults, but the thermal optimum for neonate black rat snakes was higher than that of adults.
7. Overall, our results provided support for the thermal coadaptation hypothesis.

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Keywords: Thermal coadaptation hypothesis; Black rat snake; *Elaphe obsoleta*; Northern water snake; *Nerodia sipedon*; Performance breadth; Optimal performance; Body temperature

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1. Introduction

Behavioural and physiological capacities of ectotherms are greatly influenced by body temperature (T_b : Huey and Stevenson, 1979; Stevenson et al., 1985; Hailey and Davies, 1986). Because ectotherms have low rates of metabolic heat production, their T_b is largely dependent on heat exchange with the physical environment (Pough, 1980). Ectotherms use behavioural

thermoregulation to avoid reduced capacities associated with excessively high or low T_b (Stevenson et al., 1985). The extent to which species engage in behavioural thermoregulation is variable (Ruibal, 1961). Thermoregulatory strategies range from precise thermoregulation to perfect thermoconformity. Precise thermoregulators invest substantial effort in thermoregulation and thus generally experience stable T_b s during activity, except for species inhabiting exceptionally challenging thermal environments where even substantial thermoregulatory efforts do not result in high and stable T_b s (Huey, 1982).

Thermoconformers invest little effort in thermoregulation and tend to experience variable T_b s during activity, except for species inhabiting benign thermal environments where the lack of thermoregulation does not result in low and variable T_b s (Huey, 1982).

The thermal coadaptation hypothesis proposes that thermal dependencies of important physiologically dependent processes (e.g., locomotion, digestion, ecdysis) should vary among species, and should reflect the range of T_b experienced by each species during activity (Bennett, 1980; Hertz et al., 1983; Huey and Bennett, 1987; Huey and Kingsolver, 1989; Dorcas et al., 1997; Angilletta et al., 2002). Therefore, the optimal temperature for performance (T_o) should match the preferred body temperature range of the species (T_{set}). In addition, species that experience variable T_b s during activity (generally thermoconformers) should perform well over a broader range of T_b s than species that experience stable T_b s during activity (generally precise thermoregulators). The expected tradeoff for thermoconformers is that proficiency over a range of temperatures is realised at the expense of maximum performance at the optimum temperature (Huey and Hertz, 1984; Gilchrist, 1995). Our general goal in this study was to test the thermal coadaptation hypothesis with performance and behavioural data for black rat snakes (*Elaphe obsoleta*) and northern water snakes (*Nerodia sipedon*). Although several behaviours were measured on each species, our study has the limitations associated with comparative studies of two species (Garland and Adolph, 1994).

Numerous studies have examined the influence of T_b on various locomotor, behavioural, and physiological processes of reptiles (e.g., Hailey and Davies, 1986; Mautz et al., 1992; Irschick and Losos, 1998). Few of these studies, however, were on populations that live in extreme climatic conditions and thus exposed to a broad range of environmental temperatures. Instead, most studies have focused on warm-temperate species that rarely experience T_b far from their optimum for performance. For a general understanding of the effects of T_b on performance, we also need information on species that live in high-cost environments (habitats where the lack of thermoregulation results in T_b unfavourable for performance). Therefore, we con-

ducted this study on populations at the northern extreme of their respective ranges (≈ 40 km from the northern limit of black rat snakes and ≈ 150 km from the northern limit of northern water snakes) and close to the northern extreme of reptile distributions (Conant and Collins, 1991).

Black rat snakes are large constricting colubrids that feed mostly on small mammals and birds. Although black rat snakes are primarily terrestrial, juveniles and adults do not hesitate to cross large water bodies and the total home ranges of many individuals encompass expanses of open water (Blouin-Demers and Weatherhead, 2002). Northern water snakes are medium-sized colubrids that feed on fish and amphibians. As their name implies, northern water snakes are primarily aquatic (Scribner and Weatherhead, 1995) and both adults and juveniles inhabit shallow marshes (Brown and Weatherhead, 2000). Speed of locomotion is intimately linked to fitness in animals because it affects the success of individuals at critical activities such as capturing prey, escaping predators, and finding mates. Both species studied here regularly swim so swimming speed was the first performance we scored. We could not measure crawling speed of black rat snakes in a standardized fashion because rat snakes tends to coil and strike instead of fleeing when prodded to move (G. Blouin-Demers, pers. obs.). Tongue flicking was the second behaviour we scored. Tongue flicking is a stereotyped behaviour that snakes use to acquire chemical information about their environment (Greenberg, 1993). Because tongue flicking is used, among other things, to detect prey and mates, it seems likely to affect fitness. Because tongue flicking is not strictly under muscular control, some researchers may not consider it a traditional performance measure like speed of locomotion or stamina. However, tongue flicking was used in previous studies as “another measure of neuromuscular performance... its purpose... is to gather information about the environment” (Stevenson et al., 1985, p. 49). Striking speed was the final behaviour we scored. Striking also seems likely to affect fitness because snakes strike to defend themselves and to capture prey.

Our previous studies on the two snake populations used here with temperature-sensitive radio telemetry revealed important differences in their thermal ecology. Although the preferred T_b range in a laboratory thermal gradient (T_{set}) was almost identical for the two species [26.5–29.8°C for rat snakes (Blouin-Demers and Weatherhead, 2001) and 24.7–29.8°C for water snakes (Brown and Weatherhead, 2000)], the extent to which individuals in the wild experienced T_b within their T_{set} differed between species. The mean deviation of T_b from T_{set} in rat snakes (4.8°C: Blouin-Demers and Weatherhead, 2001) was double that experienced by water snakes (2.4°C: Brown and Weatherhead, 2000). In addition,

free-ranging black rat snakes had T_b within their T_{set} 9.7% of the time overall, whereas free-ranging water snakes experienced this condition 23.5% of the time. Thus, within our study area, black rat snakes experience lower and more variable T_b s than water snakes. From the thermal coadaptation hypothesis, we predicted that black rat snakes should be able to perform well under a broader range of T_b than northern water snakes. The optimum T_b for a given performance should correspond to the mean T_b of individuals when this performance is performed in the wild (Hertz et al., 1983). Because the differences in thermoregulation between the two species arose from rat snakes experiencing lower T_b on average than water snakes (Brown and Weatherhead, 2000; Blouin-Demers and Weatherhead, 2001), we predicted that rat snakes would achieve their maximum performance at lower T_b than water snakes. Our first objective was to test these predictions by comparing swimming and tongue-flicking performance curves for adult black rat snakes and adult northern water snakes. We used two different types of motor performance to assess whether the predicted difference between the two species was consistent across the two actions.

Studies have reported that, although many processes in reptiles are temperature dependent, the influence exerted by temperature on specific processes can vary substantially (e.g. Greenwald, 1974; Stevenson et al., 1985; Dorcas et al., 1997). Different behaviours often have different performance curves within a species or population. Because racing speed is often used as the sole performance measure in studies of coadaptation, this can lead to erroneous conclusions if the performance curves of other biologically important functions differ (Huey, 1982). We predicted that coadaptation should be evident across a range of behaviours. Our second objective was to test this prediction by comparing swimming, tongue flicking, and striking performance curves within adult black rat snakes and swimming and tongue-flicking performance curves within adult northern water snakes.

If coadaptation occurs and if the thermal ecologies of adults and juveniles are similar, there should be no ontogenetic shifts in the performance curves. Therefore, we predicted that coadaptation should also be evident among neonates. Our third objective was to test this prediction by comparing swimming performance curves for adult and neonate black rat snakes and for adult and neonate northern water snakes.

2. Materials and methods

We conducted this study at the Queen's University Biological Station, 40 km north of Kingston, Ontario, Canada. Snakes used in our investigation were captured as part of concurrent studies (Blouin-Demers et al.,

2000a; Brown and Weatherhead, 2000). Captured snakes were brought to the laboratory where they were weighed, measured for snout-vent length with a flexible measuring tape (Blouin-Demers, 2003), and sexed by probing the cloaca for the presence of hemipenes. Each snake was implanted sub-cutaneously with a passive integrated transponder (Anitech Information System Inc., Markham, Ontario) for individual identification. Water snakes were housed in groups of 3–6 in tanks (75 cm × 75 cm × 75 cm) throughout the summer as a part of their use in laboratory studies. Black rat snakes were housed singly in plastic cages (50 cm × 40 cm × 15 cm) during the testing period only (2 weeks at most for any given individual). The room in which the snakes were held received natural light through four windows (natural photoperiod) and was kept at 20°C. The snakes had access to a heating rock for thermoregulation, a water dish for drinking, and a piece of plastic pipe for refuge. Water snakes were fed fresh fish ad libitum once a week, but black rat snakes were not fed because they were only kept in captivity for a short time. Neonate black rat snakes came from 16 clutches (from wild snakes) that we incubated in the laboratory at 30°C on moist vermiculite (1:1 mass ratio of water to vermiculite). Neonate northern water snakes were born to 10 gravid females held in captivity under the same conditions as the other animals used in this study. All neonates were tested within 7 days of hatching or birth. Snakes used in the current study were subsequently released at their point of capture. Our experimental protocols were approved by the Carleton University Animal Care Committee.

2.1. General testing procedures

The three measures of performance we examined were swimming speed, striking speed, and tongue-flicking frequency. We tested each individual snake at T_b of approximately 10°C, 15°C, 20°C, 25°C, 30°C, and 35°C. The order in which the treatments were administered was randomized. Some studies of temperature dependence of performance tested subjects at a given temperature before and after all experimental treatments to identify individuals that may have become ill during the experiments (e.g., Hertz et al., 1983). We did not take this precaution, but our treatments were administered over short time periods (at most 2 weeks per individual) and none of the animals we used appeared ill, weak, or otherwise abnormal during the course of our experiments. We did not test at temperatures above 35°C because it is too close to the lethal temperature for many snake species (40°C: Jacobson and Whitford, 1970; Dawson, 1975). Black rat snakes and northern water snakes from our study area become uncoordinated at $\approx 38^\circ\text{C}$ and die at $\approx 40^\circ\text{C}$ (G. Blouin-Demers, unpublished data). Some individuals were used in more

than one test of performance (e.g., both tongue-flicking and striking). The majority of tests for a given temperature were separated by at least 1 day, so that snakes had time to rest before being tested again. In a limited number of tongue-flicking and striking tests, individuals were tested at up to three temperatures in 1 day with at least 3 h separating each test. None of the females used in the study was gravid at the time of testing. Prior to each test, we immersed the snakes in warm water or placed them in a cooling chamber to equilibrate their T_b to the appropriate test temperature. In all cases, a test consisted of two consecutive trials and in our analyses we only used the fastest of the two trials for each test temperature. We recorded the T_b of the snakes immediately before and after each test by inserting a temperature probe 3 cm into their cloaca. We used the mean of these two T_b in our analyses.

2.2. Swimming speed trials

To measure swimming speed, we used a modified version of the technique used by Weatherhead and Robertson (1992). We conducted swimming trials in a plywood trough that measured 7.35 m long, 0.6 m high, and 0.4 m wide. The trough was lined with fiberglass and was filled with approximately 15 cm of water. We placed markers 1.5 m from either end to mark the central swimming distance (4.35 m). The water temperature in the trough equalled that of the testing temperature. After the T_b of the snake to be tested had equilibrated to the test temperature, we placed the snake in the water and chased it down the length of the trough. We encouraged the snake to swim at its maximum speed by gently tapping its tail throughout the trial. The time it took the snake's head to cross the two markers was recorded with a stopwatch. If the snake stopped or turned around during the trial, we immediately returned the snake to the end of the trough and restarted the trial. We measured swimming speed in neonates with the same technique, but the trough was 14 cm wide, 10 cm high, and the central swimming distance was 2.0 m.

2.3. Tongue-flicking trials

Tongue flicking is a stereotyped behaviour in snakes, as it is in most squamate reptiles (Greenberg, 1993). In these species, the tongue is projected outward and down from the mouth and is returned by sweeping upward and back into the mouth (Cooper, 1998). We measured tongue-flicking frequency for each adult snake at each test T_b . After the T_b of the snake to be tested had equilibrated to the trial temperature, we positioned the snake in front of a video camera and recorded two tongue-flicking bouts. Using frame-by-frame play back, we determined the duration of each tongue-flicking bout

(each frame is 1/60 s) and the number of times the tongue changed direction in the vertical plane. Tongue-flicking frequency was calculated as the number of vertical direction changes divided by the duration of the tongue-flicking bout.

2.4. Striking speed trials

To measure striking speed, we constructed a white plywood cage that allowed distance to be measured in three dimensions. The cage measured 1.5 m long, 0.35 m high, and 0.35 m wide. The front of the cage was clear plastic so that the strike could be recorded with a video camera. We scribed a black 5 cm grid on all faces of the cage and positioned a mirror at 45° above the cage so that all three planes of movement could be recorded on film at once. We placed our video camera in front of this apparatus to record each strike. We placed the snake in the cage and used a stuffed glove attached to the end of a stick to induce defensive striking. For a strike to be used in analysis, there could have been no contact with the glove at any point because contact could change the trajectory and speed of striking. We determined the duration and distance (in three dimensions) of each strike with frame-by-frame play back of the videotape. We attempted to measure striking speed for all adult snakes. Water snakes consistently refused to strike at all temperatures, however, so we were only able to measure striking speed for rat snakes.

2.5. Analyses

Based on previous work (Hertz et al., 1983; Stevenson et al., 1985; Huey and Kingsolver, 1989; Anguiletta et al., *in press*), we fitted a logistic-exponential curve with non-linear curve fitting (Eq. (1)) to the data for each snake and for each behaviour. The critical thermal minimum (CT_{min}) and the critical thermal maximum (CT_{max}) were set at 4°C and at 38°C, respectively, for both species because rat snakes and water snakes loose muscle tone outside this temperature range (G. Blouin-Demers, unpublished data). For each fitting, the experimental data points received a weight of one and the CT_{min} and CT_{max} received a weight of five. We used the equation obtained for each individual snake and for each behaviour to determine (1) the T_b for which performance was maximal (the optimal temperature: T_o) and (2) the two T_b for which performance was 80% of the maximum (the upper and lower bound of the 80% performance breadth: B_{80} Stevenson et al., 1985). Because non-linear curve fitting can be sensitive to starting parameter values (van Berkum, 1986), we ensured that each curve had a good fit by inspecting the error sum of squares. We obtained

tight fits in all cases:

$$\text{Performance} = S \left(\frac{1}{1 + k_1 e^{-k_2(T_b - CT_{\min})}} \right) (1 - e^{k_3(T_b - CT_{\max})}) \quad (1)$$

We performed our analyses using JMP Version 5 (SAS Institute, 2002) and Mathematica Version 4.1 (Wolfram Research, 2000) on a Macintosh desktop computer. The assumptions of normality and homogeneity of variance were verified using box plots. We considered results statistically significant at $\alpha = 0.05$. Means are reported ± 1 SE.

2.6. Sample sizes and test temperatures

Swimming-speed trials were performed on 21 adult black rat snakes and 37 adult northern water snakes (Table 1). Trials were conducted at mean T_b s of $10.4 \pm 0.5^\circ\text{C}$, $15.6 \pm 0.6^\circ\text{C}$, $19.9 \pm 0.8^\circ\text{C}$, $25.1 \pm 0.5^\circ\text{C}$, $30.1 \pm 0.6^\circ\text{C}$, and $34.5 \pm 0.4^\circ\text{C}$. Mean difference between the T_b before and after the trial was 1.3°C , indicating that the snakes' T_b did not change substantially over the course of the swimming trial. Swimming trials were also conducted on 15 neonate black rat snakes from three clutches and 14 neonate northern water snakes from three litters (Table 1). Because of the small thermal inertia of neonate snakes, their T_b equalled the water temperature before and after all trials. Trials were therefore conducted at exact T_b s of 10°C , 15°C , 20°C , 25°C , 30°C , and 35°C . Tongue-flicking frequency was measured on 17 black rat snakes and 30 northern water snakes (Table 1). Mean T_b s at which snakes were tested were $10.4 \pm 0.6^\circ\text{C}$, $15.1 \pm 0.5^\circ\text{C}$, $19.3 \pm 0.8^\circ\text{C}$, $25.0 \pm 0.7^\circ\text{C}$, $29.9 \pm 0.6^\circ\text{C}$, and $34.3 \pm 0.4^\circ\text{C}$. The mean difference between the T_b before and after the trial was 2.4°C . Striking-speed trials were conducted on 26 black rat snakes (Table 1). Striking-speed trials were conducted at mean T_b s of $10.7 \pm 0.7^\circ\text{C}$, $15.1 \pm 0.8^\circ\text{C}$, $19.9 \pm 0.4^\circ\text{C}$, $24.7 \pm 0.7^\circ\text{C}$, $30.0 \pm 0.7^\circ\text{C}$,

and $34.3 \pm 0.5^\circ\text{C}$. The mean variation in the T_b before and after the trials was 2.3°C . Although we attempted to get at least two strikes per temperature, there were occasions when striking could not be elicited. Such trials often occurred at the colder temperatures. Some individual snakes also consistently refused to strike. We excluded 10 black rat snakes from the striking speed analyses because no striking response was elicited at some temperatures. Because this apparent behavioural shift in response to temperature could have interesting implications (Hertz et al., 1982; Crowley and Pietruska, 1983), we scored the proportion of individuals striking at each test temperature.

3. Results

Relationships between performance and T_b for swimming speed, tongue-flicking frequency, and striking speed (Table 1) were as expected (Stevenson et al., 1985), with an initial increase in performance with increasing T_b , followed by a sharp decline in performance as T_b rose above 35°C in adult black rat snakes and northern water snakes (Fig. 1). Similar relationships were found for swimming speed in hatchling black rat snakes and neonatal northern water snakes (Fig. 2). The proportion of adult black rat snakes striking at each test temperature varied significantly. However, the relationship was not linear (ANOVA: $F_{(1,4)} = 3.89$, $p = 0.12$, $R^2 = 0.49$), but quadratic (ANOVA: $F_{(2,3)} = 20.56$, $p = 0.018$, $R^2 = 0.93$, Fig. 3). Therefore, adult black rat snakes tended to strike at intermediate T_b s, but hid their heads inside body coils at low and high T_b s.

3.1. Coadaptation of performance curves in adult snakes

B_{80} of swimming performance was wider for adult black rat snakes than for adult northern water snakes (ANOVA: $F_{(1,56)} = 4.05$, $p = 0.048$, $R^2 = 0.068$, Fig. 4).

Table 1

Mean (± 1 SE) parameter values of the logistic-exponential equations fitted to the performance data for adult and neonate black rat snakes and adult and neonate northern water snakes

Species	Age	Behaviour	<i>N</i>	<i>S</i>	<i>k</i> ₁	<i>k</i> ₂	<i>k</i> ₃
BRS	Adult	Flicking	17	21.3 \pm 1.0	26.98 \pm 4.79	0.334 \pm 0.036	0.916 \pm 0.052
		Striking	16	238.2 \pm 86.9	58.21 \pm 10.21	0.402 \pm 0.053	0.791 \pm 0.080
		Swimming	21	2.55 \pm 0.85	94.90 \pm 36.86	0.419 \pm 0.054	0.556 \pm 0.083
	Baby	Swimming	15	0.261 \pm 0.026	26.56 \pm 3.35	0.308 \pm 0.035	0.775 \pm 0.088
NWS	Adult	Flicking	30	30.7 \pm 2.1	30.73 \pm 4.57	0.294 \pm 0.026	0.856 \pm 0.049
		Swimming	37	1.29 \pm 0.17	417.05 \pm 201.68	0.349 \pm 0.028	0.716 \pm 0.054
	Baby	Swimming	14	0.682 \pm 0.140	49.06 \pm 9.36	0.299 \pm 0.018	0.292 \pm 0.039

Note: The equation fitted was $\text{Performance} = S \left(\frac{1}{1 + k_1 e^{-k_2(T_b - CT_{\min})}} \right) (1 - e^{k_3(T_b - CT_{\max})})$.

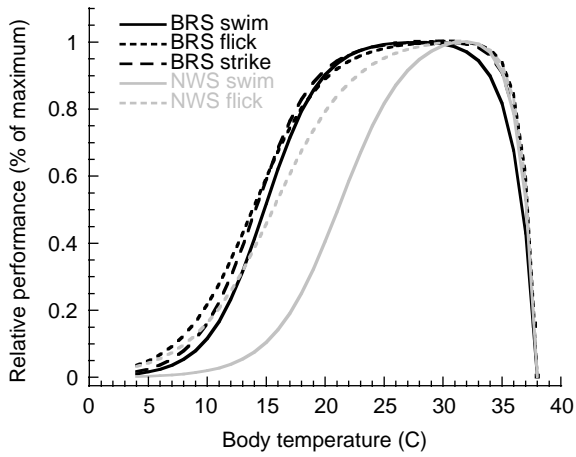


Fig. 1. Relative performance as a function of body temperature for swimming, tongue flicking and striking by adult black rat snakes (BRS) and northern water snakes (NWS) in Ontario.

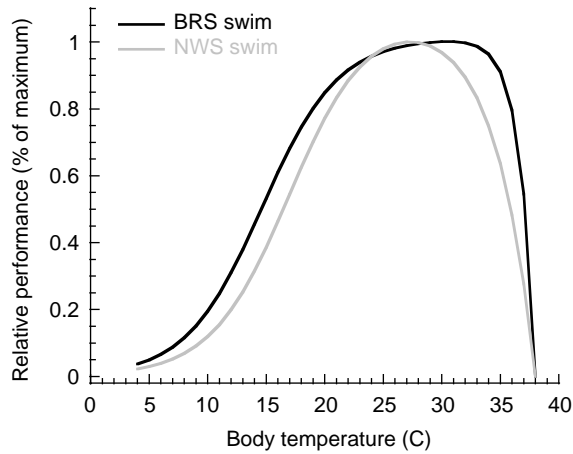


Fig. 2. Relative performance as a function of body temperature for swimming neonate black rat snakes (BRS) and northern water snakes (NWS) in Ontario.

Also, T_0 for this behaviour was lower for black rat snakes than for northern water snakes (ANOVA: $F_{(1,56)} = 22.07$, $p < 0.001$, $R^2 = 0.283$, Fig. 4). B_{80} of tongue-flicking performance was again wider for black rat snakes than for northern water snakes, but this difference was only marginally significant (ANOVA: $F_{(1,45)} = 2.70$, $p = 0.107$, $R^2 = 0.057$, Fig. 4). T_0 for tongue-flicking performance did not differ between the two species (ANOVA: $F_{(1,45)} = 0.24$, $p = 0.629$, $R^2 = 0.005$, Fig. 4). Thus, black rat snakes performed at $\geq 80\%$ of their maximum over a broader range of T_b than water snakes and for swimming, rat snakes achieved their maximum performance at lower T_b than water snakes.

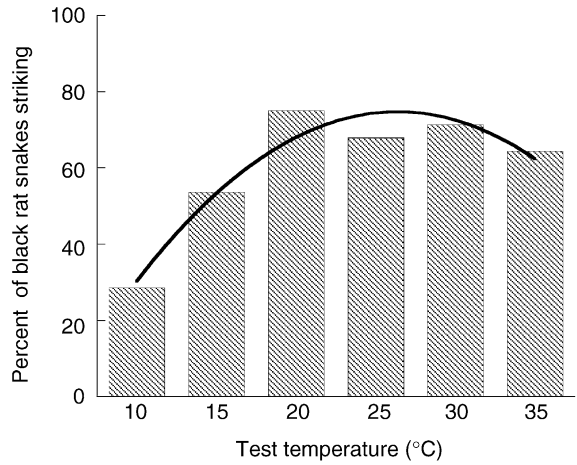


Fig. 3. Proportion of adult black rat snakes striking as a function of body temperature in Ontario. Quadratic fit is indicated by the line.

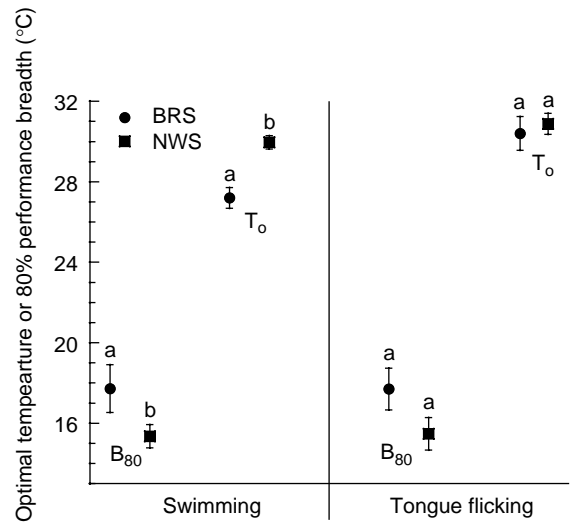


Fig. 4. 80% performance breadths (B_{80}) and optimal body temperatures (T_0) for swimming and tongue-flicking performance curves of adult black rat snakes (BRS) and northern water snakes (NWS) in Ontario. Means (± 1 SE) with the same letters are not significantly different.

3.2. Similarity of performance curves

For adult black rat snakes, B_{80} of swimming, tongue flicking, and striking performance were not significantly different (ANOVA: $F_{(2,51)} = 0.31$, $p = 0.732$, $R^2 = 0.012$, Fig. 5). T_0 for these same behaviours differed, however (ANOVA: $F_{(2,51)} = 3.89$, $p = 0.027$, $R^2 = 0.132$, Fig. 5). Tukey-Kramer HSD tests indicated that T_0 for

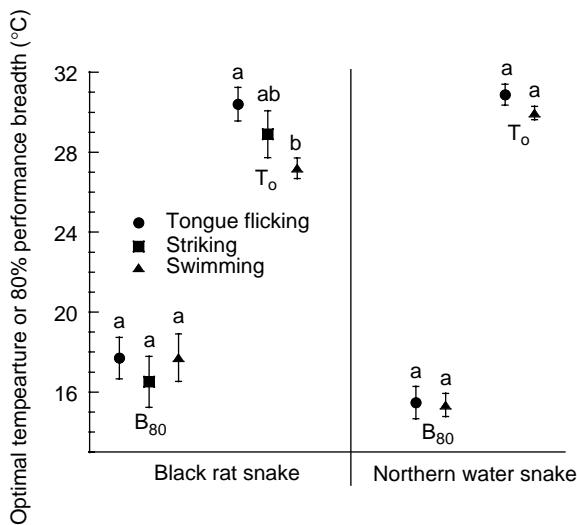


Fig. 5. 80% performance breadths (B_{80}) and optimal body temperatures (T_o) for tongue-flicking, striking, and swimming performance curves of adult black rat snakes and northern water snakes in Ontario. Means (± 1 SE) with the same letters are not significantly different.

tongue flicking was higher than T_o for swimming (Fig. 5). For northern water snakes, B_{80} of swimming and tongue flicking did not differ significantly (ANOVA: $F_{(1,65)} = 0.01$, $p = 0.904$, $R^2 < 0.001$, Fig. 5), nor did T_o for those same behaviours (ANOVA: $F_{(1,65)} = 2.41$, $p = 0.125$, $R^2 = 0.036$, Fig. 5).

3.3. Ontogenetic changes in performance curves

In black rat snakes, B_{80} of the swimming performance curves were not significantly different between adults and neonates (ANOVA with mother nested within age class: $F_{(1,13)} = 1.09$, $p = 0.315$, $R^2 = 0.632$, Fig. 6). T_o for these same performance curves were higher for neonates than for adults (ANOVA with mother nested within species: $F_{(1,13)} = 12.44$, $p = 0.004$, $R^2 = 0.693$, Fig. 6). In northern water snakes, B_{80} of the swimming performance curves were significantly different between adults and neonates (ANOVA with mother nested within species: $F_{(1,12)} = 5.22$, $p = 0.041$, $R^2 = 0.857$, Fig. 6). T_o for these same performance curves were lower for neonates than for adults (ANOVA with mother nested within species: $F_{(1,12)} = 64.22$, $p < 0.001$, $R^2 = 0.933$, Fig. 6).

3.4. Coadaptation of performance curves in neonate snakes

B_{80} of swimming performance was wider for neonate black rat snakes than for neonate northern water snakes,

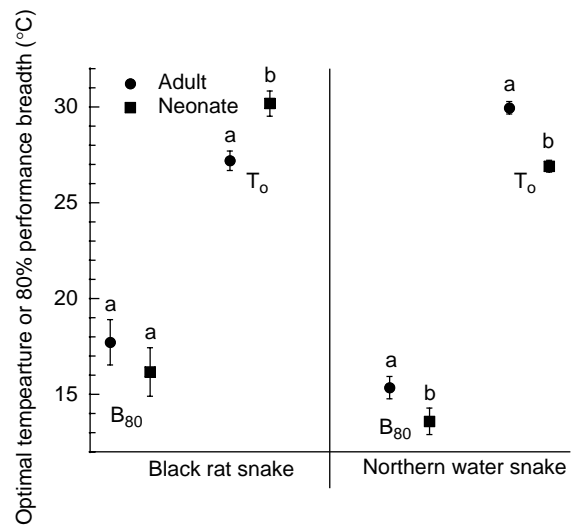


Fig. 6. 80% performance breadths (B_{80}) and optimal body temperatures (T_o) for swimming performance curves of adult and neonate black rat snakes and northern water snakes in Ontario. Means (± 1 SE) with the same letters are not significantly different.

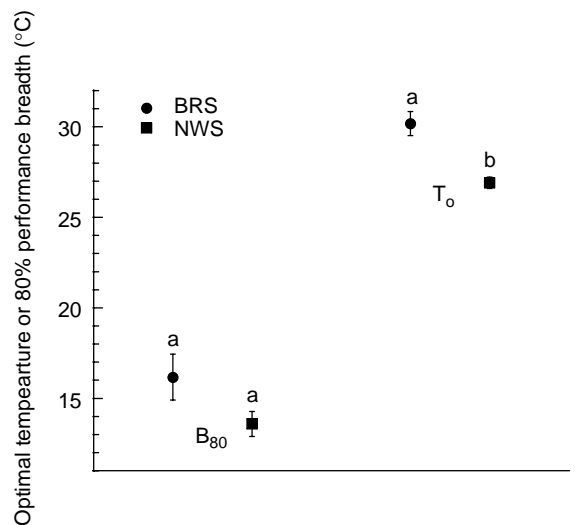


Fig. 7. 80% performance breadths (B_{80}) and optimal body temperatures (T_o) for swimming performance curves of neonate black rat snakes (BRS) and northern water snakes (NWS) in Ontario. Means (± 1 SE) with the same letters are not significantly different.

but this difference was not significant (ANOVA with mother nested within species: $F_{(1,26)} = 2.72$, $p = 0.149$, $R^2 = 0.112$, Fig. 7). Contrary to adult snakes, however, T_o for swimming was higher for black rat snakes than for northern water snakes (ANOVA with mother nested within species: $F_{(1,26)} = 19.65$, $p < 0.001$, $R^2 = 0.448$, Fig. 7).

4. Discussion

The shape of swimming, tongue flicking, and striking performance curves was an initial increase in performance with increasing T_b followed by a sharp decline as T_b approached 35°C. Similar trends are apparent in numerous studies that have investigated the thermal dependence of locomotor and physiological processes in reptiles (e.g., Licht, 1964; Hailey and Davies, 1986; Dorcas et al., 1997).

Although black rat snakes and northern water snakes select almost identical T_b in laboratory thermal gradients, free-ranging black rat snakes experience lower T_b than northern water snakes in our study populations (Brown and Weatherhead, 2000; Blouin-Demers and Weatherhead, 2001). The thermal coadaptation hypothesis predicts that T_o should match T_{set} among species and that T_o should match T_b during activity within species. If the latter prediction of the thermal coadaptation hypothesis is valid, we predicted that black rat snakes should have broader performance curves that peak at lower T_b than those of water snakes. Consistent with that prediction, B_{80} for both swimming and tongue flicking were significantly wider for black rat snakes than for water snakes. Also consistent with the thermal coadaptation hypothesis, T_o for swimming was lower for black rat snakes than for water snakes. T_o for tongue flicking, however, did not differ between the two species. One reason that the results for tongue flicking may not have been consistent with those for swimming is that snakes were not exposed to prey odours when tested. We chose this approach to keep our study comparable to previous studies (Stevenson et al., 1985) and to avoid potential difficulties that could arise from errors in quantifying prey odours, from individual differences in prey preference (e.g., individual specialization) or from differences in motivation (e.g., hunger). Because snakes were passively sampling their environment in our study, their performance may not have reflected how they would perform in an ecologically more relevant context.

We were unable to use striking speed as a third measure to test the thermal coadaptation hypothesis because we were unsuccessful in eliciting striking from water snakes. Perhaps this difference between species is due to the anti-predator behaviours exhibited by black rat snakes and water snakes. Although water snakes regularly strike when initially captured in the field, they become quite docile when in captivity. Black rat snakes, on the other hand, tend to be less aggressive than water snakes when first captured in the field but they do not become docile in captivity. When confronted with the stuffed glove at cold and warm T_b , black rat snakes tended to hide their head inside a ball of body coils instead of striking defensively. This presumably represents a shift to a last resort anti-predator behaviour under conditions where rat snakes cannot launch a

defensive strike effectively. Similar shifts in defensive behaviour in response to temperature have been documented in lizards (Hertz et al., 1982; Crowley and Pietruska, 1983).

Bennett (1980) found a qualitative match between the mean T_b of free-ranging lizards and their T_o for locomotor performance. In black rat snakes, mean values of T_o (tongue flicking = 30.4°C, striking = 28.9°C, C, and swimming = 27.2°C) were similar to those for T_{set} (28.1°C) in a laboratory thermal gradient. For northern water snakes, however, mean values of T_o (tongue flicking = 30.9°C and swimming = 30.0°C) were higher than those for T_{set} (27.1°C) in a laboratory thermal gradient. The mean T_b (25.2°C) of free-ranging black rat snakes when the thermal environment allowed snakes to reach the lower bound of their T_{set} (Blouin-Demers and Weatherhead, 2001) was lower than the mean T_b in a thermal gradient and the mean T_o for performance. Therefore, it seems that T_o of black rat snakes matches their T_{set} , but because they live in a thermally challenging environment (Blouin-Demers and Weatherhead, 2001), they can rarely achieve their T_{set} . For water snakes, however, the mean T_b (26.8°C) of free-ranging snakes when the thermal environment allowed T_{set} to be reached was close to the mean T_b selected in the gradient, but still lower than the mean T_o for performance. Thus, although both species of snakes we studied experience temperatures that are, on average, below their T_{set} , that difference is smaller for water snakes. This difference appears to have allowed northern water snakes to become thermal specialists (narrower B_{80} , higher T_o) relative to black rat snakes.

One underlying assumption of the thermal coadaptation hypothesis is that performance curves for different behaviours or processes of an individual are similar. If the performance curves of all behaviours differ, coadaptation is not possible because no single T_b can maximize organismal performance (Huey, 1982). Previous studies investigating the thermal dependence of various physiological and biological processes found that the thermal sensitivity of several measures of performance differed (Greenwald, 1974; Stevenson et al., 1985; Dorcas et al., 1997), suggesting that no single T_b is best for all of the physiological, ecological, and behavioural activities performed by reptiles. Despite these results, many investigations continue to use locomotion as the sole measure of organismal performance (Angiletta et al., in 2002). This approach would only seem to be justified when the goal of the study is specifically to assess how locomotion varies with T_b .

We compared the B_{80} of the various performances within each species to see if the thermal dependencies of different behaviours were consistent. Contrary to previous studies, our results demonstrate that there is considerable conservatism in the influence that T_b exerts on performance, at least for the processes tested. All B_{80}

within black rat snakes and northern water snakes were the same. The only T_o that differed were swimming and tongue flicking for black rat snakes. One possible explanation for the disagreement between our study and previous studies is that the behaviours and processes measured were different. For example, [Stevenson et al. \(1985\)](#) measured crawling speed, swimming speed, tongue flicking, digestion rate, and oxygen consumption. In their study, the curve that differed most from the others was oxygen consumption, a parameter we did not measure and that some researchers would argue is not a performance. Bio-mechanically, a caveat must be made about comparing striking speed and swimming speed. Even if muscle fibres had identical performance curves, there would be a difference in the performance curves for swimming and for striking because at high speeds snakes in water will experience more drag than snakes in air. However, the difference remains interesting in an ecological context.

To determine whether there were ontogenetic differences in the thermal dependency of performance, we compared the performance curves for swimming between adults and neonates of both species. The B_{80} for swimming of neonates and adults differed only in water snakes. The T_o for swimming, however, differed between adults and neonates of both species. The T_o for swimming of neonate black rat snakes was higher than that of adults, while the T_o for swimming of neonate water snakes was lower than that of adults. Interestingly, the T_{set} of neonate black rat snakes in a laboratory thermal gradient (35.0°C) is much higher than that of adults, while the T_{set} of neonate northern water snakes in a similar gradient (29.3°C) overlaps that of adults ([Blouin-Demers et al., 2000b](#)). These results suggest that the thermal ecology of neonate black rat snakes may be very different from that of adults, a pattern not uncommon among ectotherms. For example, [Lillywhite et al. \(1973\)](#) demonstrated that the thermal ecology of adult and juvenile toads (*Bufo boreas*) differed substantially because juveniles had evolved a behavioural thermoregulatory mechanism that maximized growth to reduce age at maturity. Many factors important for behavioural thermoregulation differ between adult and neonate black rat snakes. Juveniles have lower heat absorption rates because they are pale grey with dark blotches while adults are black. Juveniles have lower thermal inertia because their body mass is much less than that of adults. Finally, because juvenile snakes are much smaller than adults, they are susceptible to a much broader array of predators which would influence the costs and benefits associated with behavioural thermoregulation ([Huey and Slatkin, 1976](#)). Determining how these differences affect the thermoregulatory behaviour of neonate snakes will have to await the advent of temperature-sensitive radio-transmitters small enough to be implanted in neonates.

To determine whether coadaptation was also evident in juvenile snakes, we compared the swimming performance curves of neonate water snakes and neonate rat snakes. Similar to adults, the B_{80} for swimming was wider in black rat snakes than in northern water snakes, suggesting that coadaptation also occurs in neonates. Contrary to adults, however, T_o was higher in rat snakes than in water snakes, suggesting that there is an ontogenetic shift in performance, at least in black rat snakes. This last result is also consistent with the observation that the T_{set} of neonate black rat snakes in a thermal gradient is higher than that of adults ([Blouin-Demers et al., 2000b](#)). Again, understanding these patterns will require detailed information on the thermal ecology of free-living neonate snakes.

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