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HABITAT USE IS LINKED TO COMPONENTS OF FITNESS THROUGH THE TEMPERATURE-DEPENDENCE OF PERFORMANCE IN RATSNAKES (*ELAPHE OBSOLETA*)

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ABSTRACT

For ectothermic reptiles, habitat selection is mechanistically linked to fitness through the temperature-dependence of performance. Many reptiles occupy thermally heterogeneous environments and regulate their body temperature through selective use of habitats within their environments, making reptiles ideal subjects to understand the fitness consequences of habitat use. Our goal here was to investigate the link between habitat selection, thermoregulation, and fitness by comparing the expected distribution of performance for real ratsnakes that thermoregulate through selective use of habitat with the performance of hypothetical snakes that are assumed to use habitats randomly. Thermal data for real snakes were obtained using temperature-sensitive radio transmitters implanted in free-living snakes, whereas thermal data for hypothetical snakes were obtained by sampling environmental temperatures that a randomly moving snake would encounter. Thermal data were then transformed into performance using an experimentally derived equation relating performance (swimming speed) to temperature. Habitat selection allowed snakes to avoid lethal temperatures and resulted in an average improvement of 18% in locomotor performance. A more exact measure of the fitness improvement accrued through habitat selection will have to await data relating body temperature to ultimate measures of fitness and a deeper understanding of the contribution of different performances to fitness.

Keywords: thermal reaction norm, thermoregulation, reptiles, locomotion

INTRODUCTION

The vast majority of animals are ectotherms that, by definition, have limited capacity for buffering the ubiquitous effects of body temperature on all of their physiological processes. Indeed, body temperature affects such fundamental processes as speed of locomotion, feeding, and growth rates (Stevenson et al., 1985; Angilletta et al., 2004).

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Because variation in body temperature can have a significant impact on fitness, many ectotherms use behavioral thermoregulation to avoid reduced capacities associated with excessively high or low body temperatures (Cowles and Bogert, 1944; Huey, 1991). Although reptiles have some physiological means to thermoregulate (Seebacher and Franklin, 2005), body temperature regulation is achieved chiefly through behavior and choice of microclimate (Reinert, 1993; Christian and Weavers, 1996).

Terrestrial reptiles offer unique opportunities to understand the consequences of habitat use because behavioral thermoregulation and the temperature dependence of performance provide a clear mechanistic link between habitat use and fitness. Despite the wealth of studies documenting the link between thermoregulation patterns and habitat use in reptiles (e.g., Huey et al., 1989; Diaz, 1997), and despite the application of this approach in seminal papers on thermoregulation (Huey, 1991; Hertz et al., 1993), very few studies have quantified the improvement in components of fitness, such as performance, accrued through habitat selection in reptiles, except in the specific case of nest-site selection (e.g., Qualls and Andrews, 1999; Shine, 1999). Our goal here is to use data on body temperature, habitat use, and a thermal reaction norm to estimate the gain in performance achieved through habitat selection by ratsnakes (*Elaphe obsoleta*).

Ratsnakes preferentially use edges, the transition zones between forest and open habitats, such as rocky outcrops and old fields (Weatherhead and Charland, 1985; Durner and Gates 1993; Blouin-Demers and Weatherhead, 2001a, 2002; Carfagno and Weatherhead, 2006). Blouin-Demers and Weatherhead (2001b) showed experimentally that ratsnakes use edges to thermoregulate. Ratsnakes were fed in the field to induce a thermophilic response. Snakes that were fed when in edges remained there, whereas snakes fed in the forest moved to edges, thus experimentally demonstrating the link between habitat use and thermoregulation.

An important challenge in the use of thermal reaction norms to infer the fitness consequences of habitat use is the choice of an appropriate performance metric (Huey, 1991; Hertz et al., 1993). Because it is challenging to measure fitness per se as a function of body temperature, researchers rely on measures that seem likely to be correlated with fitness. The strength of the correlation between performance and fitness, however, is likely to vary between performance measures (Stevenson et al., 1985; Huey, 1991). For instance, for animals with indeterminate growth, such as reptiles, we can envision a stronger link between growth rates and fitness than between tongue flicking speed and fitness (Dubois et al., 2008). To complicate matters further, thermal reaction norms can differ among different performance measures (Huey, 1991; Angilletta et al., 2003, 2006). Thus, the optimal body temperature for growth may not be the optimal body temperature for locomotion. Here we use locomotion as our measure of performance. Locomotion is commonly used in studies of performance because it is directly associated with activities that affect fitness (Irschick and Garland, 2001): reptiles such as ratsnakes must move to capture prey, to elude predators, to find mates, and to compete with rivals. Superior locomotion should improve performance in all of these activities and thereby enhance fitness.

The approach we take is to compare the expected distribution of performance for real snakes that thermoregulate through selective use of habitats with the performance

of hypothetical snakes that are assumed to use habitats randomly. Thermal data for real snakes are obtained using temperature-sensitive radio transmitters implanted in free-living snakes, whereas thermal data for hypothetical snakes are obtained by sampling environmental temperatures that a randomly moving snake would encounter. Thermal data are then transformed into performance measures using an experimentally derived equation relating performance to temperature.

MATERIALS AND METHODS

STUDY AREA

We collected data from 1997 to 2000 in a 10 km × 3 km area at the Queen's University Biological Station, 100 km south of Ottawa, Canada (44º33′N; 76º19′W). Habitat was predominantly mature, second-growth deciduous forest. Lakes, wetlands, and rocky outcrops provided natural gaps and edge habitats in the forest. Artificial gaps and edges were created by small hayfields (Blouin-Demers and Weatherhead, 2001a).

RADIO-TELEMETRY

We captured snakes at communal hibernacula during spring emergence and, opportunistically, throughout the active season (Blouin-Demers et al., 2000a). From all snakes captured, we selected a subset for implantation of temperature-sensitive radio transmitters (Model SI-2T, Holohil Systems Inc., Carp, Ontario, 8.6 g, 20 months' battery life at 20 °C). Snakes selected to be implanted had to be large enough to bear the transmitter (maximum ratio of transmitter mass:body mass = 0.025:1). We used isoflurane, delivered via a precision vaporizer, to anesthetize the snakes and then sterile surgical techniques to implant the radio transmitters in the body cavity and the antennae under the epidermis (Blouin-Demers et al., 2000b; Weatherhead and Blouin-Demers, 2004). From May 1997 to November 1999, we followed 53 ratsnakes for periods ranging from 1 to 30 months (mean ± SE = 13.1 ± 1.1 months). Twenty-three snakes were followed in multiple years and therefore we have data for 79 "snake-years".

Radio transmitters had pulse rates proportional to temperature. Calibration curves were supplied by the manufacturer for each transmitter (pulse rates from 0 °C to 40 °C in 5 °C increments). We used polynomial regressions (including all terms up to degree 4) and eight calibration points for each radio transmitter to derive an equation to predict temperature based on pulse rate. All calibration equations provided a very high degree of fit (all $R^2 \geq 0.99$).

BODY TEMPERATURES

We obtained body temperature readings from ratsnakes with two automated radio-telemetry receivers (SRX 400, Lotek Engineering Inc., Newmarket, Ontario) and associated antennae towers from mid-April to early October 1997–1999 (for details see Blouin-Demers and Weatherhead, 2001c). We entered the calibration equations for each radio transmitter in both loggers and then programmed the loggers to scan

the frequency of each radio transmitter every 10 min. Each time a snake was within transmission range (the signal of the radio transmitter was clearly distinguished against the background electrostatic noise), the loggers calculated the pulse rate as the average duration of three pulse intervals, computed the corresponding temperature from the calibration equation of that transmitter, and stored the date, time, transmitter frequency, and temperature.

OPERATIVE ENVIRONMENTAL TEMPERATURES

Operative environmental temperatures are steady-state possible body temperatures available to an ectotherm in the field. A simple approach for determining operative environmental temperatures is to install in the field a series of physical models that have the same thermal characteristics as the species of interest (Bakken et al., 1985; Shine and Kearney, 2001). We constructed two models of ratsnakes using copper pipes. The models were 40 cm long and had a diameter of 4 cm. We painted the models with glossy black metal paint to approximate the reflectance of ratsnakes (Peterson et al., 1993). We suspended a thermocouple in the center of each model with stiff metal wire, filled the models with water, and then sealed both ends of each model with a plastic cap and silicone. The thermocouple was connected to a temperature data logger (HOBO Temp, ONSET Computer Corporation, Pocasset, Massachusetts) that recorded the model's internal temperature every 10 min. We ensured the models accurately approximated the thermal properties of ratsnakes by calibrating them with two fresh carcasses (Blouin-Demers and Weatherhead, 2001c).

Excluding open water that is not used by ratsnakes, the principal habitats in the study area are forest (71.7%), rock outcrop (3.6%), old field (11.1%), and marsh (13.6%) (Blouin-Demers and Weatherhead, 2001a; Row and Blouin-Demers, 2006). We measured operative temperatures by placing model snakes in 4–8 locations in each of the four principal habitats for a total duration of 3–6 weeks. We then used weather data (air temperature, wind speed, and solar radiation all read every minute and averaged for each hour) collected at the field station to build predictive multiple regression equations of model temperatures in each habitat (Blouin-Demers and Weatherhead, 2001c). All equations were highly significant and explained a large proportion of the total variance (mean R^2 = 0.85, range in R^2 = 0.56–0.94; Blouin-Demers and Weatherhead, 2001c). We used these equations and microclimatic data to calculate operative environmental temperatures in each habitat every hour for the duration of the study. We have shown previously that, from a thermal perspective, all 3 open habitats (field, marsh, rock outcrop) are equivalent (Blouin-Demers and Weatherhead, 2001c). Therefore, for this study we pooled field, marsh, and rock outcrop and considered the study area to be composed of 71.7% forest and 28.3% open habitats. We weighted the operative environmental temperatures accordingly to reflect the availability of each habitat.

SWIMMING PERFORMANCE

We measured swimming speed instead of crawling speed because ratsnakes coil and strike defensively rather than attempt to escape when one tries to coax them to crawl

quickly (Blouin-Demers et al., 2003). In addition, testing in water allowed more precise control of body temperature during performance (see below) than testing in air. In 2000, we measured the swimming speed of 21 ratsnakes at body temperatures of 10, 15, 20, 25, 30, and 35 °C (Blouin-Demers et al., 2003). Order of treatments was randomized and tests for each temperature were separated by at least one day so that snakes had time to rest between tests. Prior to each test, we immersed the snakes in warm water or placed them in a cooling chamber to equilibrate their body temperature to the appropriate test temperature. In all cases, a test consisted of two consecutive trials and in our analyses we used only the faster of the two trials for each test temperature. We recorded the body temperature 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 body temperature readings in our analyses.

We conducted swimming trials in a plywood trough that measured 735 cm long, 60 cm high, and 40 cm wide. The trough was lined with fiberglass and was filled with water to a depth of approximately 15 cm. We placed markers 150 cm from each end to mark the central swimming distance (435 cm). The water temperature in the trough equalled that of the testing temperature. After the body temperature 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. The snake was encouraged to swim at 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.

Based on previous work (Huey and Stevenson, 1979; Hertz et al., 1983; Stevenson et al., 1985; Huey and Kingsolver, 1989; Angilletta et al., 2006), we obtained a general equation predicting swimming speed based on body temperature by fitting a logistic-exponential curve with nonlinear curve fitting to the swimming data (see below). In this equation, S is a scaling factor, k_1, k_2, and k_3 are fitted parameters, $CT_{\min}$ and $CT_{\max}$ are the critical thermal minimum and maximum, and T_b is the body temperature. Critical thermal minimum and maximum temperatures were set at 4 °C and 38 °C, respectively, because ratsnakes lose muscle tone outside this temperature range (G. Blouin-Demers, unpublished data).

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

ANALYSES

We conducted statistical analyses and curve fitting with JMP version 6.0 (SAS Institute Inc.). Because nonlinear curve fitting can be sensitive to starting parameter values (van Berkum, 1986), we ensured that the curve had a good fit by varying the parameter values and inspecting the error sum of squares. We used Kolmogorov–Smirnov tests to compare distributions. We conducted analyses on the distributions of daytime hourly mean body temperatures and swimming speeds pooled across the 53 snakes (n = 16,921; see below), as well as on distributions of means for each individual (n = 53, weighted by sample size for each individual) to maintain statistical independence. These analyses gave almost identical results (Table 1). We present all means ± 1 SE.

Table 1
Quantiles and means for the distributions of operative environmental temperatures available in the habitat (T_e, thermoconformity), body temperatures experienced by ratsnakes in Ontario (T_b, thermoregulation), and their conversions to swimming speeds by the thermal performance equation

	T_e (°C)	Swim speed T_e (cm/s)	T_b (°C)	Swim speed T_b (cm/s)
Quantiles				
100%	63.6	63.9	37.0	63.9
75%	34.1	63.4	27.8	63.9
50%	24.4	60.2	23.6	63.3
25%	18.6	22.5	18.8	60.2
0%	0.3	0.0	9.9	22.2
Mean (95% CI)	23.8 (23.6–24.0)	48.7 (48.2–49.1)	23.3 (23.1–23.2)[1]	60.4 (60.3–60.5)[1]
			23.3 (22.8–23.7)[2]	60.4 (59.9–60.9)[2]
% max (95% CI)		76.2 (75.4–76.8)		94.5 (94.4–94.7)

[1]Based on data pooled for the 53 snakes.
[2]Based on individual means for the 53 snakes, weighted by sample size.

RESULTS

TEMPERATURES

We recorded 150,368 body temperature readings from the 53 individuals over 3 years. We reduced these observations to 34,211 hourly mean body temperatures. Because ratsnakes are diurnally active in our study area and their average active season is from late April to early October (Blouin-Demers and Weatherhead, 2001c), we analyzed 16,921 hourly mean body temperatures recorded during the day (0600 h–1800 h) from 1 May to 30 September. Body temperatures ranged from 9.9 to 37.0 °C with a mean of 23.3 °C (Table 1).

Similarly, we obtained 10,716 hourly mean diurnal operative environmental temperatures in the 2 habitat types (forest and open) over the 3 active seasons. The distribution of environmental temperatures was significantly wider than the distributions of pooled and individual mean body temperatures (Kolmogorov–Smirnov tests, $p < 0.001$). Environmental temperatures ranged from 0.3 to 63.6 °C with a mean of 23.8 °C (Table 1).

SWIMMING PERFORMANCE

Trials were conducted at mean body temperatures of 10.4 ± 0.5, 15.6 ± 0.6, 19.9 ± 0.8, 25.1 ± 0.5, 30.1 ± 0.6, and 34.5 ± 0.4 °C. The mean difference between the body temperature before and after the trial was 0.96 ± 0.06 °C. The fitted parameters in eq 1 were $S = 64.02$, $k_1 = 18.71$, $k_2 = 0.39$, and $k_3 = 0.77$ and generated a typical performance curve with an initial increase in performance with increasing body temperature, fol-

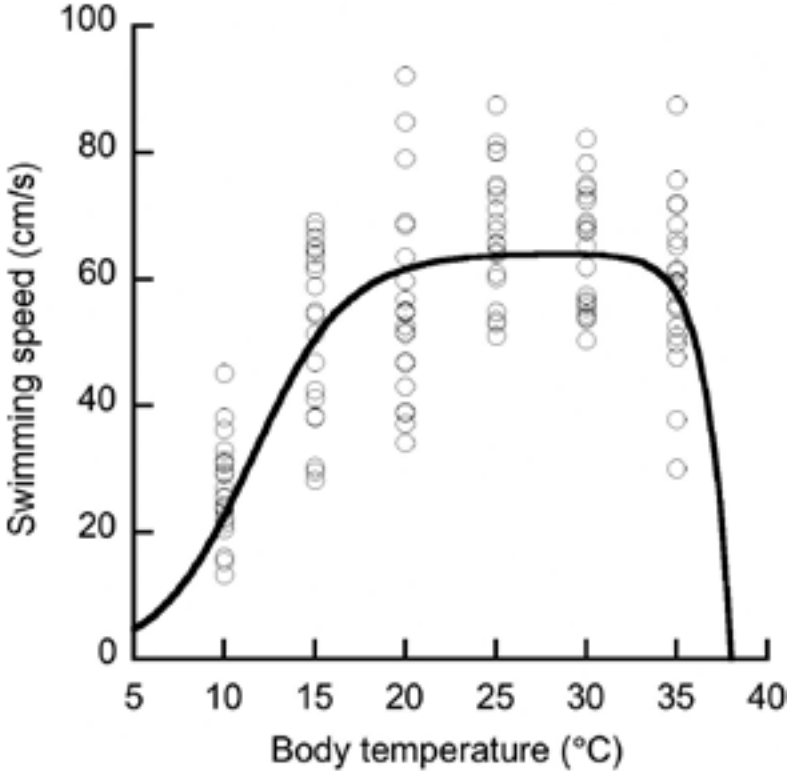

Fig. 1. Swimming speed as a function of body temperature in ratsnakes from Ontario (open symbols) with the fitted predictive logistic-exponential equation (solid line). Performance falls to 0 at the experimentally determined critical thermal maximum and minimum.

lowed by a sharp decline in performance as body temperature rose above 34 °C (Fig. 1). Consistent with ratsnakes being thermal generalists, the performance curve has a broad plateau from approximately 18 to 33 °C.

We assumed that snakes that were not using habitats selectively would realize a distribution of body temperatures equivalent to the operative environmental temperatures. Applying the thermal performance equation to those temperatures produced a bimodal distribution of swimming speeds with a substantial proportion of zeros (11.7%, Fig. 2). Most of the zeros arose because environmental temperatures were above the range of body temperatures ratsnakes can tolerate (lethal temperature is approximately 40 °C) in the open during midday. Thus, if ratsnakes were pure thermoconformers, they would frequently die from overheating. The distribution of actual body temperatures was narrower than the distribution of environmental temperatures (Fig. 2) and resulted in a highly skewed distribution of swimming speeds that was significantly different from

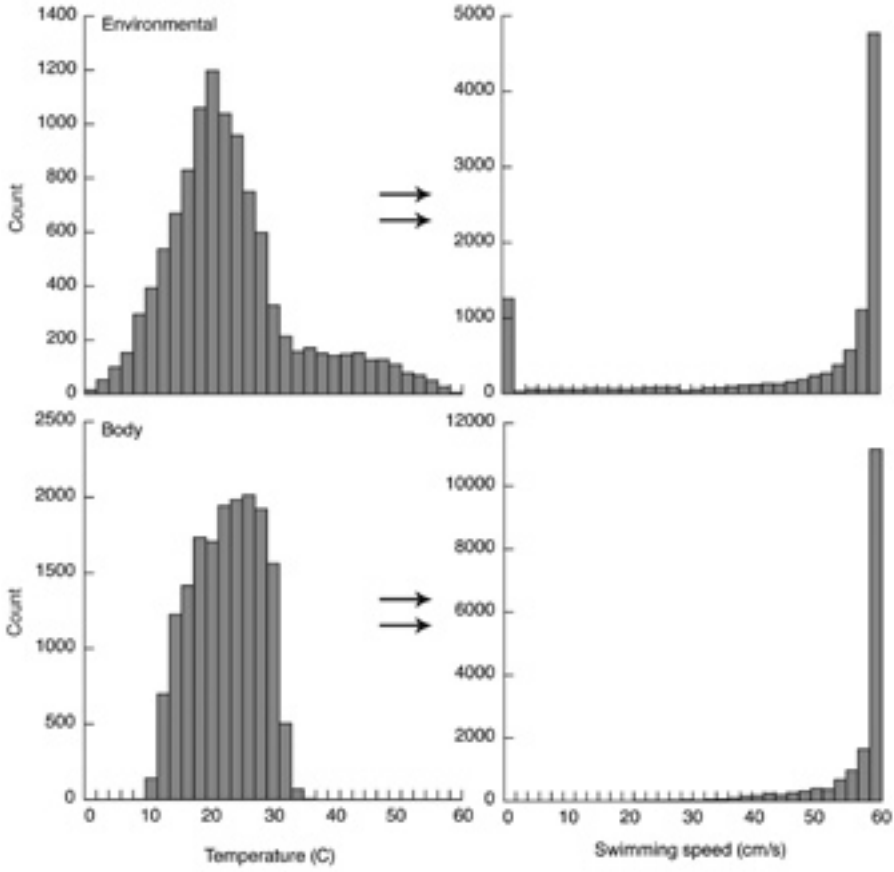

Fig. 2. Distributions of environmental operative temperatures (i.e., those that would be realized by a ratsnake that used habitats randomly) and of body temperatures experienced by free-ranging ratsnakes in Ontario, with their corresponding swimming speeds. Swimming speeds were derived by applying the thermal performance equation to the temperature distributions.

the distribution generated from the environmental temperatures based on pooled data or individual means (Fig. 2, Kolmogorov–Smirnov tests, $p < 0.001$); very few ratsnakes experienced body temperatures that resulted in slow swimming speeds, and none that produced zeros. In fact, 75% of the diurnal body temperatures recorded from ratsnakes during their active season resulted in performance >94% of the maximum speed recorded (Table 1). The mean speed that ratsnakes would achieve if they were thermoconformers is 76.2% (95% CI = 75.4–76.8%) of the maximum speed recorded, whereas the mean speed they achieve by thermoregulating through habitat selection is 94.5% (95% CI = 94.4–94.7%) of the maximum (Table 1), or an average improvement in performance of 18.3% (95% CI = 17.6–19.3%).

DISCUSSION

As previously reported (Blouin-Demers and Weatherhead, 2001c), we showed that ratsnakes do not use their habitat randomly with respect to available environmental temperatures. Through habitat selection, ratsnakes realized body temperatures that resulted in an 18% improvement in performance relative to what they would have achieved were they to use their habitat randomly (i.e., thermoconformers). In addition, habitat selection allowed ratsnakes to avoid reaching lethal body temperatures. Thus, through the temperature-dependence of performance, habitat selection is clearly beneficial to ratsnakes.

Mechanistically, this 18% improvement in performance resulted from the broad plateau of the thermal reaction norm for swimming speed in ratsnakes; a thermal specialist with a more defined optimal body temperature would incur greater performance benefits from thermoregulation. Hertz et al. (1993) documented the effect of body temperature regulation on sprinting speed for three species of *Anolis* lizards. Unsurprisingly, the thermal generalist increased performance by less than 2% through thermoregulation, but even the two thermal specialists increased performance by less than 9% by careful thermoregulation. Thus, relative to these species, the 18% improvement by ratsnakes appears substantial. We are unaware of any additional similar data that would allow a broader comparison. If the available data are typical of other reptiles, however, it would appear that the improved performance that results from thermoregulation is quite modest. If so, it is possible that habitat selection may be more important in allowing animals to avoid lethal body temperatures (a set-point system) than in improving performance.

The fitness benefit of avoiding lethal temperatures is obvious. Less clear, however, are the fitness consequences of enhancing locomotor performance by 18%. As indicated above, intuitively this seems to be a rather modest improvement. Depending on the nature of the relationship (e.g., linear vs. nonlinear) between locomotor performance and survival or mating success, however, an 18% improvement in locomotor performance could represent anything from a trivial to a profound improvement in fitness. At the moment we lack the data to say anything more than that the effect will be positive.

Converting thermal benefits from habitat selection to a currency more closely related to fitness (e.g., survival, reproductive success) becomes even more difficult if we consider more than just locomotor performance. We used locomotion as a proxy for fitness because it is logistically easier to obtain thermal reaction norms for proximate measures of fitness such as locomotion or growth rates than for ultimate measures of fitness such as clutch size or number of descendants. However, habitat selection is likely to enhance fitness in several ways. Consider female ratsnakes. By maintaining body temperatures closer to optimal, females should be able to digest food and assimilate nutrients more efficiently, allowing them to grow faster. Improved condition could result directly in larger clutches, and faster growth could allow earlier reproduction and faster increases in clutch size associated with larger body size (Blouin-Demers and Weatherhead, 2007). The improvement in performance, and ultimately in fitness, resulting from habitat selection, could be quite different from what we found for locomotion. In addition, females also select nesting microhabitats based on thermal properties, which affect both incuba-

tion time and offspring phenotypes (Blouin-Demers et al., 2004). How this affects subsequent survival and reproduction of those offspring, however, remains unknown.

Radio-telemetry has allowed routine documentation of habitat use by animals. Similarly, temperature-sensitive transmitters and data loggers are allowing collection of detailed data on thermal profiles associated with habitat selection in medium and large reptiles. Although Huey (1991) and Hertz et al. (1993) pioneered the approach 15 years ago, few researchers have attempted to quantify the benefits (in terms of fitness components) that reptiles realize from using habitat selectively, except in the specific case of nest-site selection. Like Huey (1991), we firmly believe that the study of habitat selection in reptiles can benefit greatly from integrating habitat and thermal data with thermal reaction norms because this integration allows inferences to be made about the fitness consequences of habitat selection.

We have shown that habitat selection is likely to enhance fitness in ratsnakes, both by improving locomotor performance as well as by allowing snakes to avoid lethal temperatures. However, generating a quantitative estimate of how much fitness is improved by habitat selection requires data relating body temperature to direct measures of fitness. One approach to obtaining these data would be to determine how foraging success and growth of captive snakes are affected when thermoregulatory opportunities are varied experimentally. Although not experimental, a potentially more powerful approach would be to determine how growth, reproduction, and survival of free-living snakes vary in response to natural variation in environmental temperatures. Only in free-living snakes can one measure the integrative effect of temperature on all the factors (foraging opportunities, foraging success, predator avoidance, etc.) that affect growth, reproduction, and survival.

Improved understanding of the link between habitat selection, thermoregulation, and fitness will be valuable to our basic understanding of both habitat selection and thermal ecology of snakes. Such information will also have conservation value. Habitat loss and modification are central concerns in conservation and both will affect snakes by changing their thermoregulatory opportunities. Climate change is also a major conservation concern and is likely to affect the costs and benefits of behavioral thermoregulation. By knowing more about how snakes use habitat selection for thermoregulation and how thermoregulation affects fitness, we will improve our ability to predict and to manage the consequences for snakes of changes in both habitat and climate.

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REFERENCES

Angilletta, M.J., Wilson, R.S., Navas, C.A., James, R.S. 2003. Tradeoffs and the evolution of thermal reaction norms. Trends Ecol. Evol. 18: 234–240.

Angilletta, M.J., Steury, T.D., Sears, M.W. 2004. Temperature, growth, and body size in ectotherms: fitting pieces of a life-history puzzle. Int. Comp. Biol. 44: 498–509.

Angilletta, M.J., Bennett, A.F., Guderley, H., Navas, C.A., Seebacher, F., Wilson, R.S. 2006. Coadaptation: a unifying principle in evolutionary thermal physiology. Physiol. Biochem. Zool. 79: 282–294.

Bakken, G.S., Santee, W.R., Erskine, D.J. 1985. Operative and standard operative temperature: tools for thermal energetics studies. Am. Zool. 25: 933–943.

Blouin-Demers, G., Prior, K.A., Weatherhead, P.J. 2000a. Patterns of variation in spring emergence by black rat snakes (*Elaphe obsoleta obsoleta*). Herpetologica 56: 175–188.

Blouin-Demers, G., Weatherhead, P.J., Shilton, C.M., Parent, C.E., Brown, G.P. 2000b. Use of inhalant anesthetics in three snake species. Contemp. Herpetol. 2000: 4.

Blouin-Demers, G., Weatherhead, P.J. 2001a. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. Ecology 82: 2882–2896.

Blouin-Demers, G., Weatherhead, P.J. 2001b. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes *Elaphe obsoleta obsoleta*. J. Anim. Ecol. 70: 1006–1013.

Au: Should this be ratsnakes? (like in text).

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

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

Blouin-Demers, G., Weatherhead, P.J., McCracken, H.A. 2003. A test of the thermal coadaptation hypothesis with black rat snakes (*Elaphe obsoleta*) and northern water snakes (*Nerodia sipedon*). J. Therm. Biol. 28: 331–340.

Blouin-Demers, G., Weatherhead, P.J., Row, J.R. 2004. Phenotypic consequences of nest site selection in black rat snakes (*Elaphe obsoleta*). Can. J. Zool. 82: 449–456.

Blouin-Demers, G., Weatherhead, P.J. 2007. Allocation of offspring size and sex by female black ratsnakes. Oikos 116: 1759–1767.

Carfagno, G.L.F., Weatherhead, P.J. 2006. Intraspecific and interspecific variation in use of forest-edge habitat by snakes. Can. J. Zool. 84: 1440–1452.

Christian, K.A., Weavers, B.W. 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. Ecol. Monog. 66: 139–157.

Cowles, R.B., Bogert, C.M. 1944. A preliminary study of the thermal requirements of desert reptiles. Bul. Am. Mus. Nat. Hist. 83: 265–296.

Diaz, J.A. 1997. Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. Func. Ecol. 11: 79–89.

Dubois, Y., Blouin-Demers, G., Thomas, D.W. 2008. Temperature selection in wood turtles (*Glyptemys insculpta*) and its implications for energetics. Écoscience, in press.

Au: Update?

Durner, G.M., Gates, J.E. 1993. Spatial ecology of black rat snakes on Remington Farms, Maryland. J. Wild. Manag. 57: 812–826.

Hertz, P.E., Huey, R.B., Nevo, E. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. Evolution 37: 1075–1084.

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

Huey, R.B., Stevenson, R.D. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am. Zool. 19: 357–366.

Huey, R.B., Kingsolver, J.G. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends Ecol. Evol. 4: 131–135.

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

Huey, R.B. 1991. Physiological consequences of habitat selection. Am. Nat. 137: S91–S115.

Irschick, D.J., Garland, T. 2001. Integrating function and ecology in studies of adaptation: Investigations of locomotor capacity as a model system. Annu. Rev. Ecol. Syst. 32: 367–396.

Peterson, C.R., Gibson, A.R., Dorcas, M.E. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. In: Seigel, R.A., Collins, J.T., eds. Snakes: ecology and behaviour. McGraw-Hill, New York, pp. 241–314.

Qualls, C.P., Andrews, R.M. 1999. Cold climates and the evolution of viviparity in reptiles: cold incubation temperatures produce poor-quality offspring in the lizard, *Sceloporus virgatus*. Biol. J. Linn. Soc. 67: 353–376.

Reinert, H.K. 1993. Habitat selection in snakes. In: Seigel, R.A., Collins, J.T., eds. Snakes: ecology and behaviour. McGraw-Hill, New York, pp. 201–240.

Row, J.R., Blouin-Demers, G. 2006. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. Écoscience 13: 443–450.

Seebacher, F., Franklin, C. 2005. Physiological mechanisms of thermoregulation in reptiles: a review. J. Comp. Physiol. B: 175: 533–541.

Shine, R. 1999. Why is sex determined by nest temperature in many reptiles? Trends Ecol. Evol. 14: 186–189.

Shine, R., Kearney, M. 2001. Field studies of reptile thermoregulation: how well do physical models predict operative temperatures? Func. Ecol. 15: 282–288.

Stevenson, R.D., Peterson, C.R., Tsuji, J.S. 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. Phys. Zool. 58: 46–57.

van Berkum, F.H. 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. Evolution 40: 594–604.

Weatherhead, P.J., Charland, M.B. 1985. Habitat selection in an Ontario population of the snake, *Elaphe obsoleta*. J. Herpetol. 19: 12–19.

Weatherhead, P.J., Blouin-Demers, G. 2004. Long-term effects of radiotelemetry on black rat snakes. Wild. Soc. Bull. 32: 900–906.