Body temperature influences growth rates of Common Gartersnakes (*Thamnophis sirtalis*)

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Abstract

Habitat selection can have large impacts on animal fitness. Temperature is an important aspect of habitat suitability for ectotherms, and temperature differences between habitats can thus lead to fitness differences. Here, we use an experiment with female Common Gartersnakes (*Thamnophis sirtalis*) to examine the effect of body temperature on change in mass (i.e., growth rate), which is a component of fitness. We placed female gartersnakes in experimental enclosures in old field and in forest and monitored their body temperature and mass throughout the summer. Gartersnakes in old field were warmer than gartersnakes in forest, warmer gartersnakes were more likely to eat earthworms, and warmer gartersnakes gained more mass. We therefore provide evidence that habitat use influences body temperature, and body temperature then influences growth, a component of fitness.

Key words: Common Gartersnake; *Thamnophis sirtalis*; body temperature; fitness; growth rate; habitat; thermoregulation

Introduction

Habitat selection is a major theme in ecology (Morris 2003). An individual's choice of where to live can have profound effects that ripple throughout its life, from immediate effects on safety (Dupuch *et al.* 2009), food availability (Morris and MacEachern 2010), and physiology (Halliday and Blouin-Demers 2014), to fecundity and population level consequences (Lin and Batzli 2001). Habitats can be simply defined as "… subsets of physical and biotic conditions among which population density … of a focal species varies from adjacent subsets" (Morris 2003: 2). Habitats therefore are often defined by their impact on fitness, which highlights the importance of understanding how different abiotic and biotic conditions impact fitness.

For ectotherms, temperature is one of the most important variables in habitat selection (Huey 1991) because they, by definition, rely on environmental temperature (T_e) to maintain their body temperature (T_b), and in turn T_b greatly impacts fitness (Gilchrist 1995). Fitness typically is maximized at some optimal temperature (T_o), and decreases as temperature deviates from T_o (Bulté and Blouin-Demers 2006; Dell *et al.* 2011). Ectotherms that maximize fitness should therefore select habitats that allow them to maintain T_b as close to T_o as possible (Blouin-Demers and Weatherhead 2008).

In our previous work with Common Gartersnakes (*Thamnophis sirtalis*), we demonstrated that they selected warm fields over cool forest, and that selection of old field habitat led to higher growth rate and reproductive success (Halliday and Blouin-Demers 2016a). Despite this correlation, we did not demonstrate explicitly that warmer snakes exhibited higher growth rates. Here, we re-examine these data to explore the relationship between weekly T_b and changes in mass for individual snakes in experimental enclosures in field and forest. We directly test the prediction that warmer snakes have higher growth in mass than cooler snakes, independent of their habitat.

Methods

In June 2014, we built six experimental enclosures in an old field and six enclosures in an adjacent forest (individual dimensions [l × w × h] = 2.67 × 2.67 × 1.3 m) in Pontiac county, Quebec (45.4926°N, 75.9222°W). We built the frames of the enclosures with lumber and stapled polyethylene sheeting to the wood frame to create walls. We buried the walls in the ground at least 10 cm to prevent snakes from escaping. We placed fine mesh over the enclosures to exclude birds, and electric fences around the enclosures to exclude mammalian predators. We placed a plywood board (60 × 60 cm) in each enclosure to act as a refuge. The old field was a mix of grasses and flowering plants, including goldenrod (*Solidago* sp.), milkweed (*Asclepias* sp.), and Tufted Vetch (*Vicia cracca* L.). The forest consisted mostly of Trembling Aspen (*Populus tremuloides* Michaux) with minimal understorey growth.

We captured adult female gartersnakes between late April and early June 2014 near a wetland within 10 km

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of our experimental enclosures and placed 10 individuals in the old field enclosures and 10 in the forest enclosures, with two individuals per enclosure in four of the enclosures in each habitat and one individual per enclosure in two of the enclosures in each habitat. We used gravid females because the main goal of this experiment was to examine the fitness consequences of habitat selection, therefore we measured reproductive output (Halliday and Blouin-Demers 2016a). We randomly assigned females to habitats and enclosures, while ensuring that the body size distribution was similar between habitats. We also randomly assigned half of the females in each habitat to a "low food" treatment, and the other half to a "high food" treatment. In the low food treatment, we offered each female one large earthworm twice per week and in the high food treatment we offered each female one large earthworm four times per week. We offered earthworms to snakes by isolating the snake within its enclosures and dropping an earthworm in front of its head. This typically elicited a feeding response, whereby the snake immediately struck the earthworm or began flicking its tongue at the worm. We recorded whether the snake ate the earthworm. Snakes also had access to food naturally available in the enclosures, so our food treatments represent food supplementation.

Prior to feeding, we measured the skin temperature of each snake with an infrared thermometer (Fluke 566 infrared thermometer, Fluke Corporation, Everett, Washington, USA); skin temperature is highly correlated with internal body temperature in gartersnakes (Spearman's $\rho \geq 0.87$; Halliday and Blouin-Demers 2017a). We held the thermometer 10 cm from the snakes and aimed at the centre of their bodies. We recorded whether the snake was out and basking or whether it was under the cover board. We measured T_b four times per week at 0900. Once per week, we measured the mass of each snake with a spring scale (Pesola AG, Schindellegi, Switzerland). We continued this experiment until the beginning of September (105 days), which was the point when all gravid females had given birth. We include measurements for each female only until the week before it gave birth. By the end of this experiment, the final sample size was six gartersnakes in each habitat; however, we collected sufficient data from all 10 snakes in each habitat to include data from all 20 snakes in the analyses. The loss of snakes was due to escapes and predation.

Analyses

We first conducted a *t*-test to verify that females in each habitat had similar starting masses. We then conducted an analysis to describe the difference in T_b between habitats. We used a linear mixed effects model in R (package lme4; function lmer; Bates *et al.* 2015) with daily T_b of each individual snake as the dependent variable, combinations of food treatment, habitat, the snake's location (i.e., under cover, out of cover), and all two-way interactions as fixed effects, and with snake ID as a random effect. We compared models with Akaike's information criterion (package stats; function AIC; R Core Team 2016) and selected the model with the lowest AIC as the best model. If models were within 2 AIC units of the best model, we considered them to be competing and used the most parsimonious of the competing models as the final model.

For our second analysis, we examined whether a snake ate during a given feeding event using general linear mixed effects models with a binomial distribution (package lme4; function glmer; family: binomial). We used the occurrence/non-occurrence of a feeding event (where 1 = the snake ate the worm and 0 = the snake refused the worm) as the dependent variable and temperature, location, food treatment, habitat, and two-way interactions as fixed effects, and snake ID as a random effect.

For our final analysis, we examined the change in mass for a snake from one week to the next with linear mixed effects models, with change in mass as the dependent variable and combinations of the following independent variables as fixed effects, including two-way interactions: habitat, food treatment, mean temperature over the previous week, and days since the last food item was eaten. We included snake ID as a random effect.

Results

At the beginning of the experiment, females in field and forest habitat ($n = 10$ in each habitat) did not differ significantly in mass (mean ± SE in field: 72.0 ± 9.9 g, in forest: 72.8 ± 11.8 g; $t = 0.05$, $P = 0.96$).

On average, the T_b of gartersnakes was lower in forest than in field (mean difference = 4.6 ± 0.4°C, $t_{720} = 12.33$, $P < 0.01$; Figure 1; Appendix S1). Individuals under cover were cooler than individuals out of cover, especially for snakes in the forest ($t_{720} = 5.45$, $P < 0.01$) or in the low food treatment ($t_{720} = 2.04$, $P = 0.04$).

Gartersnakes were more likely to eat if their T_b was higher (effect size = 0.10 ± 0.03, $t_{564} = 3.76$, $P < 0.01$; Appendix S2), if they were in the low food treatment (effect size = 1.68 ± 0.47, $t_{564} = 3.58$, $P < 0.01$), and if they were in the field (effect size = 1.05 ± 0.47, $t_{564} = 2.23$, $P < 0.01$). All interaction terms in this model were non-significant (Appendix S2).

Regardless of habitat or food treatment, gartersnakes were more likely to gain mass from one week to the next if their mean T_b was higher in the previous week (slope = 0.26 ± 0.11, $t_{174} = 2.24$, $P = 0.03$; Figure 2; Appendix S3). All interaction terms in this model were non-significant (Appendix S3).

Discussion

Habitat selection by ectotherms influences T_b, which in turn influences fitness because of the direct link between T_b and fitness (Blouin-Demers and Weatherhead 2008). In this study, we demonstrate that gartersnakes in our field enclosures had a higher T_b than gartersnakes

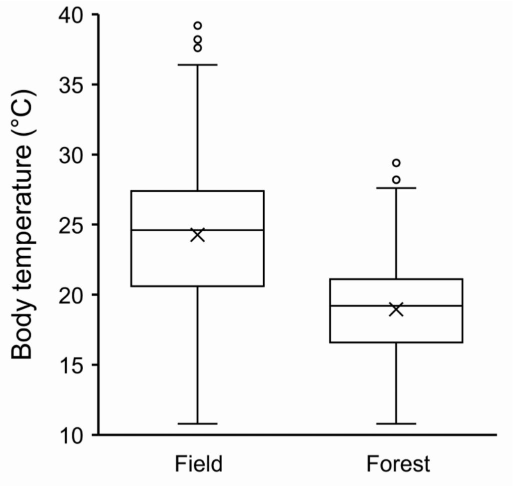

FIGURE 1. Body temperature of female Common Gartersnakes (*Thamnophis sirtalis*) living in enclosures in old field and forest habitat in Pontiac county, Quebec between June and September 2014. Boxes represent the interquartile range, lines within the box are the median, '×' in the box is the mean, whiskers are the 5th and 95th percentiles, and points above the whiskers are outliers. $n = 726$ temperature measurements on 20 individual gartersnakes.

in forest enclosures, and that gartersnakes with higher T_b are more likely to eat and have a greater mass increase regardless of habitat or food treatment. We previously demonstrated that T_e was higher in field than in forest (Halliday and Blouin-Demers 2016a) and here we demonstrate that this increased T_e translated to increased T_b. We also previously demonstrated that gartersnakes are more willing to eat at temperatures closer to their preferred T_b in the laboratory (Halliday and Blouin-Demers 2016b) and here we extend this finding to the wild; we found that gartersnakes are more likely to eat when they are warmer and that warmer gartersnakes grow more or produce larger offspring. We therefore provide direct evidence that habitat use dictates T_b, which then influences growth rate, a component of fitness.

Other studies of ectotherm habitat selection have indicated a strong preference for the habitat that most closely matched optimal temperature (Huey 1991; Calsbeek and Sinervo 2002; Halliday and Blouin-Demers 2014; Paterson and Blouin-Demers 2018). Similarly, several studies have demonstrated the link between temperature and growth rate in ectotherms (Bronikowski 2000; Patterson *et al.* 2017). Our study extends the findings of these previous studies by demonstrating that short-term changes in body temperature (over one week) can lead to changes in growth, and therefore influence fitness.

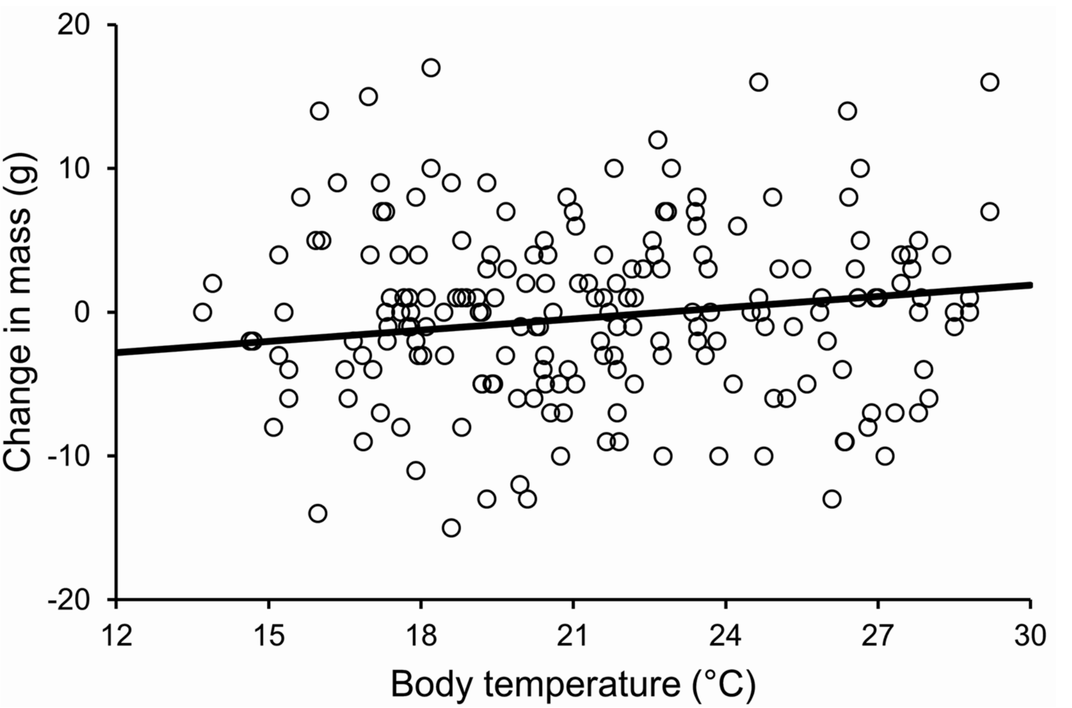

FIGURE 2. The relationship between mean body temperature in the previous week and change in mass for female Common Gartersnakes (*Thamnophis sirtalis*) living in enclosures in old field and forest habitat in Pontiac county, Quebec between June and September 2014. The line represents the relationship between body temperature and change in mass, according to a linear mixed effects model. $n = 195$ change in mass measurements on 20 individual gartersnakes.

Although willingness to eat and growth were both related to T_b, the number of worms eaten did not affect growth, and neither did the food treatment we imposed. This is likely due to an abundance of naturally available worms within our enclosures, which we could not control or account for. In another experiment with similar enclosures, we monitored worm abundance and caught worms throughout the course of our study (Halliday and Blouin-Demers 2017b). In that experiment, worm abundance was on average lower in enclosures with more snakes, which suggests that snakes were eating the worms that entered the enclosures. The worms that we fed to the snakes were an additional meal, but likely did not provide enough additional energy to affect growth detectably. The feeding treatments therefore provide evidence of the link between T_b and foraging but cannot directly link foraging and growth, even though it is logical that individuals that eat more worms should grow more. To test the link between T_b, foraging, and growth effectively one would need to completely control the food intake of study organisms, which is challenging under field conditions. While our field enclosures did not allow us to control food intake and were not entirely escape or predator proof, enclosures do offer natural habitat conditions, including natural variation in temperature and insolation, that increase the ecological realism compared to laboratory studies. Given that the main goal of our experiment was to examine the effect of habitat and temperature on fitness, we feel that field enclosures were more appropriate than more controlled laboratory conditions. Captivity stress is also likely to be lower in field enclosures than in the laboratory.

We used gravid females in our experiment complicating the interpretation of our results. Unlike juveniles, adult males, and non-gravid females, energy intake by gravid females is not only self-directed but also to the developing offspring. We use the term growth rate, but changes in mass are likely happening in both the offspring and in the females. In our previous analysis of this experiment (Halliday and Blouin-Demers 2016a), we demonstrated that females also grew in length, which implies that at least some of the change in mass is directly related to growth of the females and not just to growth of the offspring. Another potential issue associated with using gravid females in this experiment is that they often fast during pregnancy (e.g., Lourdais *et al.* 2002), which has obvious implications for a growth rate study. But this was not the case in our study: all females ate, especially if their body temperature was high.

The effect of T_b on growth was relatively weak (slope = 0.26 g/°C), probably because we measured T_b only four times each week. There was likely greater variation in snake T_b that we did not capture. We measured T_b at the same time every day, so we did not capture daily variation in T_b. A larger sample size with more continuous T_b measurements would likely lead to a stronger relationship between T_b and growth.

In summary, our study demonstrates the link between habitat use and growth, a component of fitness, via the temperature-dependence of foraging and growth. Studies on ectotherms, and to a lesser extent on endotherms, must consider temperature as an important habitat feature that can influence behaviour, physiology, and ultimately fitness.

Author Contributions

Writing – Original Draft: W.H.; Writing – Review & Editing: W.H. and G.B.-D.; Conceptualization: W.H. and G.B.-D.; Investigation: W.H.; Methodology: W.H.; Formal Analysis: W.H.; Funding Acquisition: W.H. and G.B.-D.

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Supplementary Material:

Appendix S1: Model selection and final model output for an analysis of the effect of Common Gartersnake (*Thamnophis sirtalis*) body temperature on growth.

Appendix S2: Model selection and model final output for an analysis of feeding behaviour of Common Gartersnakes (*Thamnophis sirtalis*).

Appendix S3: Model selection and final model output for an analysis examining the growth of Common Gartersnakes (*Thamnophis sirtalis*).