



Consequences of complex environments: Temperature and energy intake interact to influence growth and metabolic rate



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ABSTRACT

The field of comparative physiology has a rich history of elegantly examining the effects of individual environmental factors on performance traits linked to fitness (e.g., thermal performance curves for locomotion). However, animals live in complex environments wherein multiple environmental factors co-vary. Thus, we investigated the independent and interactive effects of temperature and energy intake on the growth and metabolic rate of juvenile corn snakes (*Pantherophis guttatus*) in the context of shifts in complex environments. Unlike previous studies that imposed constant or fluctuating temperature regimes, we manipulated the availability of preferred thermal microclimates (control vs. relatively warm regimes) for eight weeks and allowed snakes to behaviorally thermoregulate among microclimates. By also controlling for energy intake, we demonstrate an interactive effect of temperature and energy on growth—relevant temperature shifts had no effect on snakes' growth when energy intake was low and a positive effect on growth when energy intake was high. Thus, acclimation to relatively warm thermal options can result in increased rates of growth when food is abundant in a taxon in which body size confers fitness advantages. Temperature and energy also interactively influenced metabolic rate—snakes in the warmer temperature regime exhibited reduced metabolic rate (O_2 consumption rate at 25 °C and 30 °C) if they had relatively high energy intake. Although we advocate for continued investigation into the effects of complex environments on other traits, our results indicate that warming may actually benefit important life history traits in some taxa and that metabolic shifts may underlie thermal acclimation.

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1. Introduction

Organisms face increasingly dynamic and, arguably, stressful environments due to anthropogenic activities that include fossil fuel combustion, habitat modification, pollution, and the introduction of invasive species (reviewed in IPCC, 2014). The thermal effects of global climate change (GCC; e.g., 2–8 °C increase in mean global air temperature over the next 50–100 years) are expected to continue to alter ecological systems across multiple levels of biological organization (reviewed in Sears and Angilletta, 2011; IPCC, 2014). Temperature influences a myriad of biological processes—from an organism's enzymatic efficiency and metabolic rate (e.g., the rate at which O_2 is consumed [$\dot{V}O_2$]) to its behavior and reproduction—which has led to a large body of theory and empiricism on thermal biology (reviewed in Angilletta, 2009). To understand organisms' temperature sensitivity, most laboratory-based research has examined the effects of different constant temperatures on fitness-related performance traits (reviewed in Angilletta, 2009). Yet, performance in a constant environment is not always equivalent to performance in a fluctuating environment with the same mean temperature

(reviewed in Angilletta, 2009; Niehaus et al., 2012; but see Michel and Bonnet, 2010). Further, thermal environments in which animals can behaviorally thermoregulate by moving among microclimates are even more realistic and ecologically relevant than fluctuating temperature regimes (Glanville and Seebacher, 2006; Sears et al., 2011).

An unprecedented shift in global temperatures (and, thus, microclimates) is not the only potential stressor encountered by animals. They must also deal with rapidly changing complex environments wherein temperature and other environmental factors vary simultaneously (reviewed in Todgham and Stillman, 2013). For example, animals require energy to fuel their activities, and food availability is influenced by climatic variation (Both and Visser, 2005; Altermatt, 2010; Pearce-Higgins et al., 2010; Gardner et al., 2011; Allan et al., 2013; Cahill et al., 2013). Although animal traits are influenced by the independent effects of food (energy) availability and shifts in temperature (e.g., Guderley, 2004: effects on locomotor performance and muscle metabolism; LeMoine et al., 2008: effects on mitochondrial enzyme activity and transcript levels of metabolic enzymes), few studies have examined the interactive effect of food and energy (but see; Adamo et al., 2012: effects on reproduction and survival).

Juveniles may be particularly sensitive to shifts in complex environments for a host of reasons, many of which are related to body size (Peters, 1986) and variation in energy budgets due to ontogeny (sensu the ontogenetic growth model: Hou et al., 2008; Moses et al., 2008;

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West et al., 2001). Animals at this stage are typically smaller and, as a result, have a relatively high surface area to volume ratio. Therefore, the body temperature (T_{body}) of smaller ectotherms more quickly conforms to environmental temperature, and smaller animals have relatively high mass-specific rates of energy expenditure (Peters, 1986). In addition, energy intake may be constrained by the body size of juveniles (e.g., smaller snakes are gape limited and, thus, have fewer prey options than adults; King, 2002). Juveniles also have fewer energy stores, which may be required for periods of reduced food availability. In addition to energetic constraints, smaller juveniles exhibit a higher risk of predation relative to adults because they can be eaten by a larger array of predators and exhibit a reduced capacity to escape predators (e.g., slower sprint speed; Cejudo and Marquez, 2001; Peters, 1986).

Given these size-related risk factors, growth rate strongly influences fitness across animal taxa (reviewed in Dmitriew, 2011). Faster growing individuals reach reproductive maturity earlier, and they are at less risk of predation. The growth rates and/or body sizes of many taxa increase with rearing temperature in controlled, high-food conditions of the laboratory environment (e.g., reviewed in Angilletta, 2009; Montagnes et al., 2003; Seebacher and Grigaltchik, 2014). Yet, food availability varies in nature where warmer temperatures typically reduce body size in a wide array of animal taxa (e.g., Gardner et al., 2011; Caruso et al., 2014). Therefore, examining energy expenditure ($\dot{V}O_2$) in juveniles may elucidate the interplay among growth, food (energy) availability or intake, and temperature in the context of shifts in complex environments.

In addition to food availability, the net energy available to animals for growth may be influenced by digestive efficiency (the proportion of ingested nutrients that are absorbed). Although digestive efficiency can be temperature-dependent, some taxonomic groups exhibit high digestive efficiencies that are relatively insensitive to temperature (snakes: reviewed in Alexander et al., 2012). In these taxa, growth is putatively driven by food intake, resource allocation, and energy expenditure (rather than by digestive efficiency). Thus, we manipulated the availability of preferred thermal microclimates and food for 8 weeks in the juvenile corn snake (*Pantherophis guttatus*, Linnaeus) to address two alternative hypotheses based on the effects of rearing temperature and energy intake on growth (change in body length) and metabolic rate at two test temperatures (25 °C and 30 °C).

(1) Our first hypothesis proposes a lack of thermal acclimation whereby metabolic expenditure will be obligatorily tied to temperature—meaning snakes reared at warmer temperatures will expend more energy and, as a result, have less energy to allocate to growth (Fig. 1a, b). This hypothesis predicts the following: (a) The slope of the positive relationship between energy intake and growth will be steeper in snakes maintained under control conditions (those in which snakes can reach their preferred body temperature, T_{pref}) relative to those maintained under warmer conditions (those in which snakes only have thermal options higher than their T_{pref}) (Fig. 1a). (b) Energy intake will be positively related to $\dot{V}O_2$ —well-fed snakes will be heavier and, thus, consume more O_2 . However, this energy– $\dot{V}O_2$ relationship will not be influenced by temperature regime during rearing. That is, when snakes' metabolic rates are measured at a constant test temperature, they will be affected by energy intake but not by (rearing) temperature regime (Fig. 1b).

(2) Our second hypothesis proposes that snakes maintained in warm conditions will acclimate to warmer temperatures by exhibiting more efficient (lower) metabolic expenditure, and that these metabolic savings will help maintain growth (Fig. 1c, d). This hypothesis makes the following predictions: (c) The slope of the positive relationship between energy intake and growth will be similar in snakes reared under warm and control temperature conditions (Fig. 1c). (b) The positive relationship between energy intake and $\dot{V}O_2$ will be influenced by (rearing) temperature regime wherein

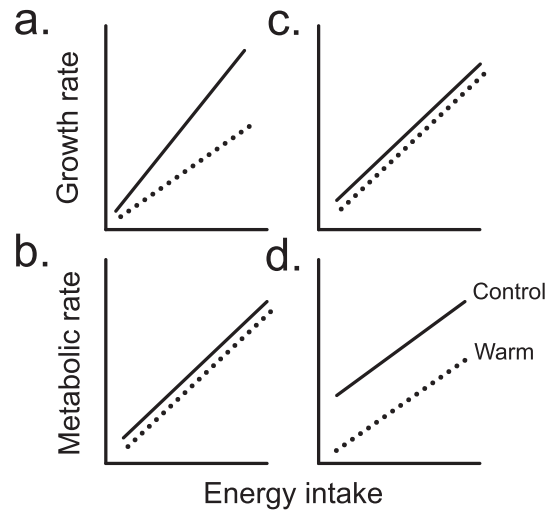


Fig. 1. Predicted effects of temperature regime (solid line: control; dotted line: warm) and energy intake on metabolic rate measured at a constant temperature (e.g., 30 °C) and growth rate based on our first (a, b) and second hypotheses (c, d). See text for details.

the offset or intercept will be lower in snakes reared in warm conditions relative to those in control conditions due to metabolic acclimation (hypometabolism) by warm snakes (sensu Seebacher and Grigaltchik, 2014; Fig. 1d).

2. Materials and methods

2.1. Study species and husbandry

Pantherophis guttatus is a medium-sized, non-venomous snake native to the southeastern United States (Gibbons and Dorcas, 2005). To address our hypotheses, we used a captive colony of *P. guttatus* ($n = 66$) that were the progeny (1st–4th generation, with no known inbreeding) of wild caught snakes in Beaufort County, South Carolina, USA. All snakes were 5–6 months old at the onset of the study, and we individually housed them in translucent plastic enclosures (270 mm × 410 mm × 150 mm) with *ad libitum* access to water in a room with a 12:12 light:dark cycle that was maintained at 20–22 °C. Prior to the study, we offered each snake a prey item (sub-adult mouse that was 15–20% of weight of the snake to which it was offered) two times per week, which represents a high-food diet for colubrid snakes (Byars et al., 2010). We thawed commercially available mice that were pre-killed and previously frozen prior to offering. To facilitate behavioral thermoregulation, we placed subsurface heating at one end of each snake's enclosure to create a thermal gradient that ranged from approximately 24.5 °C at the cool end up to approximately 33 °C at the warm end ('control' temperature regime). Because refuge availability can influence thermoregulatory decisions in snakes (Tsai and Tu, 2005), we kept folded newspaper in place on the cooler end of each enclosure to create a cool refuge similar in concept to natural conditions (e.g., a subterranean burrow). All procedures were approved by the Institutional Animal Care and Use Committee at Georgia Southern University (protocol #I14004).

2.2. Experimental design

Over the course of our 8-wk study, we manipulated temperature and food availability. We individually housed approximately half of the snakes ($n = 32$) at the control temperature regime described above (Fig. 2). This temperature range reflects thermal options in the natural range of *P. guttatus* during the active season (spring–fall) (Howze and Smith, 2012), and it also accommodates the preferred temperature for

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