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A stringent test of the thermal coadaptation hypothesis in flour beetles

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ABSTRACT

Whole-organism performance depends on body temperature and ectotherms have variable body temperatures. The thermal coadaptation hypothesis posits that thermal reaction norms have coevolved with thermal preference such that organisms attain optimal performance under a narrow range of body temperatures commonly experienced in the wild. Since thermal reaction norms are often similar, researchers interested in the effects of temperature on fitness often use one easily measured thermal reaction norm, such as locomotor performance, and assume it is a good proxy for fitness when testing the thermal coadaptation hypothesis. The extent to which this assumption holds, however, is often untested. In this study, we provide a stringent test of the thermal coadaptation hypothesis in red and in confused flour beetles by comparing the thermal reaction norm for reproductive output to the preferred body temperature range. We also test the assumption that locomotor performance can serve as a proxy for the thermal reaction norm for reproductive output, a more ultimate index of fitness. In both species, we measured the number of eggs laid, righting time, and sprint speed at eight temperatures, as well as the thermal preference in a thermal gradient. The number of eggs laid increased with female sprint speed and with male righting time, and all three performances had similar thermal reaction norms, with 80% of the maximum achieved between 23 and 37 °C. Red flour beetles had preferred body temperatures that matched the optimal temperature for performance; confused flour beetles had lower preferred body temperature than the optimal temperature for performance. We found support for the assumption that locomotor performance can serve as a proxy for reproductive output in flour beetles, but we only found evidence for thermal coadaptation in one of the two species.

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1. Introduction

Ectotherms have variable body temperature and body temperature affects whole-organism performance (Angilletta, 2009; Angilletta et al., 2002a,b; Bennett, 1980; Huey and Kingsolver, 1989). Most ectotherms thus use behavioral thermoregulation to maintain their body temperature within a narrow range and avoid reduced performance associated with body temperatures far from the optimal temperature (Angilletta, 2009; Angilletta et al., 2002a, b; Bennett, 1980; Huey and Kingsolver, 1989). For instance, ectotherms can maintain body temperatures that maximize metabolic rate (e.g., Dubois et al., 2009; Gillooly et al., 2001), growth rate (e.g., Angilletta et al., 2004), locomotion (e.g., Blouin-Demers and Weatherhead, 2008), and reproduction (e.g., Berger et al., 2008). Thermal reaction norms for whole-organism performance tend to have similar shapes, with a gradual increase in

performance with increasing temperature below the optimal temperature (T_o) followed by a sharp decrease in performance when body temperature exceeds T_o (Angilletta, 2006; Bulté and Blouin-Demers, 2006; Dell et al., 2011). According to the thermal coadaptation hypothesis, these similar shapes are due to coevolution of the thermal reaction norm for fitness and thermal preference, where the optimal temperature for fitness should evolve to closely match temperatures commonly experienced in the wild (Angilletta, 2009; Angilletta et al., 2002a, 2006; Bennett, 1980; Blouin-Demers et al., 2003; Dorcas et al., 1997; Hertz et al., 1983; Huey and Bennett, 1987; Huey and Kingsolver, 1989). Organisms with strongly left skewed thermal reaction norms (i.e. thermal specialists), however, may have sub-optimal body temperature preference (Martin and Huey, 2008).

Researchers often use easily obtained thermal reaction norms, such as that for locomotor performance (e.g., Blouin-Demers and Weatherhead, 2008), as proximate measures of the effect of temperature on fitness instead of using more ultimate measures of fitness, such as reproductive success, that can be more difficult to obtain. Indeed, the vast majority of tests of the thermal

Table 1
Literature review of tests of the thermal coadaptation hypothesis.

Reference	Group	Species	Variables measured
Anderson et al. (2011)	Nematode	*Caenorhabditis elegans*	Lifetime reproductive success, intrinsic growth rate, thermal preference
Angilletta et al. (2002a)	Lizard	*Sceloporus undulatus*	Sprint speed, sprint endurance, digestive performance, thermal preference
Bauwens et al. (1995)	Lizard	*Acanthodactylus erythurus, Lacerta monticola, L. vivipara, L. agilis, L. schreiberi, Podarcis bocagei, P. hispanicus, P. muralis, P. lilforgi, P. tiliguerta, Psammodromus algirus, Ps. hispanicus*	Sprint speed, thermal preference
Ben-Ezra et al. (2008)	Turtle	*Graptemys geographica*	Swimming speed, righting time, field active body temperatures
Bennett (1980)	Lizard	*Cnemidophorus murinus, Dipsosaurus dorsalis, Eumeces obsoletus, Gerrhonotus multicarinatus, Sceloporus occidentalis, Uma inornata*	Sprint speed, field active body temperatures
Beuchat et al. (1984)	Lizard	*Eleutherodactylus coqui, E. portoricensis*	Jumping performance, maximum jumping distance, field active body temperatures
Blouin-Demers et al. (2003)	Snake	*Elaphe obsoleta, Nerodia sipedon*	Swimming speed, tongue-flicking rate, striking speed
Dorcas et al. (1997)	Snake	*Charina bottae*	Digestive rate, passage rate, thermal preference
Gaby et al. (2011)	Lizard	*Oligosoma maccanni, Woodworthia"Otago/Southland'*	Sprint speed, thermal preference
Huey and Bennett (1987)	Lizard	*Lygosominae*	Sprint speed, thermal preference
Knowles and Weigl (1990)	Frog	*Acris crepitans, Hyla femoralis, Pseudacris triserata, Rana clamitans, R. sylvaticus,*	Maximum jumping distance, field active body temperatures
McElroy (2014)	Lizard	*Emoia cyanura, E. impar*	Sprint speed, thermal preference
Sanabria et al. (2013)	Frog	*Pleurodema nebulosum*	Locomotor performance, thermal preference
van Berkum (1986)	Lizard	*Anolis humilis, A. cupreus, A. intermedius, A lemurinus, A. limifrongs, A. lionotus, A. tropidolepis*	Sprint speed, field active body temperatures

coadaptation hypothesis to date use locomotor performance rather than reproductive success as their metric of fitness (Table 1). Nevertheless, the link between locomotor performance and fitness is not consistent across species (Angilletta et al., 2002b). In squamates, locomotor performance can predict survivorship (Calsbeek and Irschick, 2007; Jayne and Bennett, 1990) and predator escape (Irschick and Losos, 1998; Miles, 2004). Therefore, it is plausible that locomotor performance is an appropriate proxy for fitness. Given that lizards rarely use maximum sprint speed while evading human predators in the field (Irschick and Losos, 1998), however, it is also possible that locomotor performance is only loosely related to fitness. These studies provide valuable information on the variability of thermal optima between various physiological traits (Angilletta, 2009; Angilletta et al., 2002b), but more stringent tests of the thermal coadaptation hypothesis should be based on more ultimate measures of fitness.

In this study, we provide one of the most stringent tests of the thermal coadaptation hypothesis to date by comparing the thermal preference and the thermal reaction norms for righting time, sprint speed, and oviposition rate in two congeneric species of flour beetle that differ in their thermal preference (King and Dawson, 1973; see Results): the red flour beetle (*Tribolium castaneum*) and the confused flour beetle (*T. confusum*). We first test the prediction that the optimal temperatures for performance are coadapted to thermal preference in each species. Then, for the first time, we empirically test the assumption that locomotor performances (righting time and sprint speed) are good proxies for reproductive output, which is a more ultimate component of fitness. We use path analysis to determine the relative importance of temperature and locomotor performance in predicting the reproductive output of flour beetles.

2. Materials and methods

2.1. Study system

We conducted all experiments with colonies of red flour beetles (*T. castaneum*) and confused flour beetles (*T. confusum*) originally obtained from Carolina Biological Supply Company (Burlington, North Carolina, USA). At Carolina Biological Supply Company, flour beetles were maintained at 27 °C and 65% relative humidity on a 9 h:15 h light:dark cycle. For each species, the starting colonies consisted of 200 individuals, and we let the colonies grow to approximately 5000 individuals. We raised each species in large cultures containing 95% all-purpose wheat flour and 5% brewer's yeast (all future mention of flour refers to this mixture). We maintained the cultures at 30 °C and 70% relative humidity on a 12:12 h light:dark cycle for 6 months prior to experiments for *T. confusum*, and for 16 months prior to experiments for *T. castaneum*.

2.2. Thermal preference

We measured the thermal preference (T_{set}) of each species in a thermal gradient ranging from 20 to 40 °C. Although 40 °C is hot enough to induce heat shock in flour beetles (Mahroof et al., 2005), no beetles died during this experiment or were found immobile at the hot end of the gradient. We created the thermal gradient by placing a metal box (30×30 cm) with five runways (5 cm wide) and 3 cm high walls in an environmental chamber set at 20 °C and placing a heating pad under one end of the gradient. We generated a thermal map of the gradient by measuring substrate temperature every 3 cm within each lane before and after each trial. We placed 10 beetles (ca. 2 months old, mix of males and females randomly drawn from our large cultures) in the center of each lane, allowed them to acclimate to the gradient for one hour, and then used a digital camera to take pictures of the beetles in the gradient every 5 min for one hour. We assigned a temperature to each beetle in each picture based on its location within the thermal map. We used 200 individuals of each species in this experiment, for a total of 20 replicate lanes for each species. We pooled the selected temperatures for all individuals in each replicate lane and calculated T_{set} (25th, 50th, and 75th percentiles of selected temperatures; Hertz et al., 1993). We used the percentiles for each replicate lane to calculate a mean and 95% confidence