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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

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

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

**Table 2**

Order of treatments used to build righting time, sprint speed, and egg laying rate thermal reaction norms for red flour beetles (*Tribolium castaneum*) and confused flour beetles (*T. confusum*).

Day	Temperature (°C)	Performance
1 and 2	30	Egg laying rate
3	23	Righting time, sprint speed, egg laying rate
4	29	Righting time, sprint speed, egg laying rate
5	32	Righting time, sprint speed, egg laying rate
6	26	Righting time, sprint speed, egg laying rate
7 and 8	30	Egg laying rate
9	20	Righting time, sprint speed, egg laying rate
10	17	Righting time, sprint speed, egg laying rate
11	35	Righting time, sprint speed, egg laying rate
12	38	Righting time, sprint speed, egg laying rate

interval of  $T_{set}$  for each species.

### 2.3. Experimental manipulations

We randomly selected 80 pupa of each species from our large cultures, identified the sex of each pupa based on the presence/absence of ovipositors (Good, 1936), and separated males and females of each species into separate containers with *ad libitum* flour. One week following eclosion, we placed a dab of non-toxic acrylic paint onto the back of each adult beetle to identify its sex and species. Twenty-four hours after painting, we randomly selected one male and one female of the same species and measured their body length with a scale on a dissecting scope. We then placed the pair in a petri dish (10 cm diameter) with 2.5 ml of flour (pre-sifted through a 250  $\mu$ m sieve to aid in egg detection) to

create 20 mating pairs of each species. We left the pairs together for 48 h at 30 °C for a mating period to ensure that each pair would produce eggs throughout the experiment. Following this 48-h mating period, we sifted the flour with a 250- $\mu$ m sieve and counted the number of eggs laid (see Table 2 for the sequence of manipulations).

Following the mating period, we placed the pair in an environmental chamber set to the treatment temperature with 2.5 ml of fresh pre-sifted flour for 24 h, counted the number of eggs laid after 24 h, and then measured the righting time and sprint speed of each individual. We measured righting time as the time taken for an individual beetle to flip onto its ventral side after being flipped onto its dorsal side. We measured sprint speed as the time taken for a beetle to run 5 cm in a straight line on a flat surface made with the non-adhesive side of masking tape. After we completed measuring the righting time and sprint speed of each individual, we cleaned the petri dish (ensuring all flour and eggs were removed), added 2.5 ml of fresh pre-sifted flour, put the pair of beetles back in the dish, and placed the dish in the environmental chamber at the next temperature treatment. We repeated this process at different test temperatures until day 6 (Table 2).

On days 7 and 8, we provided the beetles with 2.5 ml of fresh pre-sifted flour and set the chamber to 30 °C. After 48 h, we sifted the flour and counted the number of eggs laid. This served to ensure that egg laying potential did not decrease as the experiment progressed.

On day 9, we provided the beetles with 2.5 ml of fresh pre-sifted flour, and repeated our measures of oviposition and performance at an additional four test temperatures until day 12. We used eight test temperatures ranging from 17 to 38 °C (Table 2).

**Table 3**

Model selection for non-linear functions describing thermal reaction norms for righting time (Right), sprint speed (Sprint), and egg laying (Eggs) in red flour beetles (*Tribolium castaneum*) and confused flour beetles (*Tribolium confusum*). The upper value in each cell represents the AIC for that performance measure and model, and the lower value represents  $\Delta$ AIC between that model and the model with the lowest AIC for that performance measure. The bolded model represents the best model based on the lowest AIC.

Model	<i>Tribolium castaneum</i>			<i>Tribolium confusum</i>		
	Right	Sprint	Eggs	Right	Sprint	Eggs
Stevenson et al. (1985): Linear $\times$ exponential decay: $b_0(b_1(T-5))(1 - e^{b_2(T-40)})$	698.17 2.05	-213.99 2.05	145.31 2.09	694.93 2.05	-213.76 2.05	111.36 3.68
Stevenson et al. (1985): Exponential decay $\times$ exponential decay: $b_0(1 - e^{b_1(T-5)})(1 - e^{b_2(T-40)})$	716.46 20.34	-199.59 16.45	151.56 8.34	697.06 4.18	-200.84 14.97	118.67 10.99
Stevenson et al. (1985): Logistic $\times$ exponential decay: $b_0\left(\frac{1}{1+b_1-b_2(T-5)}\right)(1 - e^{b_3(T-40)})$	739.42 43.30	-156.64 59.40	150.57 7.35	713.66 20.78	-190.88 24.93	116.35 8.67
Stevenson et al. (1985): Exponential decay + exponential: $b_0 + (1 - e^{-b_1(T-5)}) + (1 + e^{b_2(T-40)})$	710.21 14.09	-185.67 30.37	151.09 7.87	711.24 18.36	-199.27 16.54	117.04 9.36
Ratkowsky et al. (1983): Linear $\times$ exponential decay: $(b_0(T-5))(1 - e^{b_1(T-40)})$	<b>696.12</b> <b>0.00</b>	<b>-216.04</b> <b>0.00</b>	<b>143.22</b> <b>0.00</b>	<b>692.88</b> <b>0.00</b>	<b>-215.81</b> <b>0.00</b>	109.26 1.58
Quartic: $b_0 + b_1T + b_2T^2 + b_3T^3 + b_4T^4$	700.63 4.51	-213.54 2.50	146.94 3.72	695.11 2.23	-212.64 3.17	<b>107.68</b> <b>0.00</b>

We randomized the order of the test temperatures between 23 and 32 °C and conducted these treatments between days 3 and 6 (order: 23, 29, 32, 26 °C). Between days 9 and 12, we followed a more systematic order of temperature treatments to avoid potentially lethal temperatures until the end of the experiment (order: 20, 17, 35, 38 °C). Both species followed the same sequence of temperatures. The randomized order of temperature treatments allowed us to control for potential carry-over effects.

#### 2.4. Egg laying potential

For each species, we compared the number of eggs laid by a pair of beetles during days 1 and 2 to the number of eggs laid by the same pair during days 7 and 8 using a paired *t*-test in R (package: stats; function: *t*-test; R Core Team, 2014).

#### 2.5. Thermal reaction norms

We built thermal reaction norms for righting time (60 s minus time to right in seconds), sprint speed (cm/s), and oviposition rate (number of eggs laid in 24 h) using non-linear curve fitting in JMP (version 11.2.0). First, we fit six different curves to each performance measure for each species with data pooled across individuals. Four curves were from Stevenson et al. (1985), one curve was from Ratkowsky et al. (1983), and the sixth curve was a quartic curve (Table 3). We compared the fit of the different curves using Akaike's information criterion (Akaike, 1973) using the following equation (Burnham and Anderson, 2002):

$$AIC = 2L + 2K + \frac{2K(K+1)}{N-K-1}$$

where *K* is the number of parameters in the model, *N* is sample size, and *L* is calculated using the following equation:

$$L = \log \frac{RSS}{N} \times \frac{-N}{2}$$

where *RSS* is the residual sum of squares from the model. We selected the curve that best described the data for each performance measure for each species (the curve with the lowest *AIC*), and then fit that curve to the data for each individual (for righting time and sprint speed) or for each pair (for egg laying). We used the curves for each individual or pair to calculate the temperature at the maximum performance (*T<sub>o</sub>*) and at the lower and upper 80% of the maximum (*B<sub>80</sub>*; Huey and Stevenson, 1979). For each species, we compared the curves for each performance measure using multivariate analysis of variance (package: stats; function: manova) where the temperatures at the lower and upper 80% of the maximum and the temperature at the maximum were dependent variables, and where species, performance type (egg laying, righting time, and sprint speed), and their interaction were the independent variables.

We also compared the 25th, 50th, and 75th percentiles of selected temperatures for each species to their lower *B<sub>80</sub>*, *T<sub>o</sub>*, and upper *B<sub>80</sub>*, respectively, for each performance measure. In each case, we determined whether the 95% confidence intervals overlapped.

#### 2.6. Concordance of locomotor and reproductive performances

We analyzed the number of eggs laid by each pair of beetles (square root-transformed to meet the normality assumption) at each temperature treatment using linear mixed effects models (package: nlme; function: lme; Pinheiro et al., 2014). We used species, sprint speed, righting time, and the total length of the male and female in the pair, along with a polynomial term for temperature as fixed effects, and pair identity as a random effect.

We included all two-way interactions between species and the other fixed effects. We selected the appropriate polynomial term for temperature by comparing models with quadratic, cubic, and quartic terms using bias-corrected Akaike's information criteria (Akaike, 1973; package: qpcR; function: *AICc*; Spiess, 2014). We considered the model with the lowest *AICc* to be the best model. Similarly, we used *AICc* to select the best model describing the number of eggs laid. We confirmed model fit by checking the normality and homogeneity of residuals from the best model. We also used Pearson's correlations (package: stats; function: cor.test) to test for multicollinearity between righting time and sprint speed for each species and each sex.

Finally, we used path analysis (package: lavaan; function: sem; Rosseel, 2012) to examine the relative effects on reproductive output of the significant variables in the previous mixed effects model. More specifically, we determined the partial *R*<sup>2</sup> for each term in the following equations:

$$W = Sp + T + T^2 + MR + FS$$

$$MR = T + T^2$$

$$FS = T + T^2$$

where *W* is the number of eggs laid, *Sp* is species (*T. castaneum* or *T. confusum*), *T* is temperature, *T*<sup>2</sup> is temperature squared, *MR* is male righting time, and *FS* is female sprint speed. We used a quadratic effect of temperature (*T* and *T*<sup>2</sup>) because this was the best polynomial term for temperature from the linear mixed effects model.

### 3. Results

#### 3.1. Thermal preference

*T. castaneum* preferred temperatures ranging from 26.9 to 33.8 °C (interquartile range), with a median preferred temperature of 29.8 °C. *T. confusum* had a markedly lower *T<sub>set</sub>*, ranging from 23.5 to 31.4 °C, with a median preferred temperature of 26.6 °C (Table 4). Over 40 years ago, King and Dawson (1973) found that *T.*

**Table 4**

Thermal preference (*T<sub>set</sub>*) and reaction norm (TRN) summary statistics of red flour beetles (*Tribolium castaneum*) and confused flour beetles (*Tribolium confusum*) for three performance measures: righting time, sprint speed, and egg laying at temperatures ranging from 17 to 38 °C. Thermal preference is based on the 25th, 50th, and 75th quartiles of selected body temperatures in a thermal gradient. *B<sub>80</sub>* is the performance breadth: the temperature interval where at least 80% of the maximum performance (*T<sub>o</sub>*) is achieved. Values are presented as the mean followed by its 95% confidence interval. Arrows beside the values for the TRNs denote that the confidence interval for that TRN does not overlap with the confidence interval for *T<sub>set</sub>*; an arrow pointing down represents TRN below *T<sub>set</sub>*, and an arrow pointing up represents TRN above *T<sub>set</sub>*.

<i>Tribolium castaneum</i>				
Thermal preference	<i>n</i>	25th	50th	75th
	20	27.5, 26.9–28.0	29.8, 29.1–30.6	32.5, 31.3–33.8
Reaction norm	<i>n</i>	Lower <i>B<sub>80</sub></i>	<i>T<sub>o</sub></i>	Upper <i>B<sub>80</sub></i>
Righting time	39	22.7, 20.8–24.5↓	30.4, 28.6–32.2	35.5, 33.9–37.2↑
Sprint speed	40	26.8, 25.6–28.1	34.2, 33.1–35.4↑	37.5, 36.9–38.1↑
Egg laying	18	22.6, 20.3–25.0↓	30.5, 28.3–32.6	35.4, 34.2–36.6↑
<i>Tribolium confusum</i>				
Thermal preference	<i>n</i>	25th	50th	75th
	20	24.1, 23.5–24.7	26.6, 25.2–28.0	29.7, 28.0–31.4
Reaction norm	<i>n</i>	Lower <i>B<sub>80</sub></i>	<i>T<sub>o</sub></i>	Upper <i>B<sub>80</sub></i>
Righting time	39	24.8, 23.2–26.4	32.4, 30.9–33.8↑	36.5, 35.7–37.3↑
Sprint speed	40	25.0, 23.0–27.1	32.7, 31.6–33.8↑	36.7, 36.1–37.3↑
Egg laying	17	23.1, 20.5–25.8	31.0, 28.6–33.4↑	35.7, 34.4–37.0↑

*castaneum* and *T. confusum* living together in a thermal gradient segregated according to temperature, where *T. castaneum* was around 30 °C while *T. confusum* was around 25 °C. The similar values of  $T_{set}$  obtained 40 years apart for the two species suggest it is a conserved trait.

### 3.2. Egg laying potential

*T. castaneum* laid a similar number of eggs in the two 48-h egg laying periods at 30 °C (days 1–2 mean  $\pm$  S.E. =  $19.6 \pm 2.7$ , days 7–8 =  $21.9 \pm 4.0$ ;  $t_{15} = 0.3759$ ,  $p = 0.71$ ), and the same was true of *T. confusum* (days 1–2 =  $9.4 \pm 2.0$ , days 7–8 =  $11.9 \pm 2.6$ ;  $t_{14} = 2.0176$ ,  $p = 0.06$ ), although *T. confusum* laid approximately half the eggs laid by *T. castaneum*. Overall, 58% of *T. castaneum* pairs and 53% of *T. confusum* pairs increased egg output between the first and second period, 35% of *T. castaneum* pairs and 37% of *T. confusum* pairs decreased egg output between the first and second period, while 7% of *T. castaneum* pairs and 10% of *T. confusum* pairs did not change their egg output between the first and second period. Therefore, the changes in egg laying rate as a function of temperature we observed cannot be attributed to changes in egg laying potential as the experiment progressed.

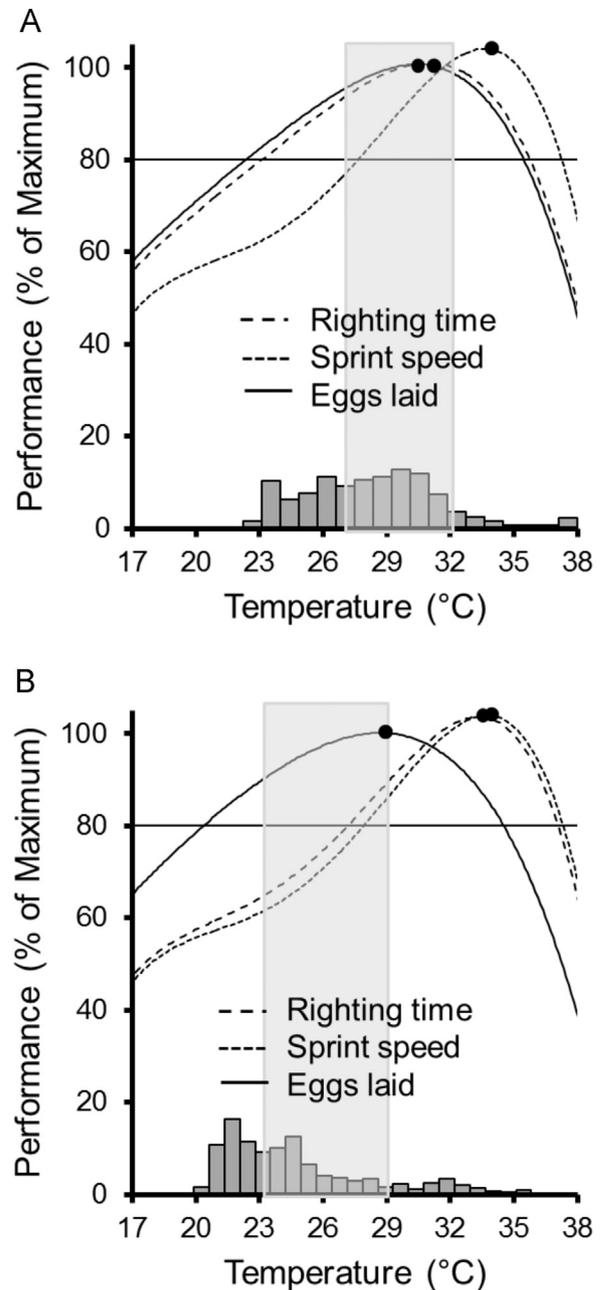
### 3.3. Thermal reaction norms

All performances, except egg laying rate in *T. confusum*, were fit best by a Ratkowsky curve (Table 3). For this reason and to ease comparison, we fit Ratkowsky curves to all individual data. *T. castaneum* achieved 80% of its maximum performance ( $B_{80}$ ) between 20 and 34 °C for righting time and for egg laying, and between 26 and 38 °C for sprint speed (Table 4, Fig. 1A). Similarly, *T. confusum* achieved 80% of its maximum performance ( $B_{80}$ ) between 23 and 37 °C for righting time and sprint speed, and between 21 and 37 °C for egg laying (Table 4, Fig. 1B). Optimal temperatures and  $B_{80}$  did not differ significantly between the two species ( $p = 0.12$ ). In both species, the values of  $T_o$  ( $p < 0.01$ ), lower  $B_{80}$  ( $p < 0.01$ ), and upper  $B_{80}$  ( $p = 0.04$ ) were lower for egg laying than for sprint speed, while the values of  $T_o$  ( $p = 0.01$ ) and lower  $B_{80}$  ( $p = 0.02$ ) were lower for righting time than for sprint speed.

We compared the thermal reaction norms of performance to the thermal preference of *T. castaneum* (Table 4, Fig. 1A). For righting time and for egg laying, the  $B_{80}$  was broader than  $T_{set}$ : the lower  $B_{80}$  was colder than the lower bound of  $T_{set}$  and the upper  $B_{80}$  was hotter than the upper bound of  $T_{set}$  while the median selected temperature matched  $T_o$ . For sprint speed,  $T_o$  exceeded the median selected temperature while the upper  $B_{80}$  exceeded the upper bound of  $T_{set}$ . For egg laying, the lower  $B_{80}$  was colder than lower  $T_{set}$  and the upper  $B_{80}$  was warmer than upper  $T_{set}$  while the median selected temperature matched  $T_o$ . We also compared the thermal reaction norms of performance to the thermal preference of *T. confusum* (Table 4, Fig. 1B). For all three reaction norms,  $B_{80}$  extended into warmer temperatures than  $T_{set}$ :  $T_o$  and upper  $B_{80}$  were warmer than the median selected temperature and the upper bound of  $T_{set}$ , while the lower  $B_{80}$  matched the lower bound of  $T_{set}$ .

### 3.4. Concordance of locomotor and reproductive performances

*T. castaneum* laid more eggs than *T. confusum* ( $t_{1,219} = 2.80$ ,  $p < 0.01$ ). The number of eggs laid by both species was positively correlated with male righting time ( $t_{1,219} = 2.87$ ,  $p < 0.01$ ; Table 5, Fig. 2a) and with female sprint speed ( $t_{1,219} = 3.66$ ,  $p < 0.001$ ; Fig. 2b), although in both species the variance in egg laying rate explained by locomotor performance was relatively small. Within each sex, righting time and sprint speed were moderately correlated (female:  $r = 0.25$ ; male:  $r = 0.28$ ).

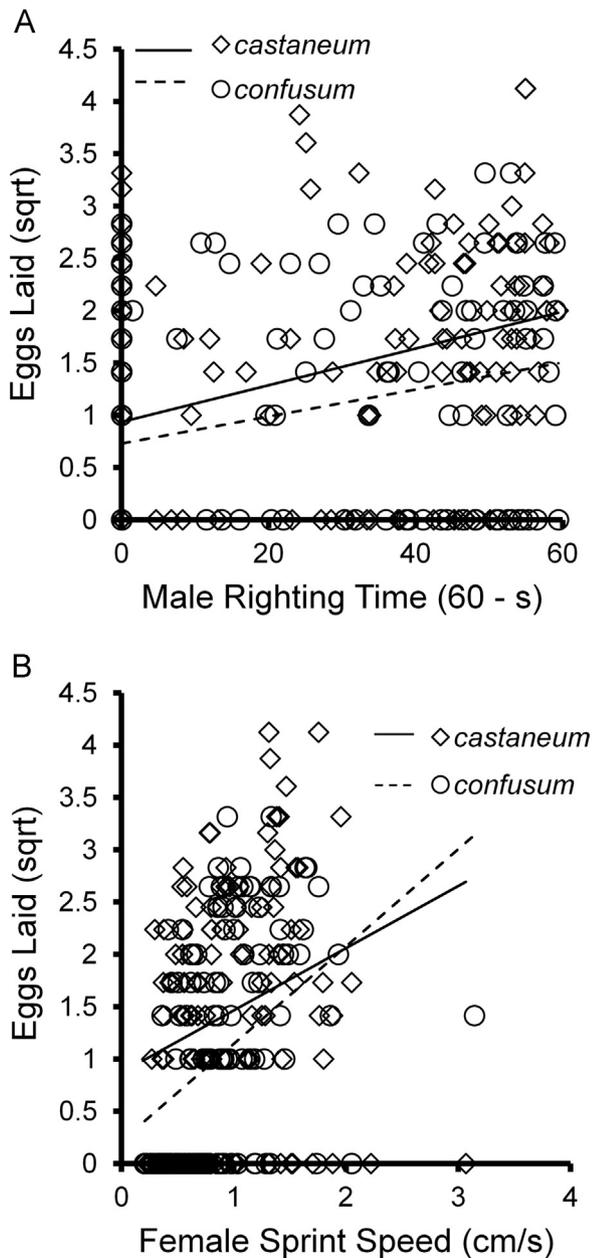


**Fig. 1.** Thermal reaction norms of red flour beetles (*Tribolium castaneum*) (A) and confused flour beetles (*Tribolium confusum*) (B) for righting time, sprint speed, and eggs laid over 24 h. All three performance measures were transformed to a percent of their maximum value. The histograms at the bottom of the figures represent the temperatures selected by the species in a thermal gradient ranging from 20 to 40 °C, and the gray boxes represent the thermal preference ( $T_{set}$ ; interquartile range) for the species. Curves represent the lines of best fit for a non-linear curve with a linear increase and exponential decay from Ratkowsky et al. (1983). The horizontal line at 80% is to help visualize the performance breadth ( $B_{80}$ ). The optimal temperature ( $T_o$ ) for each performance measure is marked by a dot at the peak of the curve.

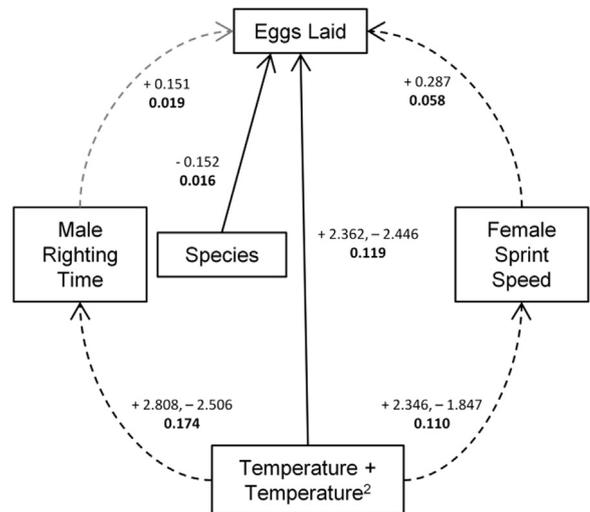
Among the variables considered, path analysis (Fig. 3) demonstrated that the combined effect of temperature and temperature squared had the strongest effect on the number of eggs laid (partial  $R^2 = 0.12$ ), with female sprint speed having the next strongest effect (partial  $R^2 = 0.06$ ), and male righting time (partial  $R^2 = 0.02$ ) and species (partial  $R^2 = 0.02$ ) having the smallest contributions to the number of eggs laid. Temperature also had an effect on female sprint speed (partial  $R^2 = 0.11$ ) and on male

**Table 5**  
Model selection for models predicting the number of eggs laid by red flour beetles (*Tribolium castaneum*) and by confused flour beetles (*Tribolium confusum*). \* denotes two-way interactions between species and all variables inside the parentheses. The bolded model is the best model according to AICc.

Model	k	AICc	ΔAICc
<b>Eggs = species + temperature + temperature<sup>2</sup> + male righting time + female sprint speed</b>	<b>8</b>	<b>683.08</b>	<b>0.00</b>
Eggs = species + temperature + temperature <sup>2</sup> + male righting time + female sprint speed + male sprint speed + female length	10	692.23	9.15
Eggs = species + temperature + temperature <sup>2</sup> + female righting time + male righting time + female sprint speed + male sprint speed + female length + male length	12	706.91	23.83
Eggs = species*(temperature + temperature <sup>2</sup> + female righting time + male righting time + female sprint speed + male sprint speed + female length + male length)	20	733.85	50.77



**Fig. 2.** The number of eggs laid (square root-transformed) by red flour beetles (*Tribolium castaneum*) and confused flour beetles (*Tribolium confusum*) increase with a faster righting time of males (A) and a faster sprint speed of females (B).



**Fig. 3.** Path analysis demonstrates that the number of eggs laid, righting time, and sprint speed are all affected by temperature, and that male righting time and female sprint speed affect the number of eggs laid. Solid lines represent direct effects and dashed lines represent indirect effects. Black lines represent  $p < 0.01$  and gray lines represent  $0.01 \leq p \leq 0.05$ . Numbers adjacent to each line represent the standardized estimate of that relationship, and bolded numbers are the partial  $R^2$  for that same relationship. On all lines involving the effect of temperature, the first number refers to the linear effect while the second number refers to the curvilinear effect.

righting time (partial  $R^2 = 0.17$ ). Overall, however, the effect sizes of the variables considered were small to moderate. The effect of male righting time on the number of eggs laid was almost entirely indirect (99.8%) and mediated by temperature. The effect of female sprint speed on the number of eggs laid, on the other hand, was mostly direct (89.7%).

**4. Discussion**

Temperature-dependent processes that influence fitness should be coadapted so that optimal performance is achieved under the temperature range commonly experienced in the wild, and animals should choose body temperatures that maximize fitness (reviewed in Angilletta (2009)). In *T. castaneum*, there was generally a good correspondence between the preferred body temperature range and the optimal temperature range for performance; the correspondence between  $B_{80}$  and  $T_{set}$  was especially good for egg laying rate and for righting time. In *T. confusum*, on the other hand, the correspondence between the preferred body temperature range and the optimal temperature range for performance was less marked: the preferred body temperature range was colder than the optimal temperature range for performance. It is notable, however, that there was a much better correspondence between  $B_{80}$  and  $T_{set}$  for egg laying rate, a more ultimate measure of fitness, than for the two locomotor performances. Our data for *T. castaneum* therefore offer strong support for the thermal coadaptation hypothesis, but our data for *T. confusum* only offer partial support for the hypothesis. This is the first study, to the best of our knowledge, to test whether easily measured, more proximal measures of fitness (righting time and sprint speed) can be used as proxies for more ultimate components of fitness (egg laying rate). In this respect, we show that the concordance between proximal and more ultimate measures of fitness was good in *T. castaneum*, but poor in *T. confusum*. In addition, our path analysis revealed weak, and mostly indirect, effects of locomotor performance on reproductive output. Therefore, using the thermal reaction norm of locomotor performance as a proxy for the thermal reaction

norm of fitness could prove problematic, at least for some species.

The thermal reaction norms for *T. castaneum* and *T. confusum* were similar for egg laying, righting time, and sprint speed in the sense that the confidence intervals for  $B_{80}$  and  $T_o$  for each performance measure for each species overlapped (Table 4), albeit the interspecific overlap was less complete for righting time than for the other two performances. The  $B_{80}$  for each curve for each species fit within a range of 12 °C from ca. 25 to 37 °C. This suggests that the underlying temperature-dependent physiological processes governing oviposition, righting time, and sprint speed are well conserved between the two species, yet their preferred temperatures have diverged.

Available evidence suggests that the thermal preference and the thermal reaction norm for egg laying rate are conserved traits in flour beetles.  $T_{set}$  for *T. castaneum* in the present study was similar to that in a previous study (30 °C; Halliday and Blouin-Demers, 2014), and so was the  $B_{80}$  of the thermal reaction norm for egg laying (between 30 and 35 °C; Halliday et al., 2015). A study over 60 years ago (Park and Frank, 1948) examined reproduction by *T. castaneum* and *T. confusum* at three temperatures (24, 29, 34 °C) and showed similar patterns to those uncovered in the present study: highest reproductive output and quickest development time at 34 °C for both species, although the differences between these variables at 29 and 34 °C were small. Langer and Young (1976) and King and Dawson (1973) obtained  $T_{set}$  values for *T. castaneum* and for *T. confusum* that were also similar to those reported here. Finally, Howe (1956) found that the number of eggs laid was maximized and the time spent in the egg stage was minimized at 35 °C, the upper end of the  $B_{80}$  reported here. Therefore, the available evidence indicates that domestication of flour beetles has not altered their thermal traits, contrary to some other invertebrates that have rapidly adapted to laboratory conditions (Anderson et al., 2007; Good, 1993; Huey and Rosenzweig, 2009).

The ancestral habitat of flour beetles may have been more thermally variable than grain warehouses in which they currently occur. Farmers are encouraged to cool or heat their warehouses to outside the optimal temperature range of insect pests (below 15 °C or above 40 °C; Phillips and Throne, 2010). It appears that the ancestral range of *Tribolium* encompassed India, southwest Asia, and the eastern Mediterranean (Good, 1936). In their historical distribution in North America, *T. castaneum* was more common in the southern United States, whereas *T. confusum* was more common in the northern United States (Good, 1936). This interspecific pattern in abundance in North America may have been a function of the difference in thermal preference between the two species.

Our path analysis demonstrated that among all factors considered, temperature had the most influence on the number of eggs laid and, unsurprisingly, also influenced male righting time and female sprint speed. A more interesting result is that female sprint speed had a larger and more direct effect (89.7% direct, partial  $R^2=0.06$ ) on the number of eggs laid than male righting time (99.8% indirect, partial  $R^2=0.02$ ), although both performances explained a relatively low proportion of the variance in the number of eggs laid. The weak and indirect influence of male righting time indicates that it is probably not an important driver of reproductive success in flour beetles. Nevertheless, males that right themselves more slowly may have fewer opportunities to mate. The effect of female sprint speed on reproductive output could potentially be a reflection of the overall effect of condition. Presumably, females in better condition can lay more eggs, and presumably they can also sprint faster. This link between condition and reproductive success in females has been demonstrated in a plethora of species (e.g., Festa-Bianchet et al., 1998; Naulleau and Bonnet, 1996; Weimerskirch, 1992). Female condition probably has more influence on the number of egg laid than male condition

because of the intersexual difference in how energy is allocated to reproduction. Using diet manipulations to vary male and female condition would be one way to test this hypothesis.

One possible limitation of our study is that we used the number of eggs laid over 24 h as our most ultimate measure of fitness, yet female flour beetles lay eggs continuously throughout their adult life, which can be up to 2 years in captivity (Good, 1936). Therefore, the number of eggs laid over 24 h may not be a good measure of the lifetime reproductive output of flour beetles. Moreover, the number of eggs laid is only one component of fitness; for instance, age at first reproduction could be a more important component of fitness in some species. Importantly, different components of fitness can have different thermal reaction norms. Huey and Berrigan (2001) found that across a large group of taxa, 76% of species had a warmer optimal temperature for intrinsic population growth rate than for lifetime reproductive output. Anderson et al. (2011) found that different strains of *Caenorhabditis elegans* had different thermal preferences and experienced highest lifetime fitness at their preferred temperatures, but the different strains maximized lifetime fitness via different mechanisms. Strains that preferred warm temperatures maximized lifetime fitness by increasing reproductive output at their preferred temperature, while strains that preferred cool temperatures maximized lifetime fitness via increased longevity at their preferred temperature. It is therefore possible that our two species of flour beetles maximize lifetime fitness differently through the combined effects of reproductive rate, longevity, and age at first reproduction. Future research should examine whether these different components of fitness vary between the two species across different temperatures.

Some of the original studies in which sprint speed was used as a proxy for fitness (i.e. Jayne and Bennett, 1990) demonstrated a link between sprint speed and survival: fast individuals were better at escaping predators than slow individuals. In the case of flour beetles, it seems improbable that they evade their predators with rapid sprinting. Flight response, or even death feigning, may be more appropriate metrics of fitness for *Tribolium* than sprint speed (Miyatake et al., 2004; Ridley et al., 2011). Future studies could examine thermal coadaptation within these other, potentially more ecologically relevant, proxies of *Tribolium* fitness.

In summary, our data for one species of flour beetle provided strong support for the thermal coadaptation hypothesis, but our data for the other species only provided partial support for the hypothesis. Within species, the thermal reaction norms tended to be coadapted and, thus, performance tended to be maximized within a relatively narrow optimal range of temperatures. Therefore, easily measured thermal reaction norms (e.g., locomotor performance) could potentially be used as proxies for thermal reaction norms that are more difficult to measure (e.g., reproductive success). Our data provided only partial support for this notion, where the thermal reaction norms for locomotion and egg laying were very similar in one species, but less similar in the other. Therefore, it would be prudent to use more ultimate measures of fitness in studies of thermal adaptation.

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