

## RESEARCH ARTICLE

# Phenotypic plasticity in locomotor performance of a monophyletic group of weevils accords with the ‘warmer is better’ hypothesis

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## ABSTRACT

Ectotherms may respond to variable environmental conditions by altering their phenotypes. Phenotypic plasticity was initially thought to be beneficial to an organism’s physiological fitness but several alternative hypotheses have been proposed with growing empirical support. In this study, we tested the full suite of hypotheses by investigating acclimation responses of locomotor performance for nine populations of five species of sub-Antarctic weevils, using static and fluctuating temperatures. Species showed typical locomotion thermal performance curves with temperature of the maximum speed ( $T_{opt}$ ) ranging between  $22.3 \pm 1.7^\circ\text{C}$  (mean  $\pm$  s.e.m.) and  $31.1 \pm 0.7^\circ\text{C}$ . For most species,  $T_{opt}$  was not affected by acclimation. For maximum speed ( $U_{max}$ ), significant, positive effects of acclimation were found for all species except a supralittoral one. Individuals acclimated to  $0^\circ\text{C}$  showed much lower values than the other two acclimation treatments ( $15^\circ\text{C}$  and fluctuating  $0$ – $15^\circ\text{C}$ ). Performance breadth (the index of the breadth of the curve,  $T_b$ ) typically showed little response to acclimation. None of the traits of the supralittoral species was affected by acclimation treatment. Responses to stable and fluctuating temperature treatments were similar. Our findings also revealed that the mean estimated activation energy  $0.40 \pm 0.015$  eV (mean  $\pm$  s.e.m.) was lower than for other herbivores, the category to which these weevils belong, suggesting that some form of compensation in the rate–temperature relationship may be evident. Thus, we typically found support for the ‘warmer is better’ hypothesis for acclimation of locomotor performance, although some compensation was evident.

**KEY WORDS:** Acclimation, Locomotion, Thermal performance, Ectotherm, Sub-Antarctic

## INTRODUCTION

The thermal environment experienced by an organism has direct effects on survival, growth and reproduction. This is especially significant for ectotherms because environmental temperature directly affects body temperature and therefore physiological processes (Huey and Stevenson, 1979; Sinclair et al., 2016). One way ectotherms respond to variable environmental conditions is by altering their phenotypes (Kingsolver and Huey, 1998); a response that can take place over a range of time scales (Chown and Terblanche, 2007). Phenotypic plasticity, which typically takes place within generations, may significantly influence an organism’s fitness

(Ghalambor et al., 2007) and was initially thought to be beneficial, at least in a physiological context. Formally known as the beneficial acclimation hypothesis (BAH), and defined by Leroi et al. (1994) as ‘acclimation to a particular environment gives an organism a performance advantage in that environment over another organism that has not had the opportunity to acclimate to that particular environment’, the hypothesis has now been subject to much scrutiny and its predictions have frequently not been supported (reviewed in Angilletta, 2009; see also Schou et al., 2017).

Several alternative hypotheses on short-term physiological plasticity or acclimation have been proposed, including, for example, compensation, optimal temperatures and deleterious acclimation (Huey et al., 1999; Wilson and Franklin, 2002; Deere and Chown, 2006). Of these, the thermodynamic effect, or the ‘warmer is better’ hypothesis (Bennett, 1987; Huey and Kingsolver, 1989) has been garnering much support (e.g. Van Damme and Vanhooydonck, 2001; Frazier et al., 2006; Knies et al., 2009; Angilletta et al., 2010; Phillips et al., 2014; Sørensen et al., 2018). In essence, because rates proceed faster at higher ambient temperatures, and therefore by association, higher organismal temperatures, fitness should always be higher at higher temperatures, at least up to a point. In the context of acclimation, this hypothesis predicts that organisms acclimated to a high-temperature environment will have a performance advantage over another organism held at a lower temperature. The influence of thermodynamic effects can also be thought to operate over evolutionary time, leading to performance differences among species from different thermal environments (Dell et al., 2011, 2014), in contrast to the idea of complete temperature compensation (Hazel and Prosser, 1974; Clarke, 2017).

Despite growing support (e.g. Kingsolver, 2009; Phillips et al., 2014; Pawar et al., 2015), in some organisms the thermodynamic effect does not seem to predominate. For example, maintenance of rates, suggesting some form of compensation is generally found for plant respiration rates (Heskel et al., 2016). Among the insects, contrary findings continue to be published (e.g. Alton et al., 2017; Zhu et al., 2016). In other organisms, life stage variation seems to account for the differences found, owing to differences in the mobility of the stages (Marais and Chown, 2008). Variation in the extent to which environmental variability is predictable has also been argued to play a role in phenotypic plasticity. The prediction is that in those settings where environmental variation is unpredictable relative to the timescale of the phenotypic response, cue reliability is thought to be low, so tending to result in an absence of plasticity and possibly in negative effects on population viability (Tufto, 2000; Chown and Terblanche, 2007; Reed et al., 2010). Despite a sound theoretical basis for the prediction, only a few studies have sought to determine whether this is the case, with contrasting outcomes (e.g. Deere and Chown, 2006; Niehaus et al., 2012; Manenti et al., 2015; Sinclair et al., 2016; Haupt et al., 2017). Hence, further empirical assessments of the idea are essential. Moreover, because microclimate temperatures and their variability may differ significantly from the

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macroclimatic setting (Woods et al., 2015; Suggitt et al., 2018), understanding of microclimatic variation may also alter expectations for particular phenotypic responses. How animals may respond under variable temperatures compared with more static settings is also not yet comprehensively understood (Sinclair et al., 2016; Kingsolver and Buckley, 2017; Morash et al., 2018). Overall, therefore, it is not yet clear which of the several contrasting hypotheses to explain acclimation responses have most support, and under what conditions various forms of response might be expected.

Here, therefore, we examine the beneficial acclimation, thermodynamic effect, ‘colder is better’, compensation, no plasticity and deleterious acclimation hypotheses simultaneously in strong inference context (following Huey et al.’s, 1999 recommendations) using both static and fluctuating temperatures. We do so by measuring locomotor performance for five species (a total of nine populations) of weevils, belonging to the Ectemnorhini, from sub-Antarctic Marion Island, of which one species inhabits the supralittoral and intertidal zone, and the rest are terrestrial (Chown, 1989). We use this trait because the available evidence suggests that locomotor performance is linked directly to fitness in these weevils. Although like other studies we do not have direct measurements of fitness variation among individuals with different locomotion speeds (see discussions in Angilletta, 2009; Sinclair et al., 2016), we consider locomotion speed a trait linked to fitness in these weevils for the following reasons. First, the entire group is flightless, hence all resource and mate acquisition, which includes positive assortative mating, must be undertaken by terrestrial locomotion (Chown and Scholtz, 1989; Chown, 1990, 1994). Second, predation by indigenous spiders and an indigenous land bird (the black-faced Sheathbill) is notable (weevils make up a significant portion of the latter’s diet in particular) (Burger, 1978; Lee et al., 2012; McClelland et al., 2018), and the only means of escape is through terrestrial locomotion. Third, activity is closely linked to specific weather conditions, suggesting that the ability to emerge and retreat rapidly into protected sites is important (Chown, 1993; Chown et al., 2004).

Based on understanding of the island’s marine and terrestrial climates (Deere et al., 2006; Faulkner et al., 2014) and on

information on the acclimation responses of other arthropod species from these major habitats (Deere and Chown, 2006; Haupt et al., 2017), we predict that the terrestrial weevils should show no plasticity, or perhaps some measure of compensation (Klok and Chown, 2005), whereas the marine weevil should show beneficial acclimation. Moreover, we also examine the slope of the rate–temperature relationship for all of the populations examined, comparing it with the typically expected value resulting in an activation energy approximation of 0.6–0.7 eV (Gillooly et al., 2001) and the somewhat lower value empirically found for body velocity [ $0.46 \pm 0.03$  (s.e.m.)] (Dell et al., 2014). In essence, we examine the expectation that the slope of the rate–temperature relationship might be lower in more polar species, especially those from the southern hemisphere (Addo-Bediako et al., 2002), if temperature compensation is evident, but not if thermodynamic effects predominate (Sørensen et al., 2018).

## MATERIALS AND METHODS

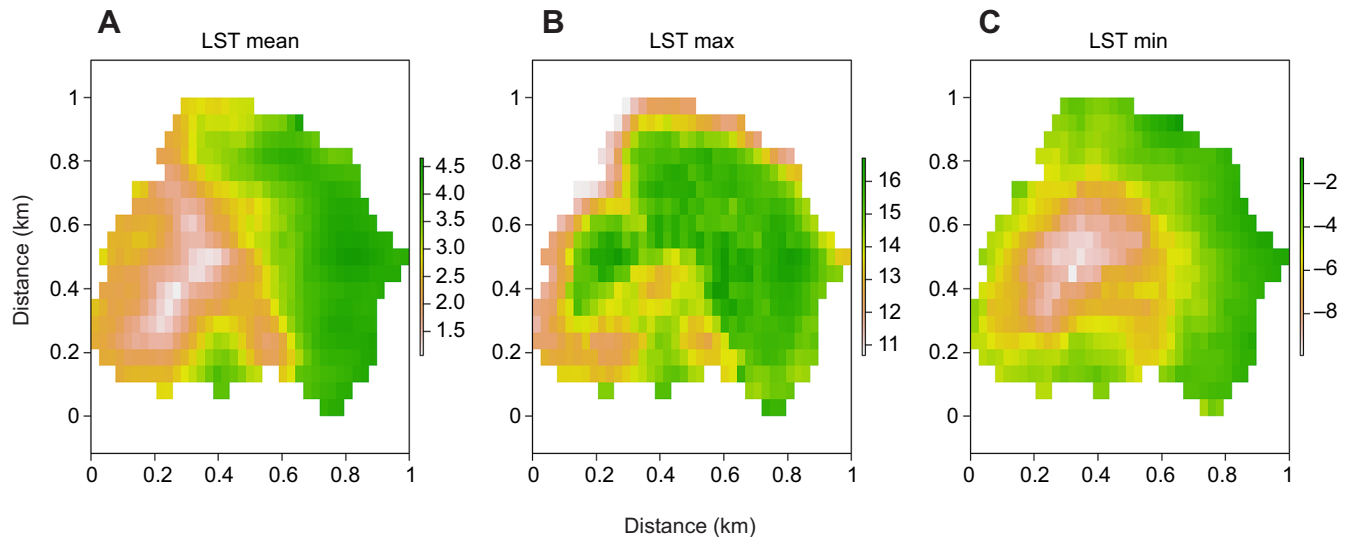
### Study area and species

Sub-Antarctic Marion Island (46°54’S, 37°45’E) is part of the Prince Edward Island group, which lies ~2300 km southeast of Cape Town, South Africa. The island is highly oceanic with a mean annual coastal temperature of ~6.5°C, total annual precipitation of ~1900 mm (as measured at the meteorological station on the north eastern coast), generally high humidity and strong winds. Temperatures vary significantly, but not straightforwardly with elevation (maximum of 1270 m; all altitudes are shown as meters above sea level). Soil temperatures and soil surface temperatures at or below 0°C can be recorded across all elevations with the passage of Southern Ocean fronts making this possible at any time of year, though more common in the winter, while relatively high maximum surface temperatures may also be found at high elevations (Chown and Froneman, 2008; data in Deere et al., 2006; Haupt et al., 2016; Leihy et al., 2018) (Table 1; Fig. 1). The climate has shown substantial change over the past 50 years, including an increase in mean annual temperature of more than 1°C and a decline in precipitation of more than 500 mm per annum (McClelland et al., 2018). The island has two major biomes:

**Table 1. Summary of soil temperatures (°C) recorded across two altitudinal transects on Marion Island, one on the eastern side of the island and one on the western side, for three winter months and three summer months**

| Altitude (m) | Winter (mid-May 2008 to mid-Aug. 2008) (°C) |      |           |           |       |                 |                 | Summer (mid-Nov. 2008 to mid-Feb. 2009) (°C) |      |           |           |       |                 |                 |
|--------------|---|------|-----------|-----------|-------|-----------------|-----------------|--|------|-----------|-----------|-------|-----------------|-----------------|
|              | <i>n</i>                                    | Mean | Abs. min. | Abs. max. | Range | Mean daily min. | Mean daily max. | <i>n</i>                                     | Mean | Abs. min. | Abs. max. | Range | Mean daily min. | Mean daily max. |
| <b>East</b>  |   |      |           |           |       |                 |                 |  |      |           |           |       |                 |                 |
| 10           | 3561  | 4.94 | 1.12      | 9.66      | 8.54  | 4.04            | 5.74            | 2652   | 8.27 | 2.00      | 18.00     | 16.00 | 6.90            | 10.36           |
| 50           | 3559  | 4.93 | 2.09      | 9.64      | 7.55  | 4.39            | 5.28            | 2654   | 7.20 | 5.00      | 18.69     | 13.69 | 6.64            | 8.11            |
| 200          | 3558  | 4.07 | 1.11      | 8.67      | 7.56  | 3.50            | 4.39            | 4750   | 7.89 | 4.13      | 12.67     | 8.54  | 6.94            | 9.01            |
| 400          | 3557  | 3.33 | −0.89     | 16.66     | 17.55 | 2.11            | 4.32            | 4754   | 6.40 | 1.08      | 16.12     | 15.04 | 4.03            | 9.18            |
| 600          | 3557  | 2.80 | 0.57      | 10.63     | 10.06 | 1.97            | 3.38            | 3492   | 5.08 | 0.00      | 21.50     | 21.50 | 3.11            | 8.66            |
| 750          | 3530  | 2.21 | −1.97     | 11.16     | 13.13 | 1.15            | 2.94            | 4751   | 4.44 | 0.05      | 20.62     | 20.57 | 2.54            | 7.02            |
| 850          | 3526  | 1.83 | −0.39     | 10.15     | 10.54 | 0.99            | 2.31            | 3494   | 2.69 | −0.91     | 16.69     | 17.60 | 1.35            | 5.38            |
| 1000         | 3641  | 1.47 | −1.39     | 10.16     | 11.55 | 0.78            | 1.92            | 4745   | 1.96 | −0.97     | 14.22     | 15.19 | 1.09            | 3.04            |
| <b>West</b>  |   |      |           |           |       |                 |                 |  |      |           |           |       |                 |                 |
| 10           | 3656  | 5.42 | 1.60      | 9.16      | 7.56  | 4.68            | 5.81            | 4751   | 8.17 | 3.64      | 14.70     | 11.06 | 7.28            | 9.28            |
| 50           | 3674  | 5.11 | 2.12      | 7.64      | 5.52  | 4.61            | 5.31            | 4751   | 7.09 | 4.17      | 11.71     | 7.54  | 6.44            | 7.86            |
| 200          | 3655  | 4.66 | 1.09      | 9.14      | 8.05  | 3.95            | 5.16            | 4750   | 6.98 | 3.63      | 13.17     | 9.54  | 6.30            | 7.92            |
| 400          | 3651  | 3.23 | 0.10      | 8.59      | 8.49  | 2.36            | 3.64            | 4751   | 5.36 | 1.58      | 14.14     | 12.56 | 4.24            | 6.56            |
| 600          | 3634  | 2.90 | 0.07      | 9.61      | 9.54  | 2.03            | 3.43            | 3923   | 3.25 | 0.00      | 13.50     | 13.50 | 2.43            | 4.73            |
| 750          | 3632  | 2.28 | −0.42     | 9.66      | 10.08 | 1.47            | 2.78            | 2374   | 2.27 | −1.50     | 15.00     | 16.50 | 1.06            | 3.74            |
| 850          | 3629  | 1.58 | −0.91     | 8.19      | 9.10  | 0.78            | 2.07            | 4750   | 2.14 | 0.07      | 10.17     | 10.10 | 1.46            | 2.97            |
| 1000         | 3625  | 1.01 | −2.38     | 8.69      | 11.07 | 0.24            | 1.32            | 3924   | 1.18 | −1.50     | 15.00     | 16.50 | 0.48            | 2.51            |

Abs. min., absolute minimum; Abs. max., absolute maximum.



**Fig. 1. Land surface temperatures recorded over the period 2001–2015 for Marion Island.** Fifteen-year means of the mean (A), maximum (B) and minimum (C) annual land surface temperatures (LST) (annual means calculated from monthly average temperatures) obtained by remote-sensing (MODIS Terra MOD11A2) satellite, including interpolated values for time periods where one or more cells had missing data. The resolution is 1×1 km. The full data set is available in Leihy et al. (2018).

tundra, which predominates in lowland areas, and polar desert, restricted to high elevations (Gremmen and Smith, 2008). Species richness of plants and invertebrates is low and no indigenous terrestrial vertebrates are found, except for the lesser sheathbill (*Chionis minor marionensis* Reichenow 1908) (see Chown and Froneman, 2008 for an overview). House mice (*Mus musculus* Linnaeus 1758) were accidentally introduced in the 1800s.

Six indigenous weevil species (Coleoptera: Curculionidae) in the Ectemnorhini are found on Marion Island (Chown, 1989; Grobler et al., 2011). Three of these are restricted to the coast with the remainder occupying most of the elevational range of the island (Table S1) (see Chown, 1989 for detailed information on diet and habitat distribution). Two of the six species are cryptic [*Bothrometopus parvulus* (Waterhouse 1885) and the recently discovered *Bothrometopus huntleyi* (Grobler et al., 2011)]. *B. huntleyi* is the more common of the two and is considered here. Moreover, some controversy exists about the number of species in the genus *Ectemnorhinus*, with some studies listing two species (e.g. Chown, 1989) and others a single species. Because the species are differentiated by size, we sampled smaller individuals from moss cushions (previously considered *Ectemnorhinus marioni* Jeannel 1940) and larger species from *Azorella selago* Hook. f. (Apiaceae) vascular cushion plants (previously considered *Ectemnorhinus similis* Waterhouse 1885) (Chown, 1990). In keeping with the current nomenclature, we do not use the formal species names here, but continue to differentiate the species by size (see also Treasure and Chown, 2014).

### Collection

Weevils of each species were collected by hand from Trypot Beach and Archway Bay, Tafelberg and Katedraalkrans, during September to November 2008 (Table S1). Individuals were kept at low density in 100 ml plastic jars with moist plaster of Paris substrates and small pieces of their preferred food of algae, bryophytes, lichens or *Azorella selago*, depending on the species (Chown, 1989), and returned to the laboratory within 2 h. In the laboratory, individuals were sorted for acclimation treatments, their identity confirmed and each individual placed into a 65 ml plastic container with moist plaster of Paris and preferred food as above. The animals were kept in climate chambers

(LABCON, Johannesburg, South Africa, accurate to  $\pm 1^\circ\text{C}$ ) at  $0^\circ\text{C}$ ,  $15^\circ\text{C}$  and  $0\text{--}15^\circ\text{C}$  (cycling on a 12 h:12 h basis). The photoperiod in each case was set to match late summer environmental day light cycles (12 h light:12 h dark), and with the light cycle and temperature cycle synchronized for the variable temperatures. These acclimation temperatures were based on microclimate temperatures found across a range of elevations (see Deere and Chown, 2006 for a rationale, and information below). Temperature within the climate chambers was measured with I-button ThermoChron dataloggers (Models DS 1921G and DS 1922H; accurate to  $\pm 0.5^\circ\text{C}$ , Dallas Semiconductors, Dallas, TX, USA). A period of 7 days was selected for acclimation. Previous studies on arthropods on both Marion and elsewhere (e.g. Klok and Chown, 2003; Weldon et al. 2011; Allen et al. 2012) suggest this is sufficient time for phenotypic responses to temperature that could alter performance. Shelf effects in the climate chambers were accounted for by keeping all containers on a single shelf in each case.

Microclimate temperatures have been logged on an hourly basis at  $\sim 100$  m intervals from sea level to 750 m (including the collection sites of the present study) across the eastern slope of Marion Island since 2002 using I-button ThermoChron dataloggers (available via Leihy et al., 2018). Data from 2002 to 2009 were processed in R version 3.5.1 (<https://www.r-project.org/>) to obtain mean daily minimum, maximum, mean and range for the three collection sites.

### Locomotion performance

A temperature-controlled walking stage (following Haupt et al., 2017) was attached to a Grant LTC 12 water bath set to regulate stage temperature. Stage temperature was monitored at each end using Type T 20-gauge thermocouples connected to CHY 507 Digital Thermometers (CHY Firemate Co, Taiwan). A single weevil was introduced to the stage at a time using tweezers. Weevils were given 2 min to equilibrate to the set temperature by placing a small round metal container (radius 2 cm×height 0.5 cm) over them. The path that the individuals then ran in 10 s was traced by hand and measured. The fastest speed from three repetitions was used for each individual (for rationale, see Garland and Losos, 1994; Angilletta et al., 2002) at eight temperatures (in this order: 2, 7, 14, 21, 24, 28, 32 and  $35^\circ\text{C}$ ). Individuals were returned for 1–2 h to their acclimation treatments in

the climate chambers between temperature runs. A total of ten individuals was used for each species×population×acclimation treatment. Because all experiments were conducted during the photophase of the climate chambers, those individuals being drawn from the fluctuating temperature experiment were always drawn from a temperature of 15°C.

A performance curve was then constructed for each individual on the basis of the fastest speed recorded at each temperature (Angilletta, 2006). From these curves, individual data on three key traits (Huey and Stevenson, 1979; Gilchrist, 1996) were estimated from the curves without model fitting: optimum speed ( $\approx$  maximum speed,  $U_{\max}$ ), temperature of the maximum speed (optimum temperature,  $T_{\text{opt}}$ ) and performance breadth (the index of the breadth of the curve,  $T_{\text{br}}$ ) estimated using Gilchrist's (1996) formula:

$$T_{\text{br}} = \sqrt{\sum \left[ \frac{U_i(T_i - T_{\text{opt}})}{U_{\max}} \right]^2}, \quad (1)$$

where  $U_i$  is the speed at  $T_i$ , i.e. the speed at a given test temperature. Mean values were then obtained for each of the traits in each of the species×population×acclimation investigations.

Ordered factorial ANOVAs with orthogonal polynomial contrasts (Huey et al., 1999) were used to test the acclimation hypotheses and implemented in R v2.12.0. In keeping with the strong inference approach, predictions for the form of the linear and quadratic aspects of the curves were made for each of the major hypotheses for each of the traits (updated from Deere and Chown, 2006; see also Dell et al. 2014) (Table 2). The ordered-factor approach requires strict adherence to the assumptions of ANOVA, in particular normally distributed residuals, a balanced design and homogeneity of variance (Huey et al., 1999). Therefore, normality of the data was checked with the Shapiro–Wilks test using the `shapiro.test` function in R. Some instances of non-normality were found, but these were generally not significant after tabulated data were subjected to sequential Bonferroni correction using the `p.adjust` function in R.

To estimate the thermal sensitivity of maximum locomotion speed, the procedure recommended by Pawar et al. (2016) was followed. Mean values at each temperature, from the lowest temperature up to  $T_{\text{opt}}$ , were used for each species×population×acclimation. An ordinary least squares regression of the natural logarithm of locomotion speed against  $1/kT$ , where  $k$  is the Boltzmann constant of  $8.617 \times 10^{-5}$  eV and  $T$  temperature in Kelvin, was used to estimate the slope of the relationship in eV (i.e. as an equivalent of activation energy). The use of this approach assumes a linear relationship, but this may not always be the case. Therefore, a quadratic term was also used to test for a curvilinear relationship. Where this model had a better fit (adjudicated using an ANOVA following Crawley, 2013),

**Table 2. Predictions of the form and sign of the linear and quadratic effects of acclimation temperature on temperature of the maximum speed ( $T_{\text{opt}}$ ), maximum speed at the optimum temperature ( $U_{\max}$ ) and performance breadth ( $T_{\text{br}}$ ) for each of the major acclimation hypotheses (adapted from Deere and Chown, 2006)**

| Hypothesis                                  | $T_{\text{opt}}$                  | $U_{\max}$                        | $T_{\text{br}}$ |
|---|-----------------------------------|-----------------------------------|-----------------|
| Beneficial acclimation (BAH)/compensation   | L <sup>+</sup>                    | n.s.                              | n.s.            |
| Thermodynamic effect/warmer is better (WIB) | L <sup>+</sup>                    | L <sup>+</sup>                    | n.s.            |
| Colder is better (CIB)                      | n.s.                              | L <sup>-</sup>                    | L <sup>-</sup>  |
| Warmer is always better (WIAB)              | n.s.                              | L <sup>+</sup>                    | L <sup>+</sup>  |
| Deleterious acclimation (DAH)               | L <sup>+/-</sup> , Q <sup>-</sup> | L <sup>+/-</sup> , Q <sup>-</sup> |                 |
| No plasticity                               | n.s.                              | n.s.                              | n.s.            |

L<sup>+</sup>, positive linear; L<sup>-</sup>, negative linear; Q<sup>-</sup>, negative quadratic; n.s., not significant.

the correction proposed by Pawar et al. (2016: eqn 10) to the estimation of activation energy was implemented.

## RESULTS

The species showed thermal performance curves typical of those of locomotion with  $T_{\text{opt}}$  ranging between  $22.3 \pm 1.7^\circ\text{C}$  (mean  $\pm$  s.e.m.) and  $31.1 \pm 0.7^\circ\text{C}$  (Table 3, Fig. 2). The acclimation treatment had no significant effect on any of the traits of the supralittoral species *Palirhoeus eatoni* (Waterhouse 1876) (Table 4, Table S2). Responses of  $T_{\text{opt}}$  to acclimation treatment varied among species and populations. Typically (5 out of 8 cases),  $T_{\text{opt}}$  was not affected by acclimation. Where it was, the effects were typically positive (Table 4, Table S2). In the case of  $U_{\max}$ , significant, positive effects of acclimation were found for all species except *P. eatoni*, with individuals acclimated to  $0^\circ\text{C}$  showing much lower values than the other two acclimation treatments (Fig. 2; Table 4, Table S2). By contrast, with the exception of *Bothrometopus randi* Jeannel 1953,  $T_{\text{br}}$  showed little response to acclimation (Table 4, Table S2).

In consequence, overall, the orthogonal polynomial contrast approach revealed support either for no acclimation effect or for the 'warmer is better' (WIB) hypothesis (Table 4). For most species, the traditional WIB hypothesis was supported, specifically for *B. randi*, *B. huntleyi* at 4–6 m and *Bothrometopus elongatus* (Jeannel 1953) at 400 m. For the remaining species, the warmer is always better (WIAB) variant was supported, with the exception of the supralittoral *P. eatoni*, where no plasticity was found.

The responses to fluctuating temperatures typically reflected those of the static 15°C acclimation (Fig. 2). Excluding the fluctuating temperature regime had no effect on the outcomes (acknowledging that a quadratic term could not be included in the models for acclimation effects) (Table S3, Table S4). That is, WIB in the broadest sense (see Deere and Chown, 2006) could not be rejected.

In terms of the rising part of the locomotion rate–temperature relationship, curvilinear relationships were found for just over half of the species×population×acclimation treatments (Table 3). Overall, activation energy ( $E$ ) varied between 0.2 and 0.52 eV, with a similar mean [ $0.40 \pm 0.015$  (s.e.m.)] and median (0.42), indicating little skew to the overall data.

## DISCUSSION

The primary aims of this study were to determine, in a short-term phenotypic plasticity setting, which of the several alternative hypotheses for the likely outcomes of acclimation (Huey and Kingsolver, 1989; Leroi et al., 1994; Deere and Chown, 2006; Frazier et al., 2006) have most support, whether very different responses are found to static and fluctuating temperatures, and whether the species found in this sub-Antarctic location show some form of thermal compensation relative to those found elsewhere.

The outcomes from the acclimation investigations indicate that the WIB hypothesis, whether interpreted in the original (Bennett, 1987; Huey and Kingsolver, 1989) or somewhat modified form (Deere and Chown, 2006), could not be rejected for eight of the nine populations (and five of the six) weevil species investigated here. These outcomes are in keeping with a growing body of work suggesting that such responses may be common over the short term owing to the fitness benefits that come from higher performance rates (Frazier et al., 2006; Angilletta et al., 2010), even though the direct connections to fitness are more difficult to determine than perhaps originally envisaged (Sinclair et al., 2016).

By contrast with arguments suggesting that such short-term responses are unlikely (Phillips et al., 2014), we found evidence for them here, with effect sizes that were non-trivial (Table S2). Thus,

**Table 3. Summary statistics (mean±s.e.m.) for the performance curve traits and activation energy for each weevil species×population×acclimation treatment**

| Species             | Altitude (m) | Acclimation (°C) | $U_{\max}$ (cm s <sup>-1</sup> ) | $T_{\text{opt}}$ (°C) | $T_{\text{br}}$ (°C) | Activation energy* |                  |               |           |
|---------------------|--------------|------------------|----------------------------------|-----------------------|----------------------|--------------------|------------------|---------------|-----------|
|                     |              |                  |                                  |                       |                      | Original $E$       | ANOVA $P$ -value | Corrected $E$ | Final $E$ |
| <i>P. eatoni</i>    | 0            | 0                | 0.55±0.04                        | 25.0±0.9              | 11.7±1.6             | 0.43272            | 0.034            | 0.47539       | 0.48      |
|                     | 0            | 0–15             | 0.60±0.07                        | 27.0±1.4              | 12.9±1.0             | 0.38386            | 0.002            | 0.42378       | 0.42      |
|                     | 0            | 15               | 0.54±0.05                        | 24.3±1.3              | 14.8±0.9             | 0.39712            | 0.026            | 0.435596      | 0.44      |
| <i>B. randi</i>     | 4–6          | 0                | 1.13±0.07                        | 24.0±1.8              | 20.3±1.1             | 0.20185            | 0.076            | N/A           | 0.20      |
|                     | 4–6          | 0–15             | 1.58±0.05                        | 29.1±1.1              | 18.9±1.2             | 0.30359            | 0.305            | N/A           | 0.30      |
|                     | 4–6          | 15               | 1.58±0.10                        | 28.8±1.0              | 16.7±0.5             | 0.39971            | 0.023            | 0.439392      | 0.44      |
| <i>B. huntleyi</i>  | 4–6          | 0                | 0.48±0.03                        | 22.3±1.7              | 18.7±1.0             | 0.39644            | 0.025            | 0.460432      | 0.46      |
|                     | 4–6          | 0–15             | 0.57±0.04                        | 27.2±1.2              | 16.8±0.7             | 0.43638            | 0.155            | N/A           | 0.44      |
|                     | 4–6          | 15               | 0.65±0.05                        | 27.7±1.0              | 16.7±1.2             | 0.39277            | 0.003            | 0.431746      | 0.43      |
|                     | 400          | 0                | 0.36±0.04                        | 28.4±1.1              | 16.4±0.9             | 0.30456            | 0.048            | 0.318562      | 0.32      |
|                     | 400          | 0–15             | 0.58±0.04                        | 28.3±1.3              | 15.2±0.9             | 0.31912            | 0.087            | N/A           | 0.32      |
|                     | 400          | 15               | 0.65±0.07                        | 29.6±1.4              | 16.2±1.2             | 0.45045            | 0.001            | 0.49456       | 0.49      |
|                     | 750          | 0                | 0.55±0.03                        | 27.8±2.0              | 18.1±0.8             | 0.29259            | 0.081            | N/A           | 0.29      |
|                     | 750          | 0–15             | 0.86±0.04                        | 31.1±0.7              | 15.7±0.8             | 0.35483            | 0.16             | N/A           | 0.35      |
|                     | 750          | 15               | 0.74±0.05                        | 26.7±2.3              | 18.0±1.4             | 0.44815            | 0.19             | N/A           | 0.45      |
|                     | 750          | 15               | 0.74±0.05                        | 26.7±2.3              | 18.0±1.4             | 0.44815            | 0.19             | N/A           | 0.45      |
| <i>B. elongatus</i> | 400          | 0                | 0.42±0.04                        | 24.1±1.8              | 17.1±1.2             | 0.2854             | 0.08             | N/A           | 0.29      |
|                     | 400          | 0–15             | 0.53±0.04                        | 28.8±1.0              | 18.6±1.3             | 0.34014            | 0.003            | 0.359887      | 0.36      |
|                     | 400          | 15               | 0.64±0.04                        | 28.5±1.2              | 15.7±0.7             | 0.41288            | 0.013            | 0.449699      | 0.45      |
|                     | 750          | 0                | 0.43±0.04                        | 23.1±2.0              | 18.9±1.8             | 0.35031            | 0.143            | N/A           | 0.35      |
|                     | 750          | 0–15             | 0.61±0.03                        | 25.7±0.8              | 16.4±0.9             | 0.40217            | 0.054            | N/A           | 0.40      |
|                     | 750          | 15               | 0.63±0.03                        | 26.5±1.2              | 15.7±0.7             | 0.45846            | 0.078            | N/A           | 0.46      |
| <i>E. marioni s</i> | 400          | 0                | 0.57±0.02                        | 27.2±0.8              | 14.4±0.8             | 0.42481            | 0.26             | N/A           | 0.42      |
|                     | 400          | 0–15             | 0.77±0.03                        | 30.3±0.8              | 16.4±1.1             | 0.4176             | 0.007            | 0.449442      | 0.45      |
|                     | 400          | 15               | 0.71±0.02                        | 26.5±1.0              | 14.8±0.5             | 0.47532            | 0.01             | 0.516264      | 0.52      |
| <i>E. marioni l</i> | 400          | 0                | 0.72±0.04                        | 28.4±0.7              | 16.2±0.9             | 0.37901            | 0.052            | N/A           | 0.38      |
|                     | 400          | 0–15             | 1.03±0.05                        | 28.1±1.1              | 14.5±0.7             | 0.46168            | 0.035            | 0.486378      | 0.49      |
|                     | 400          | 15               | 0.99±0.04                        | 30.3±1.2              | 16.2±0.7             | 0.38233            | 0.002            | 0.402071      | 0.40      |

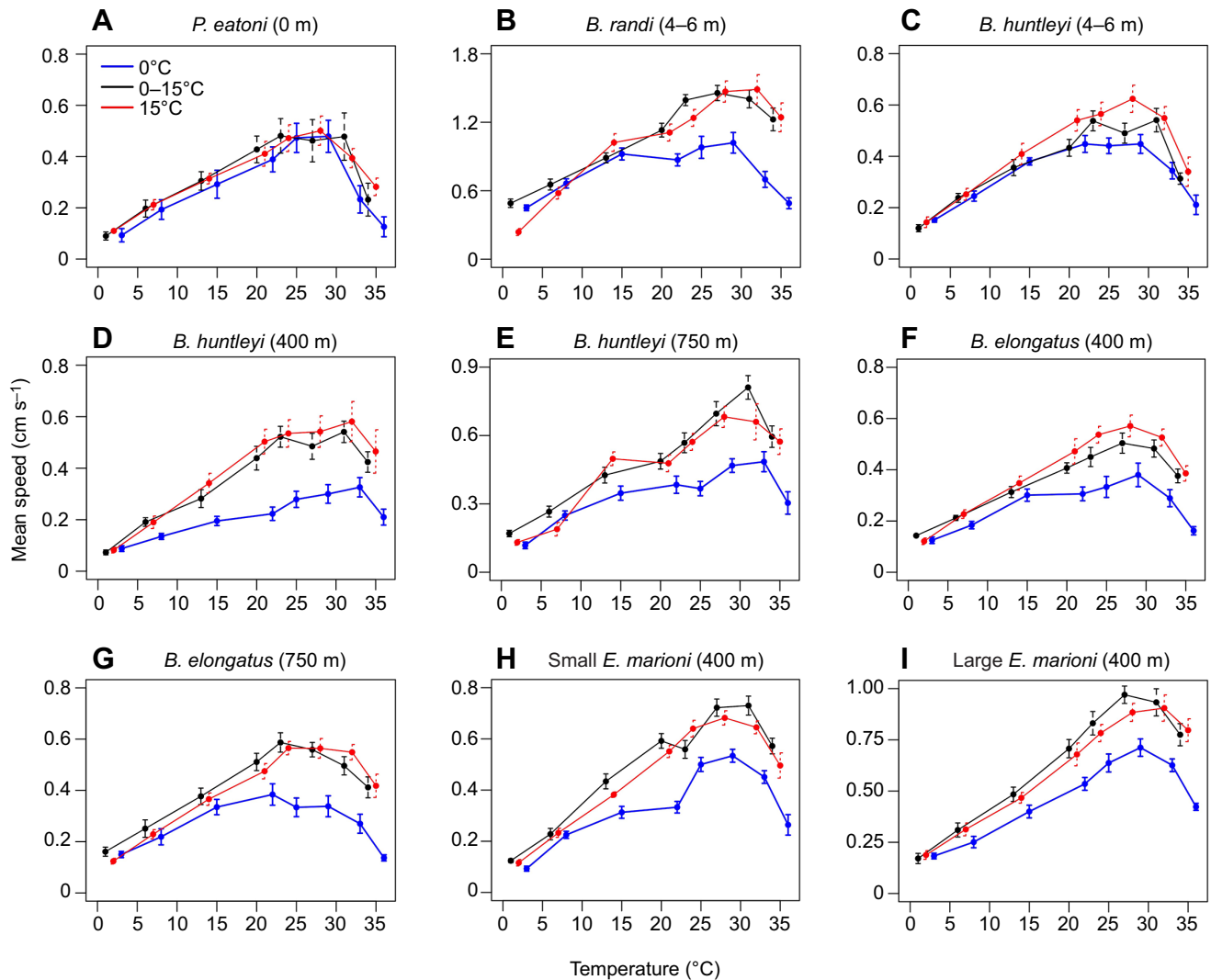
$U_{\max}$ , maximum rate of performance;  $T_{\text{opt}}$ , temperature of the maximum speed;  $T_{\text{br}}$ , performance breadth; l, large; s, small. \*Activation energy ( $E$ ) was estimated from the slope of an ordinary least squares linear regression of  $\ln$  mean locomotion speed against  $1/kT$  (where  $k$  is the Boltzmann constant and  $T$  is temperature in K). The original value shows this relationship, the ANOVA outcome a comparison with a model including a quadratic term ( $P < 0.05$  shows the quadratic model has a better fit), the corrected value the outcome of using Pawar et al.'s (2016; eqn 10) correction, and the final value the activation energy assigned to each species×population×acclimation treatment. Table S5 provides the full set of statistics. N/A, not applicable.

the idea that biochemical changes might not be able to act in concert over the short term to give effect to such a response (Phillips et al., 2014) is perhaps not as plausible as originally considered (see also evidence in Hochachka and Somero, 2002; Kingsolver, 2009). Moreover, strong support for the WIB idea, but some variation around it, as found here over the short term, and among the species, supports the idea that while the thermodynamic effect is ubiquitous, ample scope exists for variation around it. Such an outcome was found for a recent global, interspecific study (Sørensen et al., 2018), although it included very few polar species.

Of particular interest is that the current results provide little support for the hypothesis that in unpredictably variable environments, organisms are less likely to respond to environmental change via acclimation (i.e. show less phenotypic plasticity) than organisms in environments with predictable variation (Tufto, 2000; Chown and Terblanche, 2007; Niehaus et al., 2012). The climate on Marion Island is considered one of the least variable globally, although more importantly this variability in temperature is unpredictable given that within 24 h temperatures can show temporal autocorrelation that is no different from random (compared with continental sites where thermal predictability may endure for weeks) (Deere and Chown, 2006). Thus, many traits do not show acclimation responses, such as supercooling points (SCPs) and locomotion speed in a flightless moth (Klok and Chown, 1998; Haupt et al., 2017), SCPs and lower lethal temperatures (Deere et al., 2006) and locomotion performance traits (Deere and Chown, 2006) in mites, and upper and lower lethal limits in kelp fly larvae and adults (Marais et al., 2009). However,

other traits do show acclimation responses, such as SCPs and critical thermal minima in a different species of flightless moth (Klok and Chown, 1997), critical thermal minima in weevils (Klok and Chown, 2003), SCPs of a psocopteran (Slabber and Chown, 2004), several thermal tolerance traits (Slabber et al., 2007) and desiccation resistance (Chown et al., 2007) in springtails, chill coma recovery in kelp flies (although the form of the response differs between adults and larvae) (Marais and Chown, 2008) and critical thermal minima and maxima in spiders (although responses are decoupled) (Jumbam et al., 2008). More generally, the empirical basis for the relationship between predictability and plasticity in the context of thermal performance curves has yet to be resolved (Sinclair et al., 2016).

One reason for the apparent dichotomy, bearing in mind that different traits have different thermal sensitivities (Woods and Harrison, 2001; Martin and Huey, 2008), could be due to the form of the environmental variation on the island. Environmental variation is not stable, but varies both spatially and temporally. Historical views held that selection on the performance curve is determined by the typical environmental conditions of an area (Huey and Kingsolver, 1989). This view has been challenged, and it has been argued that responses of components of thermal performance curves might rather be determined by rare extreme events (e.g. brief exposure to high temperatures) (Kingsolver and Watt, 1983; Huey and Kingsolver, 1989; Kingsolver and Buckley, 2017). The principal reason for this is that the consequences of experiencing body temperatures above the optimum are much greater than those of experiencing temperatures below the optimum



**Fig. 2. Results of locomotion performance experiments for nine populations of weevils.** (A) *P. eatoni* (0 m), (B) *B. randi* (4–6 m), (C) *B. huntleyi* (4–6 m), (D) *B. huntleyi* (400 m), (E) *B. huntleyi* (750 m), (F) *B. elongatus* (400 m), (G) *B. elongatus* (750 m), (H) *E. marioni*, small (400 m), (I) *E. marioni*, large (400 m) for three acclimation treatments (0°C, 0–15°C and 15°C). The line charts show the performance curves (as mean speed in  $\text{cm s}^{-1}$ ) with s.e.m. indicated by the error bars.

(Kingsolver and Huey, 1998). On Marion Island, higher altitudes experience a wider range of temperatures than lower ones (Table 1) and temperatures of 30.0°C have been recorded on rock faces at high elevations (Boelhouwers et al., 2003; Leihy et al., 2018), a habitat of high altitude weevils. As the ability of organisms to remain active across an appropriate range of environmental temperatures is a significant component of fitness (Kristensen et al., 2007; Loeschke and Hoffmann, 2007), it would therefore be advantageous for the performance curve to incorporate high temperatures experienced in the environment. This way, the weevils avoid being negatively affected by extreme temperatures which could be damaging and potentially lethal. Continued exposure to these upper temperatures is lethal [observations from present study and critical thermal maximum values of the weevils (Klok and Chown, 2003) are close to the optima found in this study]; however, brief exposures (i.e. rare extreme events) could be responsible for selection on the performance curve (Hoffmann and Watson, 1993; Kingsolver and Buckley, 2017). Indeed, we note that  $T_{\text{opt}}$  not only for these species (23–31°C), but also for mites (20–29°C) (Deere and Chown, 2006) and a moth investigated on the island (20–25°C) (Haupt et al.,

2017), are all more in keeping with maximum than with average surface temperatures found on the island (Table 1; Fig. 1).

By contrast to the species and populations showing plasticity, for one species, the hypothesis of no plasticity could not be rejected (Table 4). This species, *P. eatoni*, is restricted to the supralittoral zone where it can be found in clumps of algae, which are often splashed by sea water (Chown, 1989). Conditions keep changing for this species, where they can be splashed by sea water one day, but not the next (see data in Faulkner et al., 2014). Thus, in this highly unpredictably variable environment, this species could be predicted to show no phenotypic plasticity. An alternative explanation for the difference among the species is the potential influence of phylogenetic relatedness, given that phylogenetic effects have been detected for other traits (Chown and Klok, 2003). One reason why this is unlikely to be important, acknowledging that no phylogenetic analysis has been undertaken here owing to the small number of species and absence of phylogeographic data on the populations, is the suggestion that the genus *Palirhoeus* is paraphyletic and resides within *Bothrometopus* (Grobler et al., 2011). Nonetheless, this question deserves broader investigation.

**Table 4. Summarised outcomes of the ordered-factor ANOVAs with orthogonal polynomial contrasts for the effects of acclimation on maximum rate of performance ( $U_{max}$ ), temperature of the maximum speed ( $T_{opt}$ ), and performance breadth ( $T_{br}$ ), for each weevil species population**

| Species                      | Altitude (m) | $T_{opt}$      | $U_{max}$                       | Hypothesis | $T_{br}$       | Hypothesis |
|------------------------------|--------------|----------------|---------------------------------|------------|----------------|------------|
| <i>P. eatoni</i>             | 0            | n.s.           | n.s.                            | n.p.       | n.s.           | n.p.       |
| <i>B. randi</i>              | 4–6          | L <sup>+</sup> | L <sup>+</sup>                  | WIB        | L <sup>-</sup> |            |
| <i>B. huntleyi</i>           | 4–6          | L <sup>+</sup> | L <sup>+</sup>                  | WIB        | n.s.           | n.p.       |
|                              | 400          | n.s.           | L <sup>+</sup>                  | WIAB       | n.s.           | n.p.       |
| <i>B. elongatus</i>          | 750          | n.s.           | L <sup>+</sup> , Q <sup>-</sup> | WIAB       | n.s.           | n.p.       |
|                              | 400          | L <sup>+</sup> | L <sup>+</sup>                  | WIB        | n.s.           | n.p.       |
| <i>E. marioni</i><br>(small) | 750          | n.s.           | L <sup>+</sup> , Q <sup>-</sup> | WIAB       | n.s.           | n.p.       |
|                              | 400          | n.s.           | L <sup>+</sup> , Q <sup>-</sup> | WIAB       | n.s.           | n.p.       |
| <i>E. marioni</i><br>(large) | 400          | n.s.           | L <sup>+</sup> , Q <sup>-</sup> | WIAB       | n.s.           | n.p.       |

L<sup>+</sup>, positive linear; L<sup>-</sup>, negative linear; Q<sup>-</sup>, negative quadratic; n.s., not significant; n.p., no plasticity; BAH, beneficial acclimation hypothesis; WIB, hotter is better. The full analytical outcomes are given in Tables S2, S3 and S4.

Accepting environmental influences, it not only seems to be plasticity that is important, but the form that this plasticity takes, as has been found for other Marion organisms (e.g. Chown et al., 2007). Even within species, it is only the high altitude populations that show the more extreme version of the WIB hypothesis (see discussion in Deere and Chown, 2006) (*B. elongatus* at 750 m and *B. huntleyi* at 400 m and 750 m) while the lower altitude populations of these species do not (*B. elongatus* at 400 m and *B. huntleyi* at 0 m) (Table 4). This pattern of plasticity has also been found in two other traits in this group of weevils: critical thermal minimum and maximum (Klok and Chown, 2003). Together with the findings of differences among species, these outcomes suggest that local differences in microclimate may have an important influence on the form of thermal performance curves and their plasticity, as is now becoming more widely appreciated (e.g. Asbury and Angilletta, 2010; Woods et al., 2015; Kingsolver and Buckley, 2017; see also Suggitt et al., 2018 and Huey 1991).

In terms of the contrast between the static and fluctuating temperatures, the latter tended to mirror the 15°C treatment most closely. Indeed, often the differences were insignificant, including for  $T_{br}$  where they might have been expected to be greater (Huey and Kingsolver, 1993; Huey et al., 1999). Although this suggests that stable and fluctuating temperature treatments show little difference, such a conclusion must be mediated by an important caveat. Our comparison did not include a 10°C treatment (the mean of 0°C and 15°C) and had we done so, a larger effect may have been detected. We note that in another species investigated in much more detail on the same island (caterpillars of the moth *P. marioni*, Haupt et al., 2017), no difference among static and fluctuating temperatures was found either. Nonetheless, the inclusion of a single fluctuating temperature regime, compared with two static regimes with different means does suggest some caution has to be applied to the outcomes. We consider the results robust, however, because of consistent responses documented across the populations (except for the supralittoral species).

Finally, assessment of the slope of the locomotion rate versus temperature relationship revealed two important outcomes. First, just over half of the relationships showed evidence of curvilinearity, so justifying the concerns raised previously about the likely impact thereof on estimations of temperature sensitivity (Pawar et al., 2016). Indeed, this effect was typically in the order of a 10%

difference in the estimate of the slope (as activation energy). Second, the mean estimated activation energy of 0.4 eV is close to, and indeed statistically indistinguishable ( $t=-1.242$ ,  $P=0.217$ ) from the average value found for 70 other investigations of the sensitivity of locomotion rate (0.46±0.03 eV) (Pawar et al., 2016). Nonetheless, it was lower than for other herbivores (0.5±0.07 eV) ( $t=-2.294$ ,  $P=0.028$ ), the category to which these weevils belong (Chown, 1989) suggesting that some form of compensation in the rate–temperature relationship, as previously suggested (Addo-Bediako et al., 2002), may be evident.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: A.M.T., S.L.C.; Methodology: A.M.T., S.L.C.; Formal analysis: A.M.T., S.L.C.; Investigation: A.M.T.; Resources: S.L.C.; Writing - original draft: A.M.T., S.L.C.; Writing - review & editing: A.M.T., S.L.C.; Funding acquisition: S.L.C.

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#### Data availability

All data are publicly available from the Monash Figshare repository (doi:10.26180/5cc247be9efe5).

#### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.195255.supplemental>

#### References

- Addo-Bediako, A., Chown, S. L. and Gaston, K. J. (2002). Metabolic cold adaptation in insects: a large-scale perspective. *Funct. Ecol.* **16**, 332–338. doi:10.1046/j.1365-2435.2002.00634.x
- Allen, J. O. L., Clusella-Trullas, S. and Chown, S. L. (2012). The effects of acclimation and rates of temperature change on critical thermal limits in *Tenebrio molitor* (Tenebrionidae) and *Cyrtobagous salviniae* (Curculionidae). *J. Insect Physiol.* **58**, 669–678.
- Alton, L. A., Condon, C., White, C. R. and Angilletta, M. J., Jr. (2017). Colder environments did not select for a faster metabolism during experimental evolution of *Drosophila melanogaster*. *Evolution* **71**, 145–152. doi:10.1111/evo.13094
- Angilletta, M. J., Jr (2006). Estimating and comparing thermal performance curves. *J. Therm. Biol.* **31**, 541–545. doi:10.1016/j.jtherbio.2006.06.002
- Angilletta, M. J., Jr (2009). *Thermal Adaptation: a Theoretical and Empirical Synthesis*. Oxford: Oxford University Press.
- Angilletta, M. J., Jr, Hill, T. and Robson, M. A. (2002). Is physiological performance optimized by thermoregulatory behaviour?: a case study of the eastern fence lizard, *Sceloporus undulatus*. *J. Therm. Biol.* **27**, 199–204. doi:10.1016/S0306-4565(01)00084-5
- Angilletta, M. J., Jr, Huey, R. B. and Frazier, M. R. (2010). Thermodynamic effects on organismal performance: is hotter better? *Physiol. Biochem. Zool.* **83**, 197–206. doi:10.1086/648567
- Asbury, D. and Angilletta, M. J., Jr (2010). Thermodynamic effects on the evolution of performance curves. *Am. Nat.* **176**, E40–E49. doi:10.1086/653659
- Bennett, A. F. (1987). Evolution of the control of body temperature: Is warmer better? In *Comparative Physiology: Life in Water and on Land* (ed. P. Dejours, L. Bolis, C. R. Taylor and E. R. Weibel), pp. 421–431. Padova: Liviana Press.
- Boelhouwers, J., Holness, S. and Sumner, P. (2003). The maritime Subantarctic: a distinct periglacial environment. *Geomorphology* **52**, 39–55. doi:10.1016/S0169-555X(02)00247-7
- Burger, A. E. (1978). Terrestrial vertebrates: a food resource for birds at Marion Island. *South Afr. J. Antarct. Res.* **8**, 87–99.
- Chown, S. L. (1989). Habitat use and diet as biogeographic indicators for subantarctic Ectemnorhini (Coleoptera: Curculionidae). *Antarct. Sci.* **1**, 23–30. doi:10.1017/S0954102089000052
- Chown, S. L. (1990). Speciation in the sub-Antarctic weevil genus *Dusmoecetes* Jeannel (Coleoptera: Curculionidae). *Syst. Entomol.* **15**, 283–296. doi:10.1111/j.1365-3113.1990.tb00064.x

- Chown, S. L.** (1993). Desiccation resistance in six sub-Antarctic weevils (Coleoptera: Curculionidae): humidity as an abiotic factor influencing assemblage structure. *Funct. Ecol.* **7**, 318-325. doi:10.2307/2390211
- Chown, S. L.** (1994). Historical ecology of sub-Antarctic weevils (Coleoptera: Curculionidae): patterns and processes on isolated islands. *J. Nat. Hist.* **28**, 411-433. doi:10.1080/00222939400770191
- Chown, S. L. and Froneman, P. W.** (eds) (2008). *The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem*. Stellenbosch: Sun Press.
- Chown, S. L. and Klof, C. J.** (2003). Water balance characteristics respond to changes in body size in sub-Antarctic weevils. *Physiol. Biochem. Zool.* **76**, 634-643. doi:10.1086/376919
- Chown, S. L. and Scholtz, C. H.** (1989). Biology and ecology of the *Dusmoecetes* Jeannel (Col. Curculionidae) species complex on Marion Island. *Oecologia* **80**, 93-99. doi:10.1007/BF00789937
- Chown, S. L. and Terblanche, J. S.** (2007). Physiological diversity in insects: ecological and evolutionary contexts. *Adv. Insect Physiol.* **33**, 50-152. doi:10.1016/S0065-2806(06)33002-0
- Chown, S. L., Klof, C. J. and McGeoch, M. A.** (2004). Weather to go out: activity of *Bothrometopus brevis* (Curculionidae) at Heard Island. *Polar Biol.* **27**, 217-221. doi:10.1007/s00300-003-0579-8
- Chown, S. L., Slabber, S., McGeoch, M. A., Janion, C. and Leinaas, H. P.** (2007). Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proc. R. Soc. B* **274**, 2531-2537. doi:10.1098/rspb.2007.0772
- Clarke, A.** (2017). *Principles of Thermal Ecology. Temperature, Energy and Life*. Oxford: Oxford University Press.
- Crawley, M. J.** (2013). *The R Book*. Chichester: Wiley.
- Deere, J. A. and Chown, S. L.** (2006). Testing the beneficial acclimation hypothesis and its alternatives for locomotor performance. *Am. Nat.* **168**, 630-644. doi:10.1086/508026
- Deere, J. A., Sinclair, B. J., Marshall, D. J. and Chown, S. L.** (2006). Phenotypic plasticity of thermal tolerances in five oribatid mite species from sub-Antarctic Marion Island. *J. Insect Physiol.* **52**, 693-700. doi:10.1016/j.jinsphys.2006.03.009
- Dell, A. I., Pawar, S. and Savage, V. M.** (2011). Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl. Acad. Sci. USA* **108**, 10591-10596. doi:10.1073/pnas.1015178108
- Dell, A. I., Pawar, S. and Savage, V. M.** (2014). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *J. Anim. Ecol.* **83**, 70-84. doi:10.1111/1365-2656.12081
- Faulkner, K. T., Clusella-Trullas, S., Peck, L. S. and Chown, S. L.** (2014). Lack of coherence in the warming responses of marine crustaceans. *Funct. Ecol.* **28**, 895-903. doi:10.1111/1365-2435.12219
- Frazier, M. R., Huey, R. B. and Berrigan, D.** (2006). Thermodynamics constrains the evolution of insect population growth rates: "warmer is better". *Am. Nat.* **168**, 512-520. doi:10.1086/506977
- Garland, T., Jr and Losos, J. B.** (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological Morphology: Integrative Organismal Biology* (ed. P. C. Wainwright and S. M. Reilly), pp. 240-302. Chicago: University of Chicago Press.
- Ghalambor, C. K., McKay, J. K., Carroll, S. P. and Reznick, D. N.** (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* **21**, 394-407. doi:10.1111/j.1365-2435.2007.01283.x
- Gilchrist, G. W.** (1996). A quantitative genetic analysis of thermal sensitivity in the locomotor performance curve of *Aphidius ervi*. *Evolution* **50**, 1560-1572. doi:10.1111/j.1558-5646.1996.tb03928.x
- Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. and Charnov, E. L.** (2001). Effects of size and temperature on metabolic rate. *Science* **293**, 2248-2251. doi:10.1126/science.1061967
- Gremmen, N. J. M. and Smith, V. R.** (2008). Terrestrial vegetation and dynamics. In *The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem* (ed. S. L. Chown and P. W. Froneman), pp. 215-244. Stellenbosch: Sun Press.
- Grobler, G. C., Bastos, A. D. S., Treasure, A. M. and Chown, S. L.** (2011). Cryptic species, biogeographic complexity and the evolutionary history of the *Ectemnorhinus* group in the sub-Antarctic, including a description of *Bothrometopus huntleyi*, n. sp. *Antarct. Sci.* **23**, 211-224. doi:10.1017/S0954102011000101
- Haupt, T. M., Sinclair, B. J., Shaw, J. D. and Chown, S. L.** (2016). Further support for thermal ecosystem engineering by wandering albatross. *Antarct. Sci.* **28**, 35-43. doi:10.1017/S0954102015000383
- Haupt, T. M., Sinclair, B. J. and Chown, S. L.** (2017). Thermal preference and performance in a sub-Antarctic caterpillar: A test of the coadaptation hypothesis and its alternatives. *J. Insect Physiol.* **98**, 108-116. doi:10.1016/j.jinsphys.2016.12.006
- Hazel, J. R. and Prosser, C. L.** (1974). Molecular mechanisms of temperature compensation in poikilotherms. *Physiol. Rev.* **54**, 620-677. doi:10.1152/physrev.1974.54.3.620
- Heskel, M. A., O'Sullivan, O. S., Reich, P. B., Tjoelker, M. G., Weerasinghe, L. K., Penillard, A., Egerton, J. J. G., Creek, D., Bloomfield, K. J., Xiang, J. et al.** (2016). Convergence in the temperature response of leaf respiration across biomes and plant functional types. *Proc. Natl. Acad. Sci. USA* **113**, 3832-3837. doi:10.1073/pnas.1520282113
- Hochachka, P. W., Somero, G. N.** (2002). *Biochemical Adaptation. Mechanism and Process in Physiological Evolution*, 2nd edn. Oxford: Oxford University Press.
- Hoffmann, A. A. and Watson, M.** (1993). Geographical variation in the acclimation responses of *Drosophila* to temperature extremes. *Am. Nat.* **142**, S93-S113. doi:10.1086/285525
- Huey, R. B.** (1991). Physiological consequences of habitat selection. *Am. Nat.* **137**, s91-s115. doi:10.1086/285141
- Huey, R. B. and Kingsolver, J. G.** (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* **4**, 131-135. doi:10.1016/0169-5347(89)90211-5
- Huey, R. B. and Kingsolver, J. G.** (1993). Evolution of resistance to high temperature in ectotherms. *Am. Nat.* **142**, S21-S46. doi:10.1086/285521
- Huey, R. B. and Stevenson, R. D.** (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* **19**, 357-366. doi:10.1093/icb/19.1.357
- Huey, R. B., Berrigan, D., Gilchrist, G. W. and Herron, J. C.** (1999). Testing the adaptive significance of acclimation: a strong inference approach. *Am. Zool.* **39**, 323-336. doi:10.1093/icb/39.2.323
- Jumbam, K. R., Terblanche, J. S., Deere, J. A., Somers, M. J. and Chown, S. L.** (2008). Critical thermal limits and their responses to acclimation in two sub-Antarctic spiders: *Myro kerguelensis* and *Prinerigone vagans*. *Polar Biol.* **31**, 215-220. doi:10.1007/s00300-007-0349-0
- Kingsolver, J. G.** (2009). The well-temperated biologist. *Am. Nat.* **174**, 755-768. doi:10.1086/648310
- Kingsolver, J. G. and Buckley, L. B.** (2017). Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate. *Philos. Trans. R. Soc. B* **372**, 20160147. doi:10.1098/rstb.2016.0147
- Kingsolver, J. G. and Huey, R. B.** (1998). Evolutionary analyses of morphological and physiological plasticity in thermally variable environments. *Am. Zool.* **38**, 545-560. doi:10.1093/icb/38.3.545
- Kingsolver, J. G. and Watt, W. B.** (1983). Thermoregulatory strategies in *Colias* butterflies: thermal stress and the limits to adaptation in temporally varying environments. *Am. Nat.* **121**, 32-55. doi:10.1086/284038
- Klof, C. J. and Chown, S. L.** (1997). Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic caterpillar, *Pringleophaga marioni* Viette (Lepidoptera: Tineidae). *J. Insect Physiol.* **43**, 685-694. doi:10.1016/S0022-1910(97)00001-2
- Klof, C. J. and Chown, S. L.** (1998). Interactions between desiccation resistance, host-plant contact and the thermal biology of a leaf-dwelling sub-antarctic caterpillar, *Embyronopsis horticella* (Lepidoptera: Yponomeutidae). *J. Insect Physiol.* **44**, 615-628. doi:10.1016/S0022-1910(98)00052-3
- Klof, C. J. and Chown, S. L.** (2003). Resistance to temperature extremes in sub-Antarctic weevils: interspecific variation, population differentiation and acclimation. *Biol. J. Linn. Soc.* **78**, 401-414. doi:10.1046/j.1095-8312.2003.00154.x
- Klof, C. J. and Chown, S. L.** (2005). Temperature- and body mass-related variation in cyclic gas exchange characteristics and metabolic rate of seven weevil species: broader implications. *J. Insect Physiol.* **51**, 789-801. doi:10.1016/j.jinsphys.2005.03.007
- Knies, J. L., Kingsolver, J. G. and Burch, C. L.** (2009). Hotter is better and broader: thermal sensitivity of fitness in a population of bacteriophages. *Am. Nat.* **173**, 419-430. doi:10.1086/597224
- Kristensen, T. N., Loeschcke, V. and Hoffmann, A. A.** (2007). Can artificially selected phenotypes influence a component of field fitness? Thermal selection and fly performance under thermal extremes. *Proc. R. Soc. B* **274**, 771-778. doi:10.1098/rspb.2006.0247
- Lee, J. E., Somers, M. J. and Chown, S. L.** (2012). Density, body size and sex ratio of an indigenous spider along an altitudinal gradient in the sub-Antarctic. *Antarct. Sci.* **24**, 15-22. doi:10.1017/S0954102011000629
- Leihy, R. I., Duffy, G. A., Nortje, E. and Chown, S. L.** (2018). High resolution temperature data for ecological research and management on the Southern Ocean Islands. *Scientific Data* **5**, 180177. doi:10.1038/sdata.2018.177
- Leroi, A. M., Bennett, A. F. and Lenski, R. E.** (1994). Temperature acclimation and competitive fitness: an experimental test of the beneficial acclimation assumption. *Proc. Natl. Acad. Sci. USA* **91**, 1917-1921. doi:10.1073/pnas.91.5.1917
- Loeschcke, V. and Hoffmann, A. A.** (2007). Consequences of heat hardening on a field fitness component in *Drosophila* depend on environmental temperature. *Am. Nat.* **169**, 175-183. doi:10.1086/510632
- Manenti, T., Loeschcke, V., Moghadam, N. N. and Sorensen, J. G.** (2015). Phenotypic plasticity is not affected by experimental evolution in constant, predictable or unpredictable fluctuating thermal environments. *J. Evol. Biol.* **28**, 2078-2087. doi:10.1111/jeb.12735
- Marais, E. and Chown, S. L.** (2008). Beneficial acclimation and the Bogert effect. *Ecol. Lett.* **11**, 1027-1036. doi:10.1111/j.1461-0248.2008.01213.x
- Marais, E., Terblanche, J. S. and Chown, S. L.** (2009). Life stage-related differences in hardening and acclimation of thermal tolerance traits in the kelp fly, *Paractora dreuxi* (Diptera, Helcomyzidae). *J. Insect Physiol.* **55**, 336-343. doi:10.1016/j.jinsphys.2008.11.016



- Martin, T. L. and Huey, R. B.** (2008). Why "suboptimal" is optimal: Jensen's inequality and ectotherm thermal preferences. *Am. Nat.* **171**, E102-E118. doi:10.1086/527502
- McClelland, G. T. W., Altwegg, R., Van Aarde, R. J., Ferreira, S., Burger, A. E. and Chown, S. L.** (2018). Climate change leads to increasing population density and impacts of a key island invader. *Ecol. Appl.* **28**, 212-224. doi:10.1002/eap.1642
- Morash, A. J., Neufeld, C., MacCormack, T. J. and Currie, S.** (2018). The importance of incorporating natural thermal variation when evaluating physiological performance in wild species. *J. Exp. Biol.* **221**, jeb164673. doi:10.1242/jeb.164673
- Niehaus, A. C., Wilson, R. S., Storm, J. J. and Angilletta, M. J., Jr.** (2012). Fall field crickets did not acclimate to simulated seasonal changes in temperature. *J. Comp. Physiol. B* **182**, 199-207. doi:10.1007/s00360-011-0611-1
- Pawar, S., Dell, A. I. and Savage, V. M.** (2015). From metabolic constraints on individuals to the dynamics of ecosystems. In *Aquatic Functional Biodiversity. An Ecological and Evolutionary Perspective* (ed. A. Belgrano, G. Woodward and U. Jacob), pp. 3-36. Amsterdam: Elsevier.
- Pawar, S., Dell, A. I., Savage, V. M. and Knies, J. L.** (2016). Real versus artificial variation in the thermal sensitivity of biological traits. *Am. Nat.* **187**, E41-E52. doi:10.1086/684590
- Phillips, B. L., Llewelyn, J., Hatcher, A., Macdonald, S. and Moritz, C.** (2014). Do evolutionary constraints on thermal performance manifest at different organizational scales? *J. Evol. Biol.* **27**, 2687-2694. doi:10.1111/jeb.12526
- Reed, T. E., Waples, R. S., Schindler, D. E., Hard, J. J. and Kinnison, M. T.** (2010). Phenotypic plasticity and population viability: the importance of environmental predictability. *Proc. R. Soc. B* **277**, 3391-3400. doi:10.1098/rspb.2010.0771
- Schou, M. F., Mouridsen, M. B., Sørensen, J. G. and Loeschcke, V.** (2017). Linear reaction norms of thermal limits in *Drosophila*: predictable plasticity in cold but not in heat tolerance. *Funct. Ecol.* **31**, 934-945. doi:10.1111/1365-2435.12782
- Sinclair, B. J., Marshall, K. E., Sewell, M. A., Levesque, D. L., Willett, C. S., Slotsbo, S., Dong, Y., Harley, C. D., Marshall, D. J., Helmuth, B. S. et al.** (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecol. Lett.* **19**, 1372-1385. doi:10.1111/ele.12686
- Slabber, S. and Chown, S. L.** (2004). Thermal tolerance and cold hardiness strategy of the sub-Antarctic psocid *Antarctopsocus jeanneli* Badonnel. *Polar Biol.* **28**, 56-61. doi:10.1007/s00300-004-0649-6
- Slabber, S., Worland, M. R., Leinaas, H. P. and Chown, S. L.** (2007). Acclimation effects on thermal tolerances of springtails from sub-Antarctic Marion Island: indigenous and invasive species. *J. Insect Physiol.* **53**, 113-125. doi:10.1016/j.jinsphys.2006.10.010
- Sørensen, J. G., White, C. R., Duffy, G. A. and Chown, S. L.** (2018). A widespread thermodynamic effect, but maintenance of biological rates through space across life's major domains. *Proc. R. Soc. B* **285**, 20181775. doi:10.1098/rspb.2018.1775
- Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie, J. J., Crick, H. Q. P., Duffield, S., Fox, R. et al.** (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nat. Clim. Change* **8**, 713-717. doi:10.1038/s41558-018-0231-9
- Treasure, A. M. and Chown, S. L.** (2014). Antagonistic effects of biological invasion and temperature change on body size of island ectotherms. *Divers. Distrib.* **20**, 202-213. doi:10.1111/ddi.12153
- Tufto, J.** (2000). The evolution of plasticity and nonplastic spatial and temporal adaptations in the presence of imperfect environmental cues. *Am. Nat.* **156**, 121-130. doi:10.1086/303381
- Van Damme, R. and Vanhooydonck, B.** (2001). Origins of interspecific variation in lizard sprint capacity. *Funct. Ecol.* **15**, 186-202. doi:10.1046/j.1365-2435.2001.00513.x
- Weldon, C., Terblanche, J. S. and Chown, S. L.** (2011). Time-course for attainment and reversal of acclimation to constant temperature in two *Ceratitis* species. *J. Thermal Biol.* **36**, 479-485.
- Wilson, R. S. and Franklin, C. E.** (2002). Testing the beneficial acclimation hypothesis. *Trends Ecol. Evol.* **17**, 66-70. doi:10.1016/S0169-5347(01)02384-9
- Woods, H. A. and Harrison, J. F.** (2001). The beneficial acclimation hypothesis versus acclimation of specific traits: physiological change in water-stressed *Manduca sexta* caterpillars. *Physiol. Biochem. Zool.* **74**, 32-44. doi:10.1086/319302
- Woods, H. A., Dillon, M. E. and Pincebourde, S.** (2015). The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *J. Therm. Biol.* **54**, 86-97. doi:10.1016/j.jtherbio.2014.10.002
- Zhu, W., Zhang, H., Li, X., Meng, Q., Shu, R., Wang, M., Zhou, G., Wang, H., Miao, L., Zhang, J. et al.** (2016). Cold adaptation mechanisms in the ghost moth *Hepialus xiaojinensis*: metabolic regulation and thermal compensation. *J. Insect Physiol.* **85**, 76-85. doi:10.1016/j.jinsphys.2015.11.008