Testing the Beneficial Acclimation Hypothesis and Its Alternatives for Locomotor Performance

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ABSTRACT: The beneficial acclimation hypothesis (BAH) is controversial. While physiological work all but assumes that the BAH is true, recent studies have shown that support for the BAH is typically wanting. The latter have been criticized for assessing the benefits of developmental plasticity rather than acclimation. Here we examine the BAH within a strong inference framework for five congeneric species of ameronothroid oribatid mites that occupy marine to terrestrial habitats. We do so by assessing responses of maximum speed, optimum temperature, and performance breadth, measured from -10°C to 35°C , to four treatment temperatures (0° , 5° , 10° , and 15°C). We show that the BAH and its alternatives often make similar empirical predictions. Weak beneficial acclimation is characteristic of one of the more marine species. In the other two upper-shore and marine species, evidence exists for deleterious acclimation and the colder-is-better hypothesis. In the two fully terrestrial species, there is no plasticity. Lack of plasticity is beneficial when cue reliability is low or costs of plasticity are high, and the former seems plausible in terrestrial habitats. However, weak plasticity in the upper-shore/marine species and the absence of plasticity in the terrestrial species might also be a consequence of phylogenetic constraint.

Keywords: performance breadth, phenotypic plasticity, maximum speed, optimal temperature, temperature compensation.

Physiologists have long held the view that phenotypic change by an individual in advance of or in response to a changing environment is beneficial (or adaptive). Indeed, the physiological literature is replete with assertions to this effect, including those regarding seasonal and shorter-term

responses of individuals to changing temperatures, water availability, and resource conditions (reviews in Prosser 1986; Hochachka and Somero 2002; Chown and Nicolson 2004). Nonetheless, this beneficial acclimation hypothesis (BAH; Leroi et al. 1994) has in recent years received vigorous criticism from several perspectives. These include the failure of many studies to include a priori the wide range of alternative hypotheses for the responses of individuals to a changing environment (Huey and Berrigan 1996; Huey et al. 1999) and the generally poor empirical support for the BAH in tests that have examined the hypothesis explicitly (Leroi et al. 1994; Zamudio et al. 1995; Bennett and Lenski 1997; Sibly et al. 1997; Woods 1999; Gibert et al. 2001; Gilchrist and Huey 2001; Woods and Harrison 2001). Thus, much of the recent literature suggests that, despite the seemingly obvious benefits of acclimation (or acclimatization), little support exists for this idea. Many of the alternative hypotheses, such as optimal developmental temperatures (Cohet and David 1977; Huey and Berrigan 1996), now appear more plausible.

Given the wide range of scenarios under which adaptive phenotypic plasticity is likely to evolve (Scheiner 1993; Agrawal 2001; Berrigan and Scheiner 2004), the lack of support for the BAH is counterintuitive, at least from a physiological perspective. Indeed, several authors take issue with many of the explicit tests of the BAH. Echoing earlier distinctions between labile and fixed traits (Scheiner 1993), Wilson and Franklin (2002b) argued that the majority of thermal acclimation tests of the BAH are neither direct nor complete because they assess the adaptive significance of developmental plasticity rather than investigating what comparative physiologists regard as acclimation (or acclimatization; e.g., Spicer and Gaston 1999, pp. 32–38; Willmer et al. 1999, pp. 9–12). That is, many past assessments of phenotypic plasticity have involved alteration of rearing regimes and subsequent assessment of adults rather than assessment of changes of phenotype within a given life stage. According to Wilson and Franklin (2002b), acclimation responses are reversible, facultative changes to the phenotype, while developmental plasticity concerns those phenotypic alterations made as a conse-

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quence of different developmental environments. While the extent to which developmental changes are nonreversible for physiological traits (as opposed to body size in organisms with determinate growth) is not well established (see Fischer et al. 2003; Zeilstra and Fischer 2005 for contrary examples), the distinction remains valid. Woods and Harrison (2002) offered a different perspective, arguing that most explicit tests of the BAH compare animals in optimal environments with those under stressful conditions. Long-term exposure to the latter is likely to impair organismal performance in all other environments, thus compromising some tests of the BAH. In addition, Woods and Harrison (2002) suggested that tests of the BAH should focus on fitness consequences of individual traits and not on the entire suite of characters that constitute fitness. Failure to do so apparently has obscured the relationship between fitness and acclimation.

Both Woods and Harrison (2002) and Wilson and Franklin (2002b) made several suggestions for ways in which tests of the BAH might be improved, especially for investigations of phenotypic plasticity within a given life stage. In essence, they proposed that the rigorous, strong inference approach adopted in analyses of developmental plasticity (e.g., Huey et al. 1999) should be used, that the range of environments investigated should perhaps not include those that impose considerable stress (but see also Hoffmann 1995; Loeschcke and Hoffmann 2002), and that a focus on individual traits is required. Clearly, aspects of the explicit critiques of previous, development-based tests of the BAH are controversial. However, implementation of the above recommendations could go some way toward resolving the surprising mismatch between what comparative physiologists consider to be self-evident (acclimation is beneficial) and what tests of the idea have indicated to date.

Here, we implement these recommendations and assess the plasticity of the temperature sensitivity of locomotor speed in five closely related species of oribatid mite. These species occur over a range of environments from strictly marine to terrestrial at sub-Antarctic Marion Island. Locomotor speed was chosen as a trait because it is a convenient measure of physiological performance in oribatid mites (Marshall and Chown 1995; Marshall et al. 1995) and is directly linked to fitness in a wide variety of organisms (Huey and Stevenson 1979; Gilchrist 1996; Gibert et al. 2001; but see also Angilletta et al. 2002 for exceptions). Mites were chosen because their small size (Mercer et al. 2001) means thermoconformation (Stevenson 1985), making them ideal for examining environmental sensitivity in physiological traits (Gilchrist 1996).

Acclimation effects on the responses of three aspects of thermal performance curves were examined: maximum speed ($u_{\max}$), temperature of the maximum speed ($\approx$ optimum

temperature, T_{opt}), and performance breadth (T_{br} ; Huey and Stevenson 1979; Gilchrist 1996). Although a variety of predictions have been made about the shape and position of performance curves for various acclimation hypotheses, particularly for $u_{\max}$ and T_{opt} and their covariation, we revisited these a priori predictions because, in some instances, it is clear that several quite similar predictions can be made for the different hypotheses. For example, Gilchrist (1996) suggested that the "hotter-is-better" hypothesis predicts a positive relationship between optimum temperature and maximum velocity (see also Carrière and Boivin 1997). However, a positive relationship between these variables, over a range of acclimation temperatures, can arise in two different ways. Thus, our predictions for the position (T_{opt} and $u_{\max}$) and shape (T_{br}) of the performance curves for the various acclimation hypotheses are as follows.

The BAH is defined as follows: "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" (Leroi et al. 1994, p. 1917). Therefore, it typically predicts covariation in T_{opt} and $u_{\max}$ and some overlap of the performance curves (fig. 1; see also Huey et al. 1999). However, the BAH can also be interpreted to mean that there is no relationship between T_{opt} and $u_{\max}$. This is complete temperature compensation (i.e., the maintenance of rate in the face of temperature changes; Clarke 2003), which is clearly a special case of beneficial acclimation (fig. 1). Partial compensation, as is apparently common for many organisms (Clarke 2003), can likewise be interpreted as a special case of beneficial acclimation. "Colder is better" (CIB) predicts that an organism acclimated to a low-temperature environment will always have a performance advantage over another organism held at a warmer environment (fig. 1). "Hotter is better" (HIB) predicts the opposite (fig. 1). In its simplest form, "inverse acclimation" is similar to the inverse compensation that has occasionally been documented in investigations of acclimation effects on metabolic rate (Huey and Berrigan 1996; fig. 1). The deleterious acclimation hypothesis (DAH; Loeschcke and Hoffmann 2002; Wilson and Franklin 2002a; Woods and Harrison 2002) predicts a substantial decline in performance for organisms held at extreme temperatures relative to those held at intermediate temperatures or those that typically do not experience such extremes in the field (fig. 1). To some extent, this hypothesis is similar to the optimal acclimation (originally optimal developmental) temperature hypothesis (Cohet and David 1977; Huey et al. 1999). Finally, the performance curves might not change in response to acclimation, revealing no variation in T_{opt} and $u_{\max}$ and no covariation between them. Such a lack of response to acclimation would indicate no

plasticity (fig. 1). An absence of phenotypic plasticity, which in some circumstances can be considered adaptive (Tufto 2000), has been predicted in models of the response of traits to environments where environmental cues are misleading or costs of plasticity are high (Moran 1992; Van Tienderen 1997; Kingsolver and Huey 1998; Tufto 2000; Sultan and Spencer 2002; Berrigan and Scheiner 2004).

When assessing the alternative acclimation hypotheses on the basis of performance curves, it is not only the values of T_{opt} and u_{max} that are significant for each acclimation treatment but also their covariation, or the positions of the curves relative to each other (see also Gilchrist and Huey 2004). Indeed, the hypotheses typically discussed as exclusive alternatives represent points along a continuum of variation in the position of performance curves (see also Huey et al. 1999; fig. 1). Thus, the performance curves that are the outcome of a combination of CIB and compensation take a form very different from those that are the outcome of CIB and inverse acclimation or of HIB and inverse acclimation (fig. 1). Nonetheless, it is clear that the positions of the curves can take a wide variety of forms and not just those illustrated in figure 1.

How acclimation-related changes in T_{br} relate to this variation and could potentially be used to assess the various acclimation hypotheses is more difficult to determine. The T_{br} could, under some circumstances, be used to distinguish the DAH from the optimal acclimation temperature hypothesis and might also be expected to change most significantly in organisms exposed to fluctuating, as opposed to constant, temperatures (Huey and Kingsolver 1993; Kingsolver and Huey 1998; Huey et al. 1999). However, if an organism has a consistent advantage after acclimation to either a low temperature (i.e., CIB) or a high temperature (HIB), it might be expected under certain circumstances that a consistent trend in T_{br} would be found from high to low acclimation temperature, or vice versa, respectively. However, such effects are likely to be dependent on the extent and nature of the trade-off between T_{br} and u_{max} (Huey and Hertz 1984; Gilchrist 1996; Angilletta et al. 2002).

Methods

Study Site and Animals

Specimens were collected from April 2002 to April 2003 on the east coast of sub-Antarctic Marion Island (46°54'S, 37°45'E), a small, isolated volcanic island in the Southern Ocean. The island has a low mean annual air temperature (ca. 5.7°C), high humidity (83%), and an evenly distributed annual precipitation of ca. 1,900 mm (Smith 2002). It is typically cloudy, with strong, predominantly westerly winds that reach gale force throughout much of the year (Schulze 1971). Although climatic (especially temperature) variation is lower than at many other sites, this variation is unpredictable on a variety of temporal scales, especially at low altitudes, because of the regular passage of fronts over the island (Schulze 1971; Smith 2002).

Five ameronothroid mite species were studied. *Halozetes marinus* and *Halozetes marionensis* are found in the littoral zones along the rocky shores, and the former species is strictly marine. *Halozetes belgicae* is found in rocky supralittoral zones, while *Halozetes fulvus* and *Podacarus auberti* are terrestrial and occupy a wide range of habitats (Mercer et al. 2000; Barendse et al. 2002). For all species (except *H. marionensis*, which was collected in situ from the rocky substrate and transferred into moistened, plaster of paris-lined vials), the vegetation on which the mite species occurred was collected and brought back to the laboratory, and animals were extracted by hand. Animals were randomly assigned to five groups of 20–40 individuals each. The performance of individuals in one group was assessed immediately (within 24 h, labeled “field-fresh”). The reason we used this group was to determine whether acclimation might have been generally stressful. In this case, significant differences between performance curves of individuals from one or more acclimation treatments and those of individuals taken directly from the field might be expected. Each of the remaining groups was placed in a large vial containing a moistened plaster of paris substrate, provided with food and water (typically lichens and algae), assigned to one of four acclimation temperatures (0°, 5°, 10°, and 15°C, $\pm 1^\circ\text{C}$ in each case), and held there for 7 days (for rationale, see Hoffmann and Watson 1993; Klok and Chown 2003; Ter-

Figure 1: Predictions from each of the major hypotheses for the response of individual performance curves to acclimation. In each case, four acclimation temperatures from low to high are indicated (as an example, we use 0°–15°C in 5° increments: 0°C [blue], 5°C [green], 10°C [purple], and 15°C [red]), and in one case the expectation for field-fresh (FF) individuals is also shown. BAH = beneficial acclimation hypothesis, COMP/BAH = complete temperature compensation (an instance of BAH), CIB = colder is better, HIB = hotter is better, IAH = inverse acclimation hypothesis, DAH = deleterious acclimation hypothesis, NP = no plasticity, CIB with COMP = combination of colder is better and compensation, CIB with IAH = combination of colder is better and inverse acclimation, and HIB with IAH = combination of hotter is better and inverse acclimation. Several of these examples represent extremes of the variation that could be found in the relative positions of the performance curves for each of the hypotheses, although, clearly, much variation could potentially be found in the positions of the curves.

blanche et al. 2006). The acclimation temperatures were based on terrestrial microclimate temperatures, which vary from a mean of approximately 0°C in winter to 12°C in summer, depending on the habitat (Chown and Crafford 1992; Blake 1996; table 1). The 15°C acclimation treatment was high, though not outside terrestrial microhabitat temperatures measured at the island (Chown and Crafford 1992; table 1). Day length was set to 14L : 10D for the 10° and 15°C acclimation treatments and to 9L : 15D for the 0° and 5°C acclimation treatments. Because the mites are small, the tubes within which they were held occupied little space on a single shelf, and therefore shelf effects in the climate chambers are unlikely to have had any influence on the temperature at which the individuals were held. Moreover, the same small areas in the climate chambers were used for each species.

Locomotion Trials

Individual mites were observed on a temperature-controlled stage using a stereo microscope ($\times 16$ magnification). To induce walking, mites were exposed to a cold light source, and the frequency of movements of the front right leg was counted for each mite over a range of temperatures (Marshall et al. 1995). Typically, eight to 10 temperatures at 5°C intervals (-10° to 35°C) were used. Mites were assessed in a pseudorandom design that used non-stressful (0° – 30°C) temperatures first and then concluded with the lowest and highest temperatures. In the latter case, mites were returned to their acclimation temperature for 1–2 h while the experimental setup equilibrated to the final, highest temperature. The species all have lower lethal temperatures less than -10° to -6°C and upper lethal temperatures greater than 35°C (Deere et al. 2006), which resulted in the extreme assessment temperatures being varied slightly between species. The lower assessment temperatures seemed to have no stressful long-term effects on individuals investigated in pilot trials. The number of leg

strokes was counted over a 20-s period but only after 20 s had elapsed once the mite had started walking. Counts were abandoned if mites faltered. To determine whether the data were representative of the capabilities of each animal, the number of leg strokes per 20 s was counted three times for each assessment temperature to provide a short-term assessment of the reliability of the counts. A sample size of 20 animals was used per acclimation temperature, but the same individuals were used at each temperature for a given species and acclimation trial. These locomotion data were used to construct performance curves (Gilchrist 1996; fig. 2), of which the key traits are T_{opt} , the thermal condition that maximizes performance, or the optimum temperature; u_{max} , the maximum rate of performance, or maximum speed (although we note that stroke interval and maximum speed are not identical unless it is presumed that stride length does not vary with stride frequency); and T_{br} , the index of the breadth of the curve, or performance breadth. Values of T_{opt} and u_{max} were obtained from the experimental data and were used to calculate T_{br} using Gilchrist's (1996) formula:

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

where T_{opt} is the temperature at which an individual had the most leg strokes per 20 s, u_{max} is the number of leg strokes per 20 s at T_{opt} , and u_i is number of leg strokes per 20 s at temperature T_i . Because each individual was assessed over the full range of temperatures, three performance curves were constructed for each individual.

The traits investigated here are in many ways similar to those that have been developed for reaction norms (David et al. 1997). However, unlike some authors, we do not consider the acute effects of temperature on performance to be similar to the effects of acclimation but rather prefer to draw a distinction between the two (see also Huey and

Table 1: Sea surface (SS) temperature and microhabitat temperature ($^\circ\text{C}$) of two terrestrial sites (0 and 200 m above sea level) for 2 years at Marion Island

Site, year	Mean	Abs min	Abs max	Mean min	Mean max	Range
SS:						
2002	5.4	3.7	8.5	4.9	6.2	4.8
2003	5.4	3.7	8	4.7	6.0	4.3
0 m:						
2002	5.3	.5	22.5	3.8	7.1	22.0
2003	7.0	1	22	5.1	8.6	21.0
200 m:						
2002	4.4	-5.0	18.5	2.2	7.0	23.5
2003	5.2	-6.0	19	3.5	6.6	25

Note: Mean, mean minimum (Mean min), mean maximum (Mean max), absolute minimum (Abs min), and absolute maximum (Abs max) temperatures and the temperature range are shown.

Figure 2: Performance curves for four experimental acclimation groups—0°C (black squares), 5°C (green triangles), 10°C (purple circles), and 15°C (red squares)—and for field-fresh individuals (black diamonds) for *Halozetes marinus*, *Halozetes marionensis*, *Halozetes belgicae*, *Halozetes fulvus*, and *Podacarus auberti*.

Berrigan 1996). In other words, we are interested in the effects of acclimation on the key traits that can be derived from the performance curve. Thus, we do not call the performance curve a reaction norm (as Angilletta et al. [2003] do).

Data Analysis

On the basis of the repeated counts, three performance curves were constructed for each individual at each acclimation temperature, and repeatability of each of the key traits derived from the performance curve was assessed using the intraclass correlation coefficient (Lessells and Boag 1987; Falconer and Mackay 1996). The effects of the acclimation treatments on each of the traits (T_{opt} , u_{max} , and T_{br}) in each of the species were assessed initially by plotting the performance curves and by formally examining the effects of the acclimation temperatures on the traits with a generalized linear model (GLZ). For optimum temperature and performance breadth, a GLZ assuming a normal distribution of errors with a log link function was used (these models gave the best fit based on deviance/df), while maximum speed (which represents count data) was analyzed using a GLZ assuming a Poisson distribution of errors with a log link function.

A formal test of the alternative hypotheses was undertaken using ordered-factor ANOVAs with single-degree-of-freedom orthogonal polynomial contrasts, as recommended by Huey et al. (1999) and implemented in R (<http://www.r-project.org/>). In keeping with the strong inference approach and the necessity of examining covariation of T_{opt} and u_{max} , predictions were made for the significance and sign of the linear and quadratic terms for T_{opt} and u_{max} for each of the alternative hypotheses (fig. 1; table 2). In many instances, no predictions were made by the alternative hypotheses for quadratic contrasts and certainly none for cubic contrasts, and in these instances contrasts were not given further consideration. In the case of the deleterious acclimation hypothesis, animals might have been exposed to stress-inducing temperatures at either or both ends of the spectrum of acclimation treatments, meaning that the linear term could be either negative or positive. For T_{br} , predictions of the sign and significance of the contrasts were more difficult to make, except in the case of no plasticity (see discussion above). The ordered-factor approach requires strict adherence to the assumptions of ANOVA, a balanced design, normally distributed residuals, and homogeneity of variances within cells (Huey et al. 1999). These conditions were typically met. Furthermore, an initial analysis (data not shown) indicated pervasive interactions between the species and acclimation treatment contrasts. Therefore, each species was analyzed separately.

Table 2: Predictions of the significance and sign of the linear and quadratic effects of acclimation temperature on optimum temperature (T_{opt}), maximum rate of performance (u_{max}), and performance breadth (T_{br}) for each of the alternative acclimation hypotheses and combinations thereof illustrated in figure 1

Hypothesis	T_{opt}	u_{max}	T_{br}
Beneficial acclimation	L ⁺	L ⁺	
Compensation/beneficial acclimation	L ⁺	NS	
Colder is better	NS	L ⁻	L ⁻
Hotter is better	NS	L ⁺	L ⁺
Inverse acclimation	L ⁻	NS	
Deleterious acclimation	L ^{+/-} , Q ⁻	L ^{+/-} , Q ⁻	
No plasticity	NS	NS	NS
Colder is better with compensation	L ⁺	L ⁻	
Colder is better with inverse acclimation	L ⁻	L ⁻	
Hotter is better with inverse acclimation	L ⁻	L ⁺	

Note: L⁺ = positive linear, L⁻ = negative linear, Q⁻ = negative quadratic, and NS = not significant.

Results

Repeatability was generally higher for u_{max} than for T_{opt} and T_{br} in all of the species across all of the acclimation temperatures, and low repeatability values were occasionally found for T_{br} and T_{opt} , especially in those individuals acclimated to 0° and 5°C (app. A in the online edition of the *American Naturalist*). Nonetheless, performance was generally consistent within individuals, and the counts provided a reasonably accurate estimate of that performance. The statistical analyses, as described above, were therefore based on the mean values of the three counts for each individual at each assessment temperature.

In the case of maximum speed (u_{max}) and performance breadth (T_{br}), no consistent differences were generally associated with acclimation temperature for any of the species (fig. 2; table 3). Moreover, the values of the traits in the acclimation groups did not differ either significantly or substantially from the values obtained from the field-fresh group of individuals. Rather, trait values appeared to be similar across the acclimation temperatures. The only exception was u_{max} in *Halozetes marinus*, which tended to decline with temperature (but only at 15°C; fig. 2). Optimum temperature showed very much the same pattern of little variation associated with acclimation temperature and no substantial or consistent differences from field-fresh values. The sole exception was found in *H. marinus*, where T_{opt} declined significantly at the highest acclimation temperature (fig. 2).

The ordered-factor approach revealed support for three

Table 3: Mean $\pm$ SE for maximum speed ($u_{\max}$), optimum temperature (T_{opt}), and performance breadth (T_{br}) for each of the species of *Halozetes* and for *Podacarus auberti*

Trait, species	Field-fresh	0°C	5°C	10°C	15°C	χ^2 (df = 4)
$u_{\max}$ (leg strokes/20 s):						
<i>H. marinus</i>	14.9 $\pm$.5 ^A	16.6 $\pm$.6 ^A	14.1 $\pm$.8 ^A	16.1 $\pm$.7 ^A	9.3 $\pm$.6 ^B	44.6***
<i>H. marionensis</i>	14.7 $\pm$.5 ^{AB}	16.1 $\pm$.7 ^A	15.6 $\pm$.5 ^A	12.6 $\pm$.5 ^B	16.8 $\pm$.6 ^A	13.6**
<i>H. belgicae</i>	24.4 $\pm$.7 ^A	23.7 $\pm$ 1.2 ^{AB}	21.4 $\pm$ 1.3 ^{ABC}	17.4 $\pm$ 1.0 ^C	19.9 $\pm$ 1.3 ^{BC}	29.3***
<i>H. fulvus</i>	16.8 $\pm$.5	16.2 $\pm$.4	15.0 $\pm$.4	14.9 $\pm$.3	15.1 $\pm$.5	3.7 NS
<i>P. auberti</i>	16.0 $\pm$.4	17.1 $\pm$.8	19.1 $\pm$.6	16.2 $\pm$.4	16.2 $\pm$.6	7.8 NS
T_{opt} (°C):						
<i>H. marinus</i>	25.0 $\pm$.5 ^A	25.0 $\pm$.01 ^A	24.7 $\pm$.5 ^A	24.7 $\pm$.3 ^A	21.1 $\pm$.5 ^B	61.6***
<i>H. marionensis</i>	24.0 $\pm$.5 ^A	21.0 $\pm$.5 ^B	21.8 $\pm$.6 ^B	21.8 $\pm$.6 ^B	24.5 $\pm$.7 ^A	33.8***
<i>H. belgicae</i>	23.3 $\pm$.6 ^{AB}	21.6 $\pm$.6 ^{AC}	25.00 $\pm$.40 ^B	20.8 $\pm$.9 ^{AC}	20.8 $\pm$.6 ^C	38.5***
<i>H. fulvus</i>	29.0 $\pm$.5 ^A	26.8 $\pm$.8 ^{AB}	25.6 $\pm$.4 ^B	24.5 $\pm$.8 ^B	28.3 $\pm$.8 ^A	32.1***
<i>P. auberti</i>	24.0 $\pm$ 1.1 ^{AB}	26.5 $\pm$ 1.1 ^{AC}	25.3 $\pm$.3 ^A	22.9 $\pm$.6 ^B	27.8 $\pm$.7 ^C	24.0***
T_{br} (°C):						
<i>H. marinus</i>	17.0 $\pm$.5 ^A	13.6 $\pm$.4 ^B	13.0 $\pm$.6 ^B	13.0 $\pm$.3 ^B	11.2 $\pm$.8 ^B	61.2***
<i>H. marionensis</i>	14.5 $\pm$.5 ^A	11.4 $\pm$.5 ^{BC}	13.6 $\pm$.6 ^{AB}	9.9 $\pm$.4 ^C	15.0 $\pm$.7 ^A	56.7***
<i>H. belgicae</i>	13.5 $\pm$.5	12.9 $\pm$.5	12.2 $\pm$.4	11.7 $\pm$.9	13.0 $\pm$.5	6.2 NS
<i>H. fulvus</i>	17.3 $\pm$.5 ^A	15.2 $\pm$ 1.0 ^{AB}	14.9 $\pm$.7 ^{AB}	14.3 $\pm$.8 ^B	18.6 $\pm$ 1.1 ^A	18.9***
<i>P. auberti</i>	15.2 $\pm$.8 ^{AB}	18.5 $\pm$.9 ^C	14.5 $\pm$.6 ^{AB}	12.7 $\pm$.6 ^B	16.5 $\pm$.5 ^{AC}	42.1***

Note: The χ^2 values are the outcome of generalized linear models (see text for details), and different letters indicate significant differences between treatments based on 95% confidence limits. NS = not significant. Using García's (2004) false-discovery-rate criterion resulted in no changes to the significance values.

** $P < .01$.

*** $P < .001$.

of the hypotheses. In the terrestrial species, *Halozetes fulvus* and *Podacarus auberti*, the hypothesis of no plasticity could not be rejected (table 4). In *H. marinus*, the deleterious acclimation hypothesis was supported, owing to a decline in performance at an acclimation temperature of 15°C, as might be expected for a fully marine species living at constantly low temperatures. By contrast, in *Halozetes marionensis*, evidence for compensation and beneficial acclimation was found, whereas in *Halozetes belgicae*, the colder-is-better hypothesis was supported, though with some indication of inverse acclimation. The inverse acclimation effect was almost certainly due to the high value of T_{opt} after the 5°C acclimation, an occurrence not repeated at 0°C (table 3).

Discussion

Explicit consideration of the predictions of each of the acclimation hypotheses has demonstrated that performance curves can show a wide range of responses to acclimation (see also Huey et al. 1999). Moreover, graphical representation of the alternative hypotheses has also shown that compensation, or conservation of rate in the face of a temperature change (Hazel and Prosser 1974; Chown and Gaston 1999; Clarke 2003), is a special instance of the beneficial acclimation hypothesis. While such compensation has regularly been assumed to be adaptive (see dis-

cussion in Huey and Berrigan 1996; Chown and Gaston 1999; Clarke 2003), appreciation of the fact that compensation can readily be included under the broad rubric of beneficial acclimation is less common. Recognition thereof could go some way toward resolving the theoretical and empirical controversy regarding whole-organismal metabolic rate compensation that has been a feature of the physiological literature for some time (Clarke 1993, 2003; Chown and Gaston 1999; Addo-Bediako et al. 2002; Hochachka and Somero 2002; Chown et al. 2003; Hodgkinson 2003; Guderley 2004; see also Huey and Berrigan 1996).

In this study, a weak effect of beneficial acclimation and, in this case, compensation was found in one of the more marine species, *Halozetes marionensis*. Such an outcome is in keeping with the expectation from the majority of the literature on acclimation within life stages (Prosser 1986; Hochachka and Somero 2002; Wilson and Franklin 2002b; Woods and Harrison 2002) and with theoretical predictions regarding adaptive phenotypic plasticity (Van Tienderen 1997; Berrigan and Scheiner 2004). Likewise, compensation can be explained by the predictably low temperatures of the lower-shore/marine habitats occupied by this species (Mercer et al. 2000; table 1) and the likely absence of opportunities to make use of frequent periods of high temperature when activity can be maximized for mate finding, feeding, reproduction, and growth (Crafford et al. 1986; Convey 1994, 1996; Gotthard and Nylin 1995;

Table 4: Summarized outcomes of the ordered-factor ANOVA with single-degree-of-freedom orthogonal polynomial contrasts for the effects of acclimation on optimum temperature (T_{opt}), maximum rate of performance (u_{max}), and performance breadth (T_{br})

Species	T_{opt}	u_{max}	Hypothesis	T_{br}	Hypothesis for T_{br}
<i>Halozetes marinus</i>	L^-, Q^-	L^-, Q^-	DAH	L^-, Q^-	
<i>Halozetes marionensis</i>	L^+	NS	COMP/BAH	L^+, Q^+	
<i>Halozetes belgicae</i>	L^-	L^-	CIB with IAH	NS	NP
<i>Halozetes fulvus</i>	NS	NS	NP	NS	NP
<i>Podacarus auberti</i>	NS	NS	NP	L^-, Q^+	

Note: The hypothesis supported in the case of T_{br} is also indicated. L^+ = positive linear, L^- = negative linear, Q^+ = positive quadratic, Q^- = negative quadratic, NS = not significant. The combined effects on T_{opt} and u_{max} indicate the acclimation hypothesis that is supported. DAH = deleterious acclimation, COMP/BAH = compensation and beneficial acclimation, NP = no plasticity, CIB with IAH = colder is better and inverse acclimation. The analytical outcomes are given in full in appendix B in the online edition of the *American Naturalist*.

Chown 1997; Gotthard et al. 2000; Addo-Bediako et al. 2002). However, what is noteworthy is that these expectations were realized in a single species only. The other species departed significantly from them.

That the most marine of the species, *Halozetes marinus*, showed evidence of deleterious acclimation is also not unexpected, given the very narrow range of temperatures that this species is likely to encounter ($2^\circ\text{--}8^\circ\text{C}$; see Mélice et al. 2003; table 1). Indeed, it was clear that the 15°C acclimation temperature led to a substantial decline in the trait values relative to those found at the other acclimation temperatures, including the field-fresh treatment. Thus, the highest-temperature acclimation appeared to be deleterious, depressing overall performance, as has been implied for long-term acclimation treatments of other species (Woods and Harrison 2002). Unfortunately, independent assessments of stress for each treatment, such as the extent of upregulation of stress proteins (Feder and Hofmann 1999) or other thermal protectants (e.g., sorbitol; Salvucci 2000), were not undertaken, and therefore it could not be determined with certainty that the higher temperatures really were detrimental.

If the 15°C acclimation temperature is ignored, it appears that performance is generally better at lower temperatures in *H. marinus*, providing evidence in favor of the colder-is-better hypothesis (table 3). Support for this hypothesis was also found in the upper-shore species, *Halozetes belgicae*. Therefore, in the three species typical of the upper shoreline or marine habitats at Marion Island (see Mercer et al. 2000), some form of acclimation response was the norm. Moreover, these responses make sense from the perspective of the predictable, constantly low temperatures of the marine zone (although we acknowledge that *H. belgicae* is also common in upper-shore areas). Reasonably strong acclimation responses are expected in predictably varying environments (Scheiner 1993; Tufto 2000; Hazel et al. 2004), although stenothermal habitats are likely to reduce the scope of these responses

(Pörtner et al. 2000; Ghalambor et al. 2006). Here, significant though reasonably weak acclimation responses were found, in keeping with both theoretical predictions and empirical findings from elsewhere.

By contrast, in the terrestrial species, *Halozetes fulvus* and *Podacarus auberti*, no evidence was found for the BAH or for compensation, nor was evidence found to support the CIB or HIB hypotheses. Rather, in each of these species, the performance curves were similar irrespective of acclimation temperature. Therefore, the only plausible alternative is the hypothesis of no phenotypic plasticity. Whether such an absence of phenotypic plasticity can be considered adaptive is not clear. Several theoretical investigations have demonstrated that if environmental cues are misleading, plasticity will not be favored (Lively 1986; Moran 1992; Kingsolver and Huey 1998; de Jong 1999; Sultan and Spencer 2002; Berrigan and Scheiner 2004), and Tufto (2000) demonstrated that if unreliable cues are associated with environmental variability in general, they are apt to limit the evolution of plasticity. Arguably, environmental unpredictability, rather than variability per se, is prone to making cues even more misleading (Levins 1968; Kingsolver and Huey 1998). It is in temporally varying circumstances such as these that bias of the phenotype toward some global optimum would be most beneficial (Tufto 2000).

Terrestrial temperatures at Marion Island certainly span a smaller range than those at many other sites, and, in this sense, the climate of the island is considered one of the least variable globally (Gremmen 1981). However, what is perhaps of more consequence is that the variability in temperature is quite unpredictable. Low and high temperatures can be encountered at virtually any time of the year, and cold snaps in summer and relatively warm days in winter are common (Schulze 1971). A comparison of temporal autocorrelation of microclimate temperatures at sea level for Marion Island and for Lambert's Bay, on the southwest coast of South Africa, readily illustrates the

Figure 3: Autocorrelation plots for hourly microclimate temperatures recorded on Marion Island during August 2002, November 2002, and June 2003. The dashed lines on each figure represent the 95% confidence intervals, while the values reported to the right of the lags on the Y-axis are the autocorrelation coefficients and their standard errors.

Figure 4: Autocorrelation plots for hourly microclimate temperatures recorded at Lambert's Bay, South Africa, during August 2002, November 2002, and June 2003. The dashed lines on each figure represent the 95% confidence intervals, while the values reported to the right of the lags on the Y-axis are the autocorrelation coefficients and their standard errors.

point. At both sites, microhabitat temperatures just below the soil surface in unshaded sites have been recorded hourly since June 2002 (and recordings are ongoing) using Thermocron iButtons (Dallas Semiconductors, Model DS1920), which have a resolution of 0.5°C. For the purposes of this comparison, the first 10 days (240 h) of data from August 2002, November 2002, and June 2003 were subjected to temporal autocorrelation analysis, and the autocorrelation values for the hourly lags for the first 168 h (7 days) were calculated and plotted. These plots indicate that at Marion Island, current temperatures provide an indication of future temperatures for a day and a half at best (fig. 3). Thereafter, temperatures are significantly negatively autocorrelated, and the pattern of autocorrelation becomes irregular with increasing time from the time of interest. By contrast, daily temperatures are perfectly predictable at Lambert's Bay for a full week. Every 24 h, temperatures are strongly correlated with those 24 h earlier (fig. 4), and by day 7 the autocorrelation has still not decayed to nonsignificant values. These patterns are typical for other months of the year at the two sites and support previous macroclimatological findings that weather conditions change in a matter of hours on the island (Schulze 1971).

Unpredictable variation in temperature on Marion Island could therefore have led to an adaptive response in the terrestrial mites in which a global optimum, with little phenotypic plasticity, is fixed (Tufto 2000). That several arthropod species here and elsewhere in the region show physiological responses that are typical of an unpredictable environment (Sinclair and Chown 2003; Sinclair et al. 2003) lends support to the idea of an adaptive absence of plasticity. Moreover, this general pattern of plasticity in marine but not terrestrial species has also been found in two other traits, supercooling point and lower lethal temperature, in these species, although *H. belgicae* showed little plasticity (Deere et al. 2006).

Nonetheless, several conditions would have to be satisfied to show that the lack of plasticity in the nonmarine mite species is indeed adaptive, including demonstration of consistent variation among individuals, a genetic basis for the traits, and a relationship between variation in locomotor performance and fitness. For plasticity of locomotor performance, these conditions are all controversial (Heinrich and Bartholomew 1979; Via et al. 1995; Gilchrist 1996; Scott et al. 1997; Hoffmann and Hewa-Kapuge 2000; Gibert et al. 2001; Angilletta et al. 2002; Sarkar 2004), and data are not available for the mite species in question. Thus, the question of an adaptive absence of phenotypic plasticity in the mite species is difficult to resolve. Demonstration of adaptive phenotypic plasticity in the other three species would be complicated for similar reasons.

An alternative explanation for both the absence of plas-

ticity in the fully terrestrial species and the weak plasticity in the marine and upper-shore ones might be that the lack of plasticity or weak presence thereof is a plesiomorphic characteristic of an ancient Gondwanan group (Marshall and Pugh 1996; Marshall and Coetzee 2000; Procheş and Marshall 2001). That both $u_{\max}$ and T_{opt} in these species are similar to those of the distantly related continental Antarctic mite species *Maudheimia petronia* (Marshall et al. 1995) suggests that this is a plausible alternative, as does the mismatch between optimum temperatures and likely habitat temperatures, which has been noted for other species (Hertz et al. 1983; Abushama and Al-Salameen 1989; Ward and Seely 1996; Bennett 2004). However, only a comprehensive investigation of the above conditions would allow the adaptive and constraint hypotheses to be distinguished.

In conclusion, this study has rejected the beneficial acclimation hypothesis for two and perhaps three labile traits within a given life stage for four of five mite species. It therefore lends support to previous arguments (summarized in Huey and Berrigan 1996) that the beneficial acclimation hypothesis requires more cautious scrutiny than it has received in the past. Moreover, this work also shows that unpredictability is an important feature of the environment that is likely to shape the nature and extent of phenotypic plasticity. It also draws attention to differences in predictability that exist between marine and terrestrial environments (see also Vasseur and Yodzis 2004) and the consequences these differences might hold for species physiological responses.

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Literature Cited

- Abushama, F. T., and M. A. Al-Salameen. 1989. Temperature reactions of desert tenebrionid beetles from Kuwait. *Journal of Arid Environments* 16:293–304.
- Addo-Bediako, A., S. L. Chown, and K. J. Gaston. 2002. Metabolic

- cold adaptation in insects: a large-scale perspective. *Functional Ecology* 16:332–338.
- Agrawal, A. A. 2001. Phenotypic plasticity in the interaction and evolution of species. *Science* 294:321–326.
- Angilletta, M. J., Jr., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27:249–268.
- Angilletta, M. J., Jr., R. S. Wilson, C. A. Navas, and R. S. James. 2003. Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology & Evolution* 18:234–240.
- Barendse, J., R. D. Mercer, D. J. Marshall, and S. L. Chown. 2002. Habitat specificity of mites on sub-Antarctic Marion Island. *Environmental Entomology* 31:612–625.
- Bennett, A. B. 2004. Thermoregulation in African chameleons. *International Congress Series* 1275:234–241.
- Bennett, A. F., and R. E. Lenski. 1997. Evolutionary adaptation to temperature. VI. Phenotypic acclimation and its evolution in *Escherichia coli*. *Evolution* 51:36–44.
- Berrigan, D., and S. M. Scheiner. 2004. Modeling the evolution of phenotypic plasticity. Pages 82–97 in T. J. DeWitt and S. M. Scheiner, eds. *Phenotypic plasticity: functional and conceptual approaches*. Oxford University Press, Oxford.
- Blake, B. E. 1996. Microclimate and prediction of photosynthesis at Marion Island. MSc thesis. University of the Free State, Bloemfontein, South Africa.
- Carrière, Y., and G. Boivin. 1997. Evolution of thermal sensitivity of parasitization capacity in egg parasitoids. *Evolution* 51:2028–2032.
- Chown, S. L. 1997. Thermal sensitivity of oxygen uptake of Diptera from sub-Antarctic South Georgia and Marion Island. *Polar Biology* 17:81–86.
- Chown, S. L., and J. E. Crafford. 1992. Microhabitat temperatures at Marion Island (46°54'S 37°45'E). *South African Journal of Antarctic Research* 22:51–58.
- Chown, S. L., and K. J. Gaston. 1999. Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Reviews* 74:87–120.
- Chown, S. L., and S. W. Nicolson. 2004. *Insect physiological ecology: mechanisms and patterns*. Oxford University Press, Oxford.
- Chown, S. L., A. Addo-Bediako, and K. J. Gaston. 2003. Physiological diversity: listening to the large-scale signal. *Functional Ecology* 17:562–572.
- Clarke, A. 1993. Seasonal acclimatization and latitudinal compensation in metabolism: do they exist? *Functional Ecology* 7:139–149.
- . 2003. Costs and consequences of evolutionary temperature adaptation. *Trends in Ecology & Evolution* 18:573–581.
- Cohet, Y., and J. David. 1977. Control of adult reproductive potential by preimaginal thermal conditions: a study in *Drosophila melanogaster*. *Oecologia (Berlin)* 36:295–306.
- Convey, P. 1994. Growth and survival strategy of the Antarctic mite *Alaskozetes antarcticus*. *Ecography* 17:97–107.
- . 1996. The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota. *Biological Reviews* 71:191–225.
- Crafford, J. E., C. H. Scholtz, and S. L. Chown. 1986. The insects of sub-Antarctic Marion and Prince Edward islands, with a bibliography of entomology of the Kerguelen biogeographical province. *South African Journal of Antarctic Research* 16:42–84.
- David, J. R., P. Gibert, E. Gravot, G. Petavy, J. Morin, D. Karan, and B. Moreteau. 1997. Phenotypic plasticity and developmental temperature in *Drosophila*: analysis and significance of reaction norms of morphometrical traits. *Journal of Thermal Biology* 22:441–451.
- Deere, J. A., B. J. Sinclair, D. J. Marshall, and S. L. Chown. 2006. Phenotypic plasticity of thermal tolerances in five oribatid mite species from sub-Antarctic Marion Island. *Journal of Insect Physiology* 52:693–700.
- de Jong, G. 1999. Unpredictable selection in a structured population leads to local genetic differentiation in evolved reaction norms. *Journal of Evolutionary Biology* 12:839–851.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. Prentice Hall, London.
- Feder, M. E., and G. E. Hofmann. 1999. Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. *Annual Review of Physiology* 61:243–282.
- Fischer, K., E. Eenhoorn, A. N. M. Bot, P. M. Brakefield, and B. J. Zwaan. 2003. Cooler butterflies lay larger eggs: developmental plasticity versus acclimation. *Proceedings of the Royal Society B: Biological Sciences* 270:2051–2056.
- García, L. V. 2004. Escaping the Bonferroni iron claw in ecological studies. *Oikos* 105:657–663.
- Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology* 46:5–17.
- Gibert, P., R. B. Huey, and G. W. Gilchrist. 2001. Locomotor performance of *Drosophila melanogaster*: interactions among developmental and adult temperatures, age, and geography. *Evolution* 55:205–209.
- Gilchrist, G. W. 1996. A quantitative genetic analysis of thermal sensitivity in the locomotor performance curve of *Aphidius ervi*. *Evolution* 50:1560–1572.
- Gilchrist, G. W., and R. B. Huey. 2001. Parental and developmental temperature effects on the thermal dependence of fitness in *Drosophila melanogaster*. *Evolution* 55:209–214.
- . 2004. Plastic and genetic variation as a function of temperature within and among parallel clines in *Drosophila subobscura*. *Integrative and Comparative Biology* 44:461–470.
- Gotthard, K., and S. Nylin. 1995. Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* 74:3–17.
- Gotthard, K., S. Nylin, and C. Wiklund. 2000. Individual state controls temperature dependence in a butterfly (*Lassiommatia maera*). *Proceedings of the Royal Society B: Biological Sciences* 267:589–593.
- Gremmen, N. J. M. 1981. *The vegetation of the sub-Antarctic islands Marion and Prince Edward*. Junk, The Hague.
- Guderley, H. 2004. Metabolic responses to low temperature in fish muscle. *Biological Reviews* 79:409–427.
- Hazel, J. R., and C. L. Prosser. 1974. Molecular mechanisms of temperature compensation in poikilotherms. *Physiological Reviews* 54:620–677.
- Hazel, W., R. Smock, and C. M. Lively. 2004. The ecological genetics of conditional strategists. *American Naturalist* 163:888–900.
- Heinrich, B., and G. A. Bartholomew. 1979. Roles of endothermy and size in inter- and intraspecific competition for elephant dung in an African dung beetle, *Scarabaeus laevistriatus*. *Physiological Zoology* 52:484–496.
- Hertz, P. E., R. B. Huey, and E. Nevo. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* 37:1075–1084.

- Hochachka, P. W., and G. N. Somero. 2002. Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press, Oxford.
- Hodkinson, I. D. 2003. Metabolic cold adaptation in arthropods: a smaller-scale perspective. *Functional Ecology* 17:562–567.
- Hoffmann, A. A. 1995. Acclimation: increasing survival at a cost. *Trends in Ecology & Evolution* 10:1–2.
- Hoffmann, A. A., and S. Hewa-Kapuge. 2000. Acclimation for heat resistance in *Trichogramma* nr. *brassicae*: can it occur without costs? *Functional Ecology* 14:55–60.
- Hoffmann, A. A., and M. Watson. 1993. Geographical variation in the acclimation responses of *Drosophila* to temperature extremes. *American Naturalist* 142(suppl.):S93–S113.
- Huey, R. B., and D. Berrigan. 1996. Testing evolutionary hypotheses of acclimation. Pages 205–237 in I. A. Johnston and A. F. Bennett, eds. *Animals and temperature: phenotypic and evolutionary adaptation*. Cambridge University Press, Cambridge.
- Huey, R. B., and P. E. Hertz. 1984. Is a jack-of-all-temperatures a master of none? *Evolution* 38:441–444.
- Huey, R. B., and J. G. Kingsolver. 1993. Evolution of resistance to high temperature in ectotherms. *American Naturalist* 142(suppl.): S1–S46.
- Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist* 19:357–366.
- Huey, R. B., D. Berrigan, G. W. Gilchrist, and J. C. Herron. 1999. Testing the adaptive significance of acclimation: a strong inference approach. *American Zoologist* 39:323–336.
- Kingsolver, J. G., and R. B. Huey. 1998. Evolutionary analyses of morphological and physiological plasticity in thermally variable environments. *American Zoologist* 38:545–570.
- Klok, C. J., and S. L. Chown. 2003. Resistance to temperature extremes in sub-Antarctic weevils: interspecific variation, population differentiation and acclimation. *Biological Journal of the Linnean Society* 78:401–414.
- Leroi, A. M., A. F. Bennett, and R. E. Lenski. 1994. Temperature acclimation and competitive fitness: an experimental test of the beneficial acclimation assumption. *Proceedings of the National Academy of Sciences of the USA* 91:1917–1921.
- Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104:116–121.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, NJ.
- Lively, C. M. 1986. Canalization versus developmental conversion in a spatially variable environment. *American Naturalist* 128:561–572.
- Loeschcke, V., and A. A. Hoffmann. 2002. The detrimental acclimation hypothesis. *Trends in Ecology & Evolution* 17:407–408.
- Marshall, D. J., and S. L. Chown. 1995. Temperature effects on locomotor activity rates of sub-Antarctic oribatid mites. *Polar Biology* 15:47–49.
- Marshall, D. J., and L. Coetzee. 2000. Historical biogeography and ecology of a continental Antarctic mite genus, *Maudheimia* (Acari, Oribatida): evidence for a Gondwanan origin and Plio-Pleistocene speciation. *Zoological Journal of the Linnean Society* 129:111–128.
- Marshall, D. J., and P. J. A. Pugh. 1996. Origin of the inland Acari of continental Antarctica, with particular reference to Dronning Maud Land. *Zoological Journal of the Linnean Society* 118:101–118.
- Marshall, D. J., I. P. Newton, and J. E. Crafford. 1995. Habitat temperature and potential locomotor activity of the continental Antarctic mite, *Maudheimia petronia* Wallwork (Acari: Oribatei). *Polar Biology* 15:41–46.
- Mélice, J.-L., J. R. E. Lutjeharms, M. Rouault, and I. J. Ansorge. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science* 99:363–366.
- Mercer, R. D., S. L. Chown, and D. J. Marshall. 2000. Mite and insect zonation on a Marion Island rocky shore: a quantitative approach. *Polar Biology* 23:775–784.
- Mercer, R. D., A. G. A. Gabriel, J. Barendse, D. J. Marshall, and S. L. Chown. 2001. Invertebrate body sizes from Marion Island. *Antarctic Science* 13:135–143.
- Moran, N. A. 1992. The evolutionary maintenance of alternative phenotypes. *American Naturalist* 139:971–989.
- Pörtner, H. O., P. L. M. van Dijk, I. Hardewig, and A. Sommer. 2000. Levels of metabolic cold adaptation: tradeoffs in eurythermal and stenothermal ectotherms. Pages 109–122 in W. Davison, C. Howard-Williams, and P. A. Broady, eds. *Antarctic ecosystems: models for wider ecological understanding*. New Zealand Natural Sciences, Christchurch.
- Procheş, S., and D. J. Marshall. 2001. Global distribution patterns of non-halacarid intertidal marine mites: implications for their origin in marine habitats. *Journal of Biogeography* 28:47–58.
- Prosser, C. L. 1986. *Adaptational biology: molecules to organisms*. Wiley, New York.
- Salvucci, M. E. 2000. Sorbitol accumulation in whiteflies: evidence for a role in protecting proteins during heat stress. *Journal of Thermal Biology* 25:353–361.
- Sarkar, S. 2004. From the reaktionsnorm to the evolution of adaptive plasticity: a historical sketch, 1909–1999. Pages 10–30 in T. J. DeWitt and S. M. Scheiner, eds. *Phenotypic plasticity: functional and conceptual approaches*. Oxford University Press, Oxford.
- Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* 24:35–68.
- Schulze, B. R. 1971. The climate of Marion Island. Pages 16–31 in E. M. van Zinderen Bakker, J. M. Winterbottom, and R. A. Dyer, eds. *Marion and Prince Edward islands: report on the South African biological and geological expedition 1965–1966*. Balkema, Cape Town.
- Scott, M., D. Berrigan, and A. A. Hoffmann. 1997. Costs and benefits of acclimation to elevated temperature in *Trichogramma carverae*. *Entomologia Experimentalis et Applicata* 85:211–219.
- Sibly, R. M., L. Winokur, and R. H. Smith. 1997. Interpopulation variation in phenotypic plasticity in the speckled wood butterfly, *Pararge aegeria*. *Oikos* 78:323–330.
- Sinclair, B. J., and S. L. Chown. 2003. Rapid response to high temperature and desiccation but not to low temperature in the freeze tolerant sub-Antarctic caterpillar *Pringlephaga marioni* (Lepidoptera, Tineidae). *Journal of Insect Physiology* 49:45–52.
- Sinclair, B. J., A. Addo-Bediako, and S. L. Chown. 2003. Climatic variability and the evolution of insect freeze tolerance. *Biological Reviews* 78:181–195.
- Smith, V. R. 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change* 52:345–357.
- Spicer, J. I., and K. J. Gaston. 1999. *Physiological diversity and its ecological implications*. Blackwell Science, Oxford.
- Stevenson, R. D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *American Naturalist* 126:362–386.

- Sultan, S. E., and H. G. Spencer. 2002. Metapopulation structure favors plasticity over local adaptation. *American Naturalist* 160: 271–283.
- Terblanche, J. S., C. J. Klok, E. S. Krafur, and S. L. Chown. 2006. Phenotypic plasticity and geographic variation in thermal tolerance and water loss of the tsetse fly *Glossina pallidipes* (Diptera: Glossinidae): implications for distribution modelling. *American Journal of Tropical Medicine and Hygiene* 74:786–794.
- Tufto, J. 2000. The evolution of plasticity and nonplastic spatial and temporal adaptations in the presence of imperfect environmental cues. *American Naturalist* 156:121–130.
- Van Tienderen, P. H. 1997. Generalists, specialists, and the evolution of phenotypic plasticity in sympatric populations of distinct species. *Evolution* 51:1372–1380.
- Vasseur, D. A., and P. Yodzis. 2004. The color of environmental noise. *Ecology* 85:1146–1152.
- Via, S., R. Gomulkiewicz, S. M. Scheiner, C. D. Schlichting, and P. H. Van Tienderen. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology & Evolution* 10:212–217.
- Ward, D., and M. K. Seely. 1996. Adaptation and constraint in the evolution of the physiology and behavior of the Namib Desert tenebrionid beetle genus *Onymacris*. *Evolution* 50:1231–1240.
- Willmer, P., G. Stone, and I. A. Johnston. 1999. *Environmental physiology of animals*. Blackwell Science, Oxford.
- Wilson, R. S., and C. E. Franklin. 2002a. The detrimental acclimation hypothesis. *Trends in Ecology & Evolution* 17:407–408.
- . 2002b. Testing the beneficial acclimation hypothesis. *Trends in Ecology & Evolution* 17:66–70.
- Woods, H. A. 1999. Patterns and mechanisms of growth of fifth-instar *Manduca sexta* caterpillars following exposure to low- or high-protein food during early instars. *Physiological and Biochemical Zoology* 72:445–454.
- Woods, H. A., and J. F. Harrison. 2001. The beneficial acclimation hypothesis versus acclimation of specific traits: physiological change in water-stressed *Manduca sexta*. *Physiological and Biochemical Zoology* 74:32–44.
- . 2002. Interpreting rejections of the beneficial acclimation hypothesis: when is physiological plasticity adaptive? *Evolution* 56: 1863–1866.
- Zamudio, K. R., R. B. Huey, and W. D. Crill. 1995. Bigger isn't always better: body size, developmental and parental temperature, and territorial success in *Drosophila melanogaster*. *Animal Behaviour* 49:671–677.
- Zeilstra, I., and K. Fischer. 2005. Cold tolerance in relation to developmental and adult temperature in a butterfly. *Physiological Entomology* 30:92–95.

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