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ORIGINAL PAPER

Fall field crickets did not acclimate to simulated seasonal changes in temperature

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Abstract In nature, many organisms alter their developmental trajectory in response to environmental variation. However, studies of thermal acclimation have historically involved stable, unrealistic thermal treatments. In our study, we incorporated ecologically relevant treatments to examine the effects of environmental stochasticity on the thermal acclimation of the fall field cricket (*Gryllus pennsylvanicus*). We raised crickets for 5 weeks at either a constant temperature (25°C) or at one of three thermal regimes mimicking a seasonal decline in temperature (from 25 to 12°C). The latter three treatments differed in their level of thermal stochasticity: crickets experienced either no diel cycle, a predictable diel cycle, or an unpredictable diel cycle. Following these treatments, we measured several traits considered relevant to survival or reproduction, including growth rate, jumping velocity, feeding rate, metabolic rate, and cold tolerance. Contrary to our predictions, the acclimatory responses of crickets were unrelated to the magnitude or type of thermal variation. Furthermore, acclimation of performance was not ubiquitous among traits. We recommend additional studies of acclimation in fluctuating environments to assess the generality of these findings.

Keywords Temperature · Acclimation · Seasonality

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Introduction

Temperature is one of the most important environmental factors that influence the phenotypes, abundances, and distributions of species (Prosser 1991; Angilletta 2009). Short-term changes in body temperature affect rates of physiological processes, which in turn affect organismal performance (Marsh and Bennett 1986; Temple and Johnston 1998; De Marco and Resende 2002). Some ectotherms can respond to thermal change by shifting their sensitivity to temperature through a process known as acclimation (Randall et al. 2002; Wilson and Franklin 2002; Seebacher and Wilson 2006; Deere and Chown 2006). For example, many species respond to changes in environmental temperature by improving their locomotor performance at novel temperatures (e.g., Fry and Hart 1948; Johnson and Bennett 1995; Wilson and Franklin 1999; Condon and Wilson 2006; Glanville and Seebacher 2006; Wilson et al. 2007). The physiological mechanisms underlying these responses include changes in the rates of biochemical reactions, the properties of muscle contraction, the proportions of muscle-fibre types, and the quantity and quality of mitochondria (Beddow and Johnston 1995; Johnson and Bennett 1995; Swank and Rome 2001; Seebacher et al. 2003; Seebacher and Wilson 2006).

Despite the plethora of studies reporting acclimation, we know very little about patterns of acclimation in ecologically relevant thermal environments (Johnston and Temple 2002; Angilletta et al. 2006; Angilletta 2009; but see Glanville and Seebacher 2006). In theory, thermal acclimation should depend on the predictability of environmental change (DeWitt and Scheiner 2004). If environmental temperature changes appreciably and predictably, organisms may use external cues to adjust their internal composition accordingly (Levins 1968). For example, Gabriel (2005) suggested that seasonal acclimation would be advantageous when organisms occur in an environment where the direction and magnitude of change is predictable between seasons. By contrast, environments that vary stochastically would favour genotypes that express a generalized phenotype (Gabriel 2005; Gabriel et al. 2005). Thus, the capacity for acclimation should be pronounced in species that experience strong seasonal changes in temperature, such as those from temperate environments. Moreover, acclimation responses of temperate species should be most evident in the presence of reliable thermal cues (Schuler et al. 2011). These ideas can be tested through experiments that document acclimation to constant and fluctuating temperatures (Schaefer and Ryan 2006; Terblanche et al. 2010).

In this study, we examined the influence of three different cooling regimes on the acclimation of several performance traits in fall field crickets (*Gryllus pennsylvanicus*). These regimes differed in the predictability of thermal change, ranging from a linear change that represented an artificial pattern to a stochastic change that mimicked the natural pattern of air temperature. After exposing crickets to the thermal treatments, we measured the thermal sensitivities of locomotion, feeding, and metabolic rate. We expected that crickets exposed to linear thermal change would perform better at low temperatures than would crickets exposed to less predictable patterns of thermal change.

Methods

Study organism and husbandry

Fall field crickets (*Gryllus pennsylvanicus*) occur commonly throughout North America and have an annual life cycle. Eggs enter diapause shortly after fertilization in autumn and young emerge as nymphs between June and early July of the following year (Alexander 1968; Carriere et al. 1996). Individuals grow and develop during the summer and begin to reproduce in August or September. Adults die in the first frosts of autumn (Alexander and Meral 1967; Alexander 1968).

Gravid crickets were captured in Vigo County, IN, USA, in August and September of 2005 and were brought back to the laboratory at Indiana State University. We used the offspring of these females for our experiment. Prior to the experiment, these offspring were maintained as groups of siblings in 5.7 L containers at 25 ± 1°C, with unlimited access to water and food (ground rabbit chow). In February of 2006, siblings were divided evenly among thermal treatments. Because we could not precisely determine the sex or age of each individual, we ensured that initial body masses were similar among the groups (mean = 0.134 g, range = 0.040–0.281 g, $N = 66$–67 crickets per treatment; $F_{2,198} = 0.44$, $P = 0.64$). During the experiment, crickets were housed individually in Petri dishes (90 × 20 mm) with access to food, water, and shelter (paper towelling). Small holes were drilled in the side of each dish for ventilation.

To determine thermal sensitivities prior to acclimation, we sampled additional crickets from the colony, which were similar in size to the experimental crickets. These control individuals ($N = 60$) were kept at 25 ± 1°C in their original rearing containers. All containers were cleaned at least once per week. The photoperiod for all treatments was 12L:12D with scotophase occurring during the day (French and Cade 1987).

Thermal treatments

To design realistic thermal treatments (Fig. 1b–d), we obtained temperatures recorded by a weather station in Terre Haute, Indiana (Fig. 1a), near the area where the crickets were collected (National Oceanic and Atmospheric Administration 2006). At the beginning of the experiment, we randomly allocated individuals to one of three thermal treatments (Fig. 1): a linear decline in temperature, a decline in temperature with predictable diel variation, or a decline in temperature with stochastic diel variation. Over the 5-week period of exposure, the mean daily temperature in all treatments declined from 25 to 12°C. Thermal treatments were maintained using programmable incubators (Precision, Model 818). All physiological measurements occurred during scotophase.

Growth, development, and sex

To estimate growth, we recorded the body masses of crickets at the beginning and the end of the thermal treatment. Body mass was recorded to the nearest 0.1 mg using an electronic balance. At the end of the experiment, we also evaluated the developmental stage of each cricket. Individuals were considered adults if their wings were fully formed. During the experiment, most crickets grew and developed enough for us to determine their sex by the

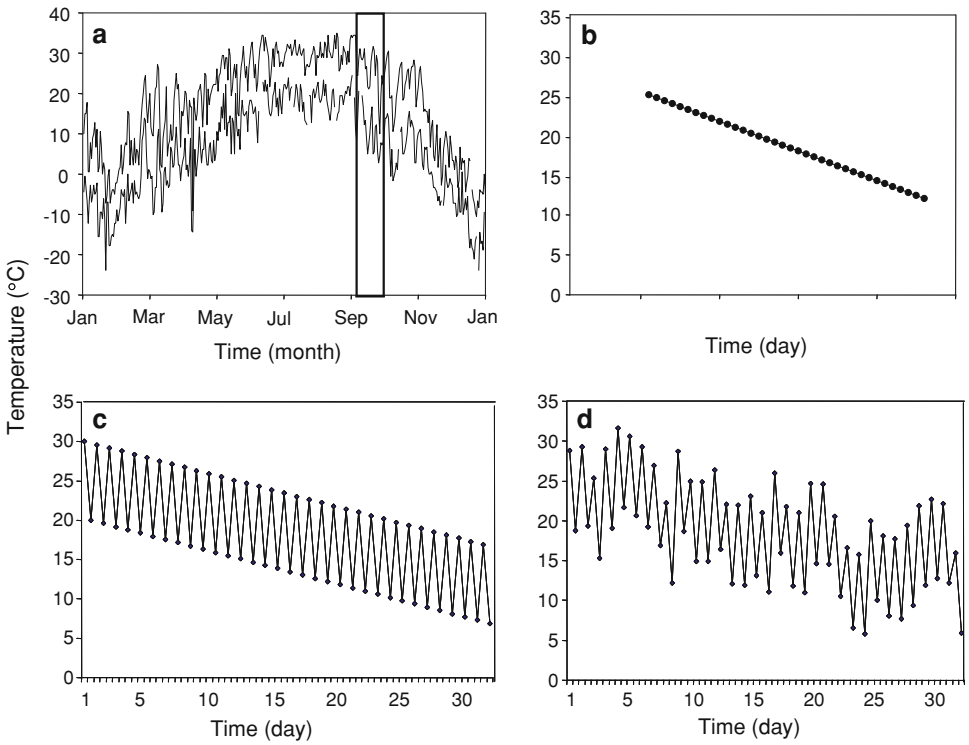

Fig. 1 **a** Air temperatures in Terre Haute, IN, USA in 2000. *Vertical lines* bracket those temperatures that we considered when designing our thermal treatments. Crickets were subjected to either a control treatment of 25°C or one of three thermal treatments: **a** linear cooling, **b** cooling with reliable diel variation, or **c** cooling with stochastic diel variation

presence or absence of an ovipositor. We compared growth and development among groups using ANOVA and a χ^2 test, respectively. These statistical analyses, and all others described below, were performed in STATISTICA 7.0 (StatSoft, OK, USA). Descriptive statistics are presented as mean ±95% confidence interval.

Locomotor performance

In a preliminary experiment, we found that jumping was thermally insensitive over a wide thermal range, so we did not assay jumping performance in this study. Rather, we assessed locomotor performance by encouraging crickets to run along a linear track (0.5 m), housed within an environmental chamber (1.9 × 2.5 × 2.5 m). A clear plastic cover was placed over the track to prevent the cricket from jumping. We motivated each cricket to run forward by tapping the cover as it moved along the track. We prevented crickets from turning within the track by pushing a wooden rod behind them as they ran.

We assayed the speed of 30 crickets from each treatment at the following temperatures: 8, 12, 16, 20, 25, 30, 35, and 44°C. These temperatures span nearly the entire range of thermal tolerance for a field cricket [during preliminary work, we established the critical thermal minimum to be <4°C ($N = 20$) and the critical thermal maximum to be 46 ± 0.29°C ($N = 20$)]. Temperatures were randomly ordered during locomotor trials, except that 44°C was reserved for last because we worried that exposure to this extreme temperature would affect subsequent performance. Between trials, temperatures were changed at a rate of 4–5°C h^{-1} within the environmental chamber, and crickets were given at least 20 min to adjust to a new test temperature. Each individual was measured at all temperatures, unless it became injured or died. Crickets from each thermal treatment were interspersed to avoid confounding the effects of time and treatment on speed. Because these assays took 3 days to complete, crickets were maintained at 12°C between trials. We recorded the mass of each cricket before and after locomotor trials; the mean mass was used as a covariate in statistical analyses.

We used the following equation to estimate the thermal breadth of locomotor performance (T_{br}) for each cricket:

$$T_{br} = \sqrt{(\Sigma\,[(u_i(T_i - T_{opt})^2)/u_{max}])}$$

where u_i refers to the running speed at a particular temperature (T_i), T_{opt} is the temperature at which an individual's maximum speed was achieved, and u_{max} is the maximal running speed (Gilchrist 1996).

We used an ANOVA for repeated measures to compare running performance between treatments and test temperatures. For this analysis, we excluded data for crickets that failed to complete one or more of the locomotor trials. We also used ANOVA to determine whether thermal treatment or body size affected the maximal speed, the thermal optimum, or the thermal breadth.

Cold tolerance

We compared cold tolerances between groups by measuring the ability to recover from chill coma (Gibert and Huey 2001). A subset of crickets from each treatment (N ranged from 14 to 20), which were not subjected to other measures of performance, were placed in Petri dishes (50 × 10 mm). These dishes were entombed in ice, causing the air temperature within each dish to fall to 0°C within 5 min. After 15 min, the dishes were removed from the ice and the crickets were transferred to sheets of paper at room temperature (25°C). Using forceps, we positioned each cricket on its back in the centre of a printed circle (diameter = 2 cm). We recorded the time between the removal of dishes from the ice and the recovery of each individual using event-recording software (Shih and Mok 2000). Recovery was scored when a cricket assumed an upright position and broke the plane of the circle; this simple, objective measure of recovery reflected the onset of motor coordination (Angilletta et al. 2007). As each cricket left its circle, we covered it with a small Petri dish to prevent the animal from interfering with others on the same sheet. Because crickets were assayed in successive trials, each trial included individuals from each of the thermal treatments. Petri dishes containing crickets from different thermal treatments were chilled together, and the positions of these dishes were rotated between trials. We used ANOVA to compare recovery times among groups.

Metabolic rate

We measured the metabolic rates of crickets at 12 and 25°C. To control for the order of temperatures, we randomly selected half of the individuals from each treatment to be tested at 25°C first and the other half to be tested at 12°C first; data from these two groups were combined for all analyses. We recorded the body mass of each cricket prior to each measurement and used the mean mass as a covariate in statistical analyses.

Rates of oxygen consumption over 12 h were recorded by closed-system respirometry (Model TR-3, Sable Systems, Las Vegas, NV, USA). Each cricket was placed inside a sealed glass respirometry chamber (250 mL) and placed in an incubator (Model KB-115, Brinkmann). To ensure that the temperature within the respirometry chambers equalled the temperature of the incubator, chambers were placed in the incubator at least 1 h prior to measurements. During this time, we calibrated the oxygen analyser (Model FC-1, Sable Systems) with a gas of known concentration. Recordings commenced at the onset of scotophase (0900 hours). Initially, all chambers were flushed sequentially with air that was purged of water and carbon dioxide. Each chamber was flushed again after 12 h. At each flush, air from a chamber flowed through the oxygen analyser at a known rate. A computer controlled the sequential flushing of chambers to ensure that each chamber was sealed for a precise duration between recordings. Given the oxygen concentration and flow rate during the second flush, we used a computer programme (CONVOL, Sable Systems) to calculate the total volume of oxygen consumed while the chamber was sealed. Hourly rates were calculated by dividing total oxygen consumption by 12 h. When recordings ended at 2100 hours, crickets were returned to 12°C and were provided unlimited food and water until the next trial commenced. An ANOVA for repeated measures was used to assess the effects of thermal treatment and test temperature on metabolic rate; body mass was used as a covariate.

Feeding rate

We measured the feeding rates of crickets (N = 19–20 per treatment) at 12 and 25°C. As with measures of metabolic rate, we randomly assigned half of the crickets from each treatment to begin at 12°C and the other half to begin at 25°C. Crickets were weighed and placed in Petri dishes at the appropriate temperature. Each dish contained a known mass of food (ground rabbit chow) and a source of water. Quantities of food were estimated as surplus to a cricket's feeding capacity. After 48 h, the mass of both the cricket and the food were recorded; food was dried before weighing to minimize error associated with variation in moisture content. Crickets were immediately placed in a new Petri dish with fresh food and water, and their feeding performance was measured at the second temperature. An ANOVA for repeated measures was used to assess the effects of thermal treatment and test temperature on feeding rate; body mass was used as a covariate.

Results

Growth and development

During the 5 weeks of acclimation, crickets in the three thermal treatments grew at different rates ($F_{2,196} = 9.30$, $P < 0.001$). Crickets exposed to a linear cooling grew more slowly than crickets exposed to cooling with either predictable or stochastic diel variation ($P < 0.05$; Fig. 2). Only 9% of crickets exposed to linear cooling matured during our experiment, compared with 33 and 22% of crickets that matured when exposed to cooling with predictable diel variation and stochastic diel variation, respectively. However, a Chi-squared analysis of log-transformed data indicated that the probability of maturation did not differ significantly among groups ($\chi^2 = 3.0$,

$df = 2$, $P = 0.22$). All groups consisted of a biased sex ratio, in which 58–66% of individuals within a treatment were males.

Locomotor performance

The speed of running depended greatly on body temperature ($F_{7,700} = 4.47$, $P < 0.001$). Crickets ran the slowest at 8°C and ran the fastest at 30–35°C (Fig. 3). Performance was poor at extremely high temperatures; in fact, several individuals were unable to run at 44°C (control: $N = 2$; linear cooling: $N = 1$; cooling with predictable diel variation: $N = 11$; cooling with stochastic diel variation: $N = 0$). Performance was unrelated to either body mass ($F_{1,100} = 2.08$, $P = 0.15$) or thermal treatment ($F_{3,100} = 1.18$, $P = 0.32$). Contrary to our expectation, crickets exposed to different thermal treatments performed similarly across temperatures (interaction effect: $F_{21,700} = 0.91$, $P = 0.58$).

Key aspects of the performance curve were relatively insensitive to the thermal conditions used in our experiment. Maximal speed was not significantly affected by body mass ($F_{1,100} = 0.14$, $P = 0.71$) or thermal treatment ($F_{3,100} = 1.82$, $P = 0.15$). The thermal optimum for running also was not significantly affected by body mass ($F_{1,100} = 0.20$, $P = 0.65$) or thermal treatment ($F_{3,100} = 1.86$, $P = 0.14$). The mean thermal breadth of locomotor performance was large for all groups, ranging from 23.0 to 24.7°C in width. However, thermal breadth did not differ significantly among thermal treatments ($F_{3,105} = 0.64$, $P = 0.59$). Interestingly, there was a trend for maximal running speed to decrease as the thermal breadth increased, but this relationship was not statistically significant ($r^2 = 0.03$, $N = 105$, $P = 0.09$).

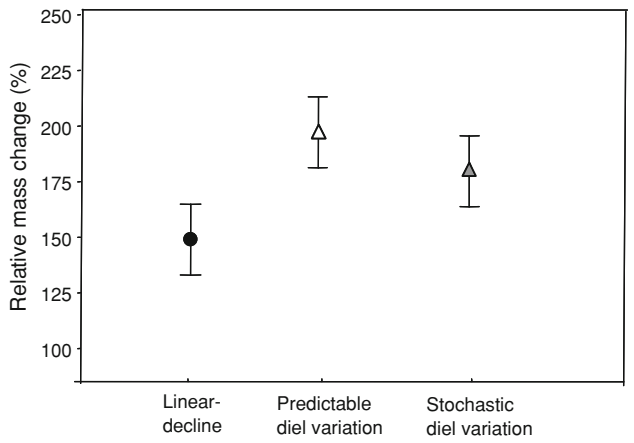

Fig. 2 Growth rates of fall field crickets (*Gryllus pennsylvanicus*) when exposed to either a linearly declining, reliably variable, or stochastically variable decrease in temperature from 25 to 12°C over 5 weeks. *Error bars* denote 95% confidence intervals

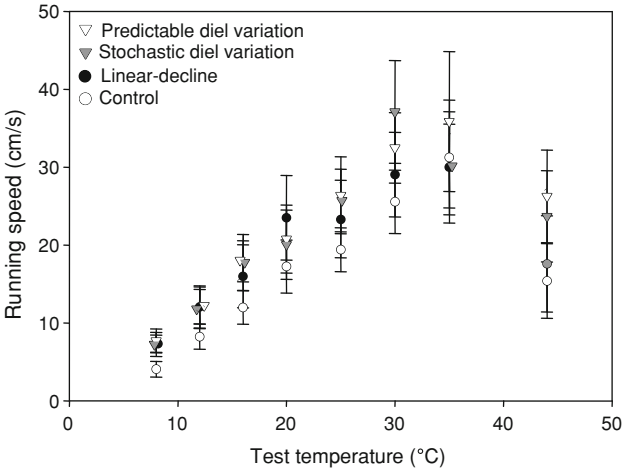

Fig. 3 The thermal sensitivity of locomotor performance for the fall field cricket (*Gryllus pennsylvanicus*) when exposed to either a constant (25°C) or variable thermal regime (linearly declining, reliably variable, or stochastically variable decrease in temperature from 25 to 12°C) for 5 weeks. *Error bars* denote 95% confidence intervals

Cold tolerance

Although larger crickets took significantly longer to recover from chill coma ($F_{1,65} = 13.2$, $P = 0.001$), thermal treatment did not affect the recovery time when means were adjusted for variation in body mass ($F_{3,65} = 0.9$, $P = 0.43$; Fig. 4).

Metabolic rate

Not surprisingly, larger crickets consumed more oxygen than smaller crickets ($F_{1,83} = 393.8$, $P < 0.001$). After adjusting the metabolic rates for variation in body size,

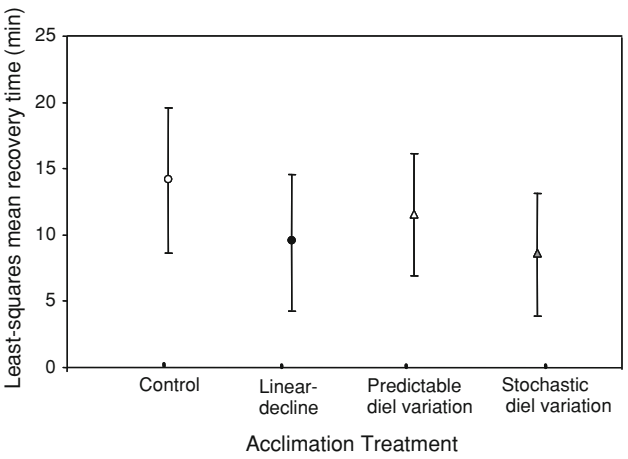

Fig. 4 Recovery time following chill coma for fall field crickets (*Gryllus pennsylvanicus*) when exposed to a constant 25°C or, linearly declining, reliably variable, or stochastically variable, decrease in temperature from 25 to 12°C, over 5 weeks. *Error bars* denote 95% confidence intervals

mean rates differed significantly among thermal treatments ($F_{3,83} = 21.3$, $P < 0.001$). At both 12 and 25°C, metabolic rate was highest in the control crickets ($P < 0.001$ for all pairwise comparisons with other groups; Fig. 5). The thermal sensitivity of metabolic rate did not vary significantly among crickets exposed to different thermal treatments ($F_{3,87} = 1.2$, $P = 0.32$). The Q_{10} of mass-specific metabolic rate ranged between 2.8 and 3.1.

Feeding rate

While statistically controlling for the positive relationship between body mass and feeding rate ($F_{1,81} = 8.4$, $P = 0.005$), we found no significant variation in feeding rate among groups exposed to different thermal conditions. Likewise, neither the mean feeding rate ($F_{3,81} = 0.5$, $P = 0.67$; Fig. 6) nor its thermal sensitivity varied among groups (mean $Q_{10} = 2.9$, range = 2.3–3.8; $F_{3,66} = 1.0$, $P = 0.41$). When averaged among groups, feeding rate was 2.6 times higher at a body temperature of 25°C than it was at a body temperature of 12°C ($F_{1,81} = 5.0$, $P = 0.03$).

Discussion

We expected that crickets exposed to a gradual and predictable change in temperature would exhibit a greater degree of acclimation than would crickets exposed to unpredictable changes in temperature. To our surprise, acclimation responses for several performance traits were unrelated to the predictability of environmental temperature, and some performance traits did not appear to acclimate at all. Because we considered several forms of thermal change, ranging from highly artificial to fairly natural, our results have implications for our understanding of patterns of acclimation in free-ranging animals.

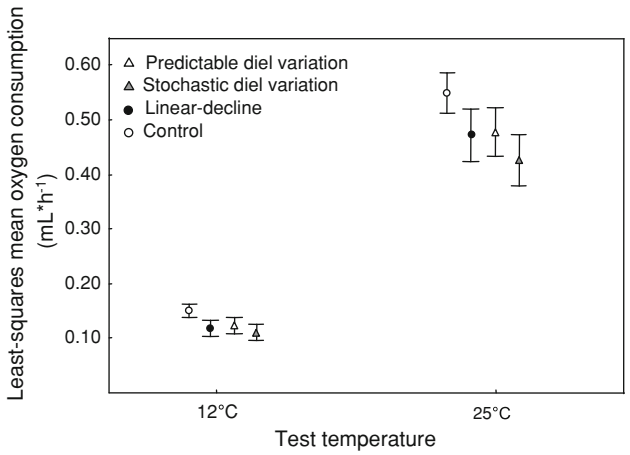

Fig. 5 Oxygen consumption rates for fall field crickets (*Gryllus pennsylvanicus*) when exposed to a constant 25°C or, linearly declining, reliably variable, or stochastically variable, decrease in temperature from 25 to 12°C, over 5 weeks. *Error bars* denote 95% confidence intervals

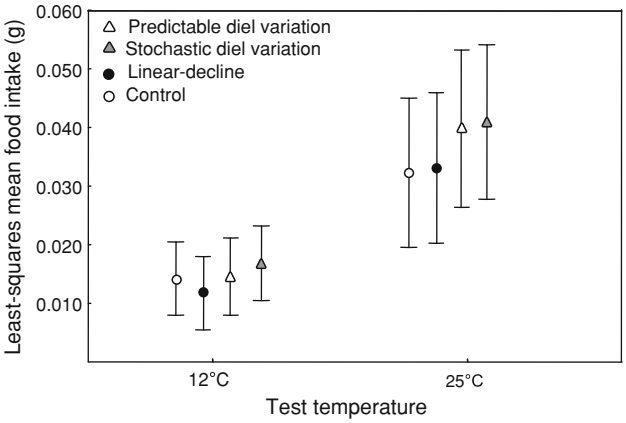

Fig. 6 Food intake rates for fall field crickets (*Gryllus pennsylvanicus*) when exposed to a constant 25°C or, linearly declining, reliably variable, or stochastically variable, decrease in temperature from 25 to 12°C, over 5 weeks. *Error bars* denote 95% confidence intervals

In our experiment, the growth rates of crickets responded to the thermal variation experienced during development. After 5 weeks, crickets exposed to cooling with diel variation were larger than were crickets exposed to linear cooling. However, crickets exposed to predictable and stochastic forms of diel variation did not grow differently. Many studies have examined the effects of thermal fluctuations on growth (Siddiqui and Barlow 1972; Hokanson et al. 1977; Brakefield and Kesbeke 1997; Sanford 2002; Du and Ji 2003; Georges et al. 2005; Folguera et al. 2011), but few have compared growth under predictable and stochastic fluctuations. Schaefer and Ryan (2006) found that zebrafish (*Danio rerio*) grew more rapidly when exposed to stochastic diel fluctuations than they did when exposed to predictable diel fluctuations. Interestingly, fish grew even faster when exposed to a constant temperature that equalled the mean temperature of the variable environments (28°C). For relatively slow-growing species, thermal sensitivities of growth rate cannot be measured within individuals because of the time required to estimate growth; however, the patterns of growth in zebrafish suggest that thermal fluctuations were stressful because extreme temperatures reduced growth. Since fish in the stochastically fluctuating environment experienced extreme temperatures for shorter durations, they were able to grow faster than fish in the predictably fluctuating environment. Importantly, the effect of predictable or stochastic thermal variations on growth depends on the mean temperature (Siddiqui and Barlow 1972). In our experiment, the mean temperature throughout the experiment decreased steadily, which led to faster growth when temperature fluctuated around the mean. The effect of thermal variation can also depend on the life stage

of the organism when thermal sensitivity acclimates during development (Niehaus et al. 2006, 2011).

Reversible acclimation should evolve when the environment varies predictably within generations (Gabriel et al. 2005), while irreversible acclimation should evolve when the environment varies primarily among generations (Gabriel and Lynch 1992). Our study indicates crickets do not conform to these predictions. Field crickets likely experience greater thermal variation within generations than among generations, but appear to acclimate poorly during simulated seasonal change. Crickets showed no plasticity in running performance, feeding rate or cold tolerance—three traits that likely affect fitness. Rapid feeding would boost the energetic reserves available for breeding (Hoback and Wagner 1997), cold tolerance could enhance longevity because freezing demarcates the end of the lifecycle (Alexander and Meral 1967), and locomotor performance can enhance the survivorship (Miles 2004; Husak 2006).

Gabriel et al. (2005) argued that organisms that enter diapause during harsh conditions should specialise to the conditions they are likely to experience during adulthood. This strategy may benefit organisms that live as adults for only a short period. Nevertheless, those organisms that experience dramatic seasonal changes after diapause might enhance their fitness by being generalists rather than specialists. Perhaps crickets failed to acclimate because their wide performance breadths prevent loss of function during thermal change (see Fig. 3). Furthermore, crickets in the wild may thermoregulate behaviourally to ameliorate the impact of environmental change (John Storm, personal observations). Recent studies of other species indicate that organisms may suffer limited potential to acclimate during thermal fluctuations. Schuler et al. (2011) found that isopods (*Porcellio scaber*) also failed to acclimate to either predictable or unpredictable declines in temperature. Terblanche et al. (2010) found that fruit flies (*Ceratitis capitata*) were less able to acclimate to changes in mean temperature when thermal variance was higher than when thermal variance was low. Collectively, these studies suggest that some organisms may possess limited capacity to acclimate to ecologically relevant thermal conditions.

We found that crickets exposed to cooling from 25 to 12°C reduced their rate of metabolism relative to crickets maintained at a constant temperature of 25°C. In some species, individuals raised at different constant temperatures had the same stage-specific metabolic rates at their respective rearing temperatures (Birchard and Reiber 1995; Angilletta et al. 2000), which suggests that metabolic compensation had occurred. Here, we observed the opposite pattern, since the pattern of acclimation to cooling exaggerated environmental effects on metabolic rate. Other species that have been acclimated to diel variation in temperature have also failed to show any acclamatory changes in metabolism (McMahon et al. 1995, Booth 1998; see also Huey and Berrigan 1996). Interestingly, the effect of acclimation of metabolic rate did not depend on the predictability of cooling.

Physiologists designing studies of acclimation have typically considered phenotypic responses to abrupt changes in the environment, even though nature changes both gradually and stochastically. Transferring organisms directly between contrasting thermal conditions could impose unexpected costs (e.g., production of heat shock proteins) that overshadow the acclimatory processes that occur during more gradual changes in temperature. Moreover, seasonal changes in temperature occur in conjunction with the more predictable changes in photoperiod, through which organisms can anticipate the need to adjust their phenotype. The current theory assumes that organisms know when temperatures will shift between seasons despite not knowing the exact magnitude of thermal change (Gabriel et al. 2005). This simplifying assumption could account for the discrepancies between theoretical predictions and empirical observations. For example, the crickets in our study experienced a constant photoperiod, although photoperiod can be a reliable indicator of seasonal change in natural environments (Moran 1992). We believe a greater number of studies should address the interactive effects of temperature and photoperiod on physiological acclimation (e.g. Martin et al. 2009; Condon et al. 2010). By designing experiments that combine realistic changes in photoperiod and temperature, we should obtain a more accurate picture of the patterns and processes of organismal acclimation in seasonal environments.

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