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The strength of temperature-mediated selection on body size in a wild insect population

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Abstract

Body size is a crucial element of an organism's ecology and evolution, and is known to be influenced by natural selection. Here, we estimated the strength of temperature-mediated selection on body size in a wild population of the striped ground cricket, *Allonemobius socius*. We found that extremely high, but naturally occurring temperatures, selected for larger body sizes, as expected. The strength of this selection pressure was strong, with the univariate selection gradients being $\beta = 0.591 \pm 0.237$; $\beta_s = 0.281 \pm 0.112$; and $\beta_\mu = 3.95 \pm 1.58$ ($\pm s_{\bar{x}}$). These results suggest that periodically occurring temperature extremes can influence the evolution of body size in wild populations of *A. socius* and other orthopterans. Furthermore, these selection pressures may contribute to the often observed size cline known as the Converse of Bergmann's rule, and become more prevalent in the future as temperatures increase due to global warming.

Key words

Gryllidae, Nemobiinae, body size, selection gradients, temperature, *Allonemobius socius*, Bergmann's rule, global warming

Introduction

Body size has a tremendous influence on the ecology and evolution of natural populations. Body size affects the biochemistry, physiology, morphology, life-history, behavior, distribution, demography, and competitive ability of most, if not all, known species (see reviews in Bonner 2006, Brown *et al.* 2004, Roff 2001, Sibly & Brown 2007). These effects, as well as body size's high levels of heritable genetic variation (Mousseau & Roff 1987, Roff & Mousseau 1987) have made it one of the most intensely studied traits in biology. And yet, biologists still struggle to identify the mechanisms that determine body size in natural populations (Atkinson & Sibly 1997, Mousseau 1997, van Voorhies 1996).

One mechanism known to have a tremendous effect on body size in wild populations is temperature-mediated selection (Bodie & Semlitsch 2000, Brown & Brown 1999, Grant & Grant 1995). Temperature-mediated selection pressures are particularly important to orthopterans and other ectotherms which lack physiological mechanisms for thermal regulation. For example, desiccation caused by extremely high temperature selects for larger individuals in many ectothermic species (Addo-Bediako *et al.* 2001, Chown & Gaston 1999, Levins 1969, Schoener & Janzen 1968). Larger individuals are better able to resist desiccation than smaller individuals because they have a greater capacity to store water (Chown 1993) and a smaller surface area-to-volume ratio, which reduces the rate of water loss (Chown *et al.* 1998). As such, natural selection tends to favor increased body size in populations of ectotherms subjected

to extremely high temperatures.

The importance of estimating the strength of selection pressures under natural conditions has long been recognized (Endler 1986), and a large number of these estimates have been published (Hoekstra *et al.* 2001, Irschick *et al.* 2008, Kingsolver *et al.* 2001). However, these previous works have focused on a relatively small number of species. For example, while Kingsolver *et al.* (2001) presented over 1,500 estimates for the strength of selection, these estimates were only distributed across 61 species, of which 15 were invertebrates, including one orthopteran (Zuk 1988). This relatively modest sampling of species, despite the robust overall sample size, suggests that while our understanding of natural selection in the wild has increased greatly over the past several years, more work needs to be done.

In this study, we estimated the strength of temperature-mediated selection acting on body size in a wild population of the striped ground cricket, *Allonemobius socius*. These small-bodied orthopterans are found throughout the eastern United States (Marshall 2004) and are frequently used in ecological and evolutionary studies (Fedorka *et al.* 2007, Winterhalter & Mousseau 2007). We collected a population of these crickets from Newberry County, South Carolina, USA (lat 34°N, long 81°W) on August 1, 1999. On this particular date, temperatures in the area reached 40.5°C (Williams *et al.* 2006), which was more than one standard deviation above the average high temperature for that time of year and marked the beginning of several days of extreme heat in the area (Fig. 1). Adult crickets were captured individually (no nymphs were observed), using an insect net. Upon capture, individuals were placed in a shaded plastic collection bin (36.2 × 24.1 × 31.1 cm) for the remainder of the collection period (~1.5 h in total). While in this container, 59 of the 103 individuals died (57.3% mortality). Based on the general ability of large-bodied individuals to resist desiccation (Addo-Bediako *et al.* 2001, Chown & Gaston 1999, Levins 1969, Schoener & Janzen 1968), we predicted that larger individuals would have a higher probability of surviving this mortality event.

Methods

After the collection was completed, we brought all individuals (both living and dead) back to the laboratory. Here, digital images of the crickets' femurs were taken using a Leica LW Scientific Mini-VID digital camera mounted to a Leica Zoom 2000 stereoscope. The length of each femur was then measured from these digital images using tpsDIG (Rohlf 2006). We used the average of the left and right femur as our estimate of body size. Because insects have determinant growth, length is generally a more consistent proxy of

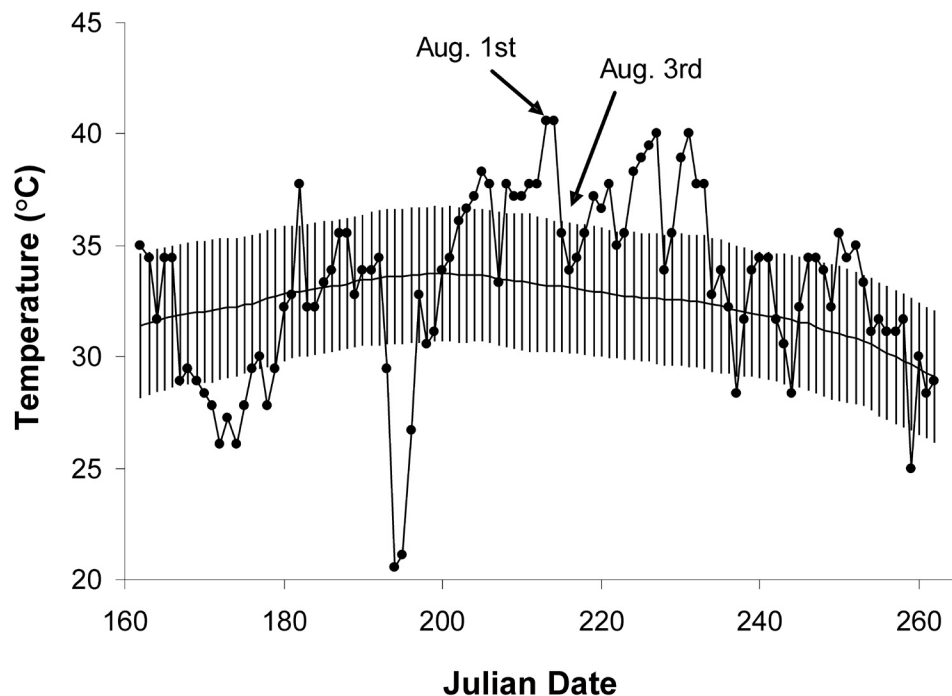


Fig 1. Daily high temperatures ($^{\circ}\text{C}$) that occurred in Newberry County, SC in 1999 (points) relative to the average high temperatures ($\pm s_{\bar{x}}$) for that time of year. The initial collection took place on August 1, 1999 and the second collection took place on August 3rd of the same year.

body size than mass. Furthermore, femur length has been used as a proxy for body size in this system (Mousseau & Roff 1989).

In order to determine the relationship between body size and mortality, we first compared the mean body size of the population before (*i.e.*, all individuals) and after (*i.e.*, just survivors) the selection event took place, using a t-test (Sokal & Rohlf 1995). We then estimated the strength of selection using the univariate variance-standardized selection gradient (β_{σ}). This selection gradient is the most commonly reported and is obtained by regressing relative fitness ($\omega_{\text{relative}} = \omega_{\text{individual}} / \omega_{\text{average}}$) onto the trait of interest (*i.e.*, body size) in units of the population's standard deviation ($Y_{\sigma} = Y_{\text{individual}} / \sigma$). The variance-standardized selection gradient describes the expected change in fitness after one standard deviation increase in the population's mean.

In addition to the univariate variance-standardized selection gradient (β_{σ}), we also present the univariate unstandardized (β) and mean-standardized (β_{μ}) selection gradients, as a convenience for those more comfortable with those formats. The unstandardized selection gradient represents the change in fitness expected after a one-unit increase in the population's mean. And the mean-standardized selection gradient represents the change in relative fitness expected after a 100% increase in the population's mean (Hereford *et al.* 2004). All three selection gradients can be used as an estimate of the strength of selection and only differ in terms of the measurement scale. The two standardized selection gradients (β_{σ} and β_{μ}) can be obtained by dividing the unstandardized selection gradient by either the population's standard deviation ($\beta_{\sigma} = \beta / \sigma$) or its mean ($\beta_{\mu} = \beta / \mu$).

We used survivorship as our estimate of fitness in this study. Each individual collected from the population was assigned either a 1 (*i.e.*, alive) or a 0 (*i.e.*, dead). Relative fitness was then estimated by dividing each of these scores by the population's mean fitness ($\omega_{\text{average}} = 0.427$). Because this measure was dichotomous, we used a logistic regression to test for the significance of our selection gradients (Janzen & Stern 1998). We visualized the selection gradients non-

parametrically using cubic splines and following Schluter (1988). Standard errors were estimated by bootstrapping the dataset 500 times.

In order to determine if the mortality we observed in our collection was the result of natural selection or simply an artifact of our collection procedures, we resampled the population two days after the initial collection (August 3, 1999). On this date, daily high temperatures were still above the average high for that time of year ($\sim 32^{\circ}\text{C}$), but within one standard deviation of the mean (Fig. 1). No mortality was observed during the resampling and a total of 42 individuals were captured on this date (no nymphs were observed).

These crickets were brought back to the laboratory and their femurs measured in the same manner as for our original collection. Our hypothesis was that if the changes in body size that we observed during the initial collection resulted from our collection protocols, then those changes would not be reflected in the second sample. To test this hypothesis, we compared the mean femur length of the crickets collected on August 3rd to the means of the initial collection, both before (*i.e.*, all individuals) and after (*i.e.*, only survivors) the mortality event, using t-tests.

All statistical analyses were performed using SAS version 9.1 (SAS 2002) with the exception of the nonparametric regression which was performed using the program *glmsWin* 1.0 (Schluter & Nychka 2000).

Results

We found that extremely high, but naturally occurring, temperatures selected for increased body size in *A. socius*. The mean femur length of our study population increased from 6.69 ± 0.05 mm ($\pm s_{\bar{x}}$) before selection to 6.82 ± 0.07 mm after selection had occurred (Fig. 2A). This change represented a 1.9% increase in the population's mean phenotype, but was not significant at the $\alpha = 0.05$ level using a one-tailed t-test ($t_{92} = 1.13$, $P = 0.13$). However,

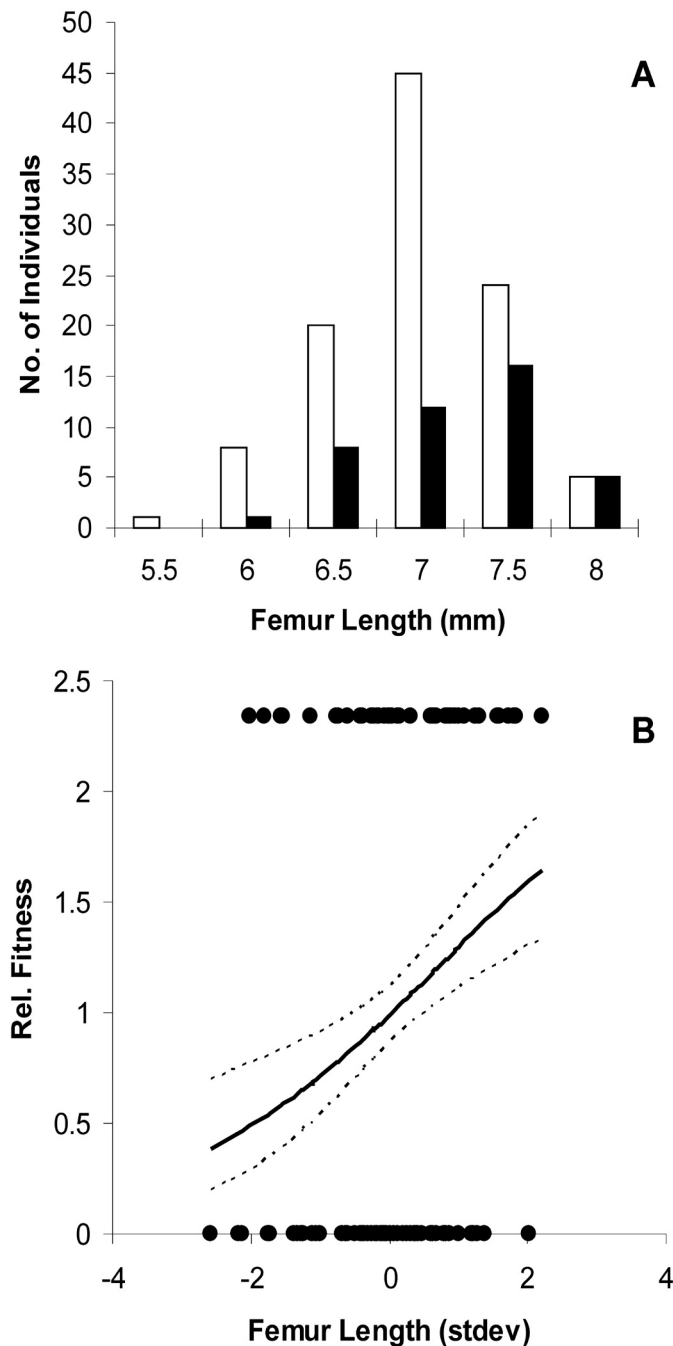


Fig 2. (A) The number of individuals at each femur length (mm) collected before selection (white bars) and after selection occurred (black bars). (B) The nonlinear selection gradient ($\pm s_{\bar{x}}$) estimated by the cubic splines. Fitness is on a relative scale (*i.e.*, $\omega_{\text{mean}} = 1$) and femur length is measured in terms of standard deviations. The raw data are also presented (closed circles).

femur length was positively and significantly related to survivorship based on our logistic regression ($X^2 = 6.18$; $P = 0.01$). The selection gradients ($\pm s_{\bar{x}}$) were estimated as: $\beta_{\sigma} = 0.281 \pm 0.112$; $\beta = 0.591 \pm 0.237$; and $\beta_{\mu} = 3.95 \pm 1.58$. The relationship between femur length and survivorship was roughly linear (Fig. 2B). By back-calculating

our selection gradients, we found that for every 1 mm increase in femur length, a cricket's probability of survival increased by 37%.

The selection pressure we observed did not appear to be caused by our collection protocols. When we resampled the population two days after the initial collection (*i.e.*, August 3rd), no mortality was observed and the average femur length of the population was 6.95 ± 0.08 mm ($\pm s_{\bar{x}}$). This mean was 3.9% larger and significantly different ($t_{143} = 2.85$, $P = 0.0052$) from the initial sample before the selection event; and 1.9% greater, but not significantly different ($t_{82} = 1.13$, $P = 0.2610$) after the selection had occurred (Fig. 3). In fact, because the mean femur length of the August 3rd collection was slightly higher (though not significantly different) from the survivors of our August 1st collection, our protocols may have led to an under-estimation of the strength of selection. As such, our selection gradients should be considered conservative.

Discussion

The magnitude of selection gradients that we observed in this study (Fig. 2) suggests that the strength of temperature-mediated selection in this system is quite strong. The variance-standardized selection gradient (β_{σ}) was 0.281 ± 0.112 ($s_{\bar{x}}$), which is 87% greater than the median strength of selection on body size reported in previous studies (body size median $\beta_{\sigma} = 0.15$, Kingsolver & Pfennig 2007). The strength of selection we observed was also 27% greater than the median values reported across all traits (all traits median $\beta_{\sigma} = 0.22$, Kingsolver & Pfennig 2007).

One factor that may have influenced our estimates of the selection gradient was the fact that we used a univariate measure of fitness as opposed to a multivariate technique (Blows 2007). If the extreme temperatures observed in this study also acted on traits that were genetically correlated with body size, then our estimates would include both direct and indirect selection pressures (Lande & Arnold 1983). In their review, Kingsolver *et al.* (2001) found a strong correspondence in the variance-standardized selection gradients between univariate and multivariate techniques. This trend suggests that the univariate methodology that we employed did not bias our estimate of β_{σ} although we could not test this hypothesis directly because only femur length was measured in this study.

In addition to providing information about the general strength of natural selection, selection gradients help us predict the evolutionary response of a population in the next generation. The change in a population's mean phenotype (in standard deviation units) that is expected in the next generation (R_{σ}) is equal to the product of the variance-standardized selection gradient and the trait's narrow-sense heritability ($R_{\sigma} = \beta_{\sigma} h^2$). Narrow-sense heritability represents the proportion of the total phenotypic variation that can be attributed to the additive effect of genes (Falconer & Mackay 1996). Based on our observed selection gradients (Table 1) and a previously published estimate of the heritability for femur length in *A. socius* ($h^2 = 0.45 \pm 0.04$ $s_{\bar{x}}$, Mousseau & Roff 1989), we predict that femur length will increase by 0.13 standard deviations in the next generation — approximately 0.06 mm or 0.8%. If these selection pressures were applied consistently and the heritability remained stable (Roff & Mousseau 1999), then the mean femur length of the population would increase by 50% in 339 generations.

Our data suggest that increases in body size brought about by exposure to extremely high temperatures can affect the body size of *A. socius* in the next generation. This observation has an important implication for broad-scale patterns of geographic variation in body size among ectotherms. Although endotherms (Ashton

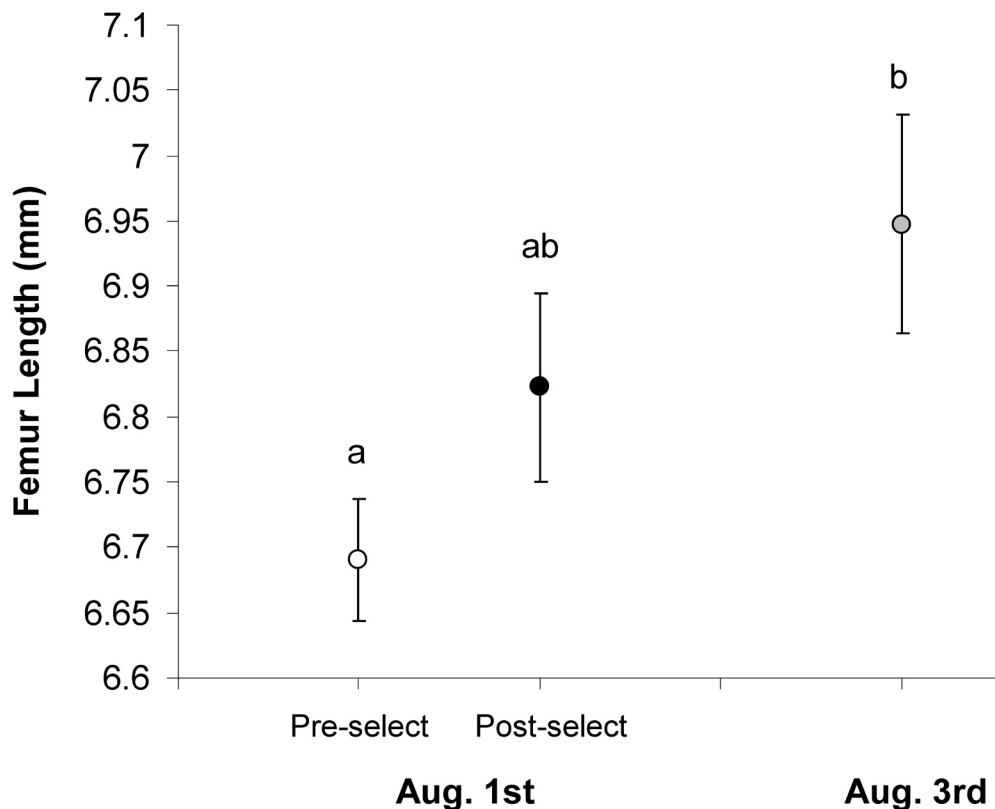


Fig 3. The mean \pm $s_{\bar{x}}$ for femur length (mm) of crickets collected on August 1st before selection (open circle) and after selection (closed circle), as well as those collected on August 3rd (gray circles). Letters indicant significant differences at the $\alpha = 0.05$ level.

et al. 2000, Zink & Remsen 1986) and many ectotherms (Ashton & Feldman 2003, Litzgus *et al.* 2004) tend to exhibit larger body sizes at higher latitudes (a pattern known as Bergmann's rule), other ectotherms (Ashton & Feldman 2003, Huey *et al.* 2000) including many orthopterans (Masaki 1967, Masaki 1978, Mousseau 1997) tend to be larger at lower latitudes (*i.e.*, they follow the converse of Bergmann's rule).

Converse Bergmann's size clines are thought to be caused primarily by the time constraints that season length places on an organism's growth (Roff 1980). Given similar growth rates, larger body sizes require longer periods of time to produce than smaller body sizes. Because season lengths tend to be longer at lower latitudes, organisms that follow the converse of Bergmann's rule are thought to have more time for growth and therefore are able to reach larger sizes.

While this explanation is generally accepted (Blanckenhorn & Demont 2004, Chown & Klok 2003, Mousseau 1997, Stillwell *et al.* 2007), our data suggest that periodically occurring extreme heating events may also contribute to the converse of Bergmann's rule. The high temperatures that we observed in 1999 were atypical for the area. In Newberry County, daily high temperatures of 40.5°C or greater have only occurred twelve times between 1948 and 2001 (including twice in 1999) or on average of once every 4.5 years (Williams *et al.* 2006). If the rate at which these high temperatures are encountered increases with decreasing latitudes (as we would expect) then selection for larger body sizes should be stronger at low, relative to high, latitudes. Our results suggest that selection pressure associated with periodically occurring extreme heating events may contribute to the converse of Bergmann's rule. Furthermore, if these extreme heating events occur with greater frequency as a result of projected global warming (IPCC 2001), we anticipate that the number of ectothermic species that follow the

converse of Bergmann's rule will increase over time.

Finally, although we have assumed that the mortality we observed was caused by desiccation, it may have been due to heat shock (Lindquist 1986). In order to distinguish between these two possibilities, populations would have to be reared in the laboratory and subjected to similarly high temperatures (~40.5°C) under both moist and dry conditions. If the mortality observed in this study was due to desiccation, then we would expect lower mortality rates in the moist treatment.

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