

METABOLIC CONSTRAINTS AND CURRENCIES IN ANIMAL ECOLOGY

Phenotypic clines, energy balances and ecological responses to climate changeLauren B. Buckley^{1*}, César R. Nufio^{2,3} and Joel G. Kingsolver¹

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Summary

1. The Metabolic Theory of Ecology has renewed interest in using energetics to scale across levels of ecological organization. Can scaling from individual phenotypes to population dynamics provides insight into why species have shifted their phenologies, abundances and distributions idiosyncratically in response to recent climate change?

2. We consider how the energetic implications of phenotypes may scale to understand population and species level responses to climate change using four focal grasshopper species along an elevation gradient in Colorado. We use a biophysical model to translate phenotypes and environmental conditions into estimates of body temperatures. We measure thermal tolerances and preferences and metabolic rates to assess rates of energy use and acquisition.

3. Body mass declines along the elevation gradient for all species, but mass-specific metabolic rates increases only modestly. We find interspecific differences in both overall thermal tolerances and preferences and in the variation of these metrics along the elevation gradient. The more dispersive species exhibit significantly higher thermal tolerance and preference consistent with much of their range spanning hot, low elevation areas. When integrating these metrics to consider metabolic constraints, we find that energetic costs decrease along the elevation gradient due to decreasing body size and temperature. Opportunities for energy acquisition, as reflected by the proportion of time that falls within a grasshopper's thermal tolerance range, peak at mid elevations. We discuss methods for translating these energetic metrics into population dynamics.

4. Quantifying energy balances and allocation offers a viable approach for predicting how populations will respond to climate change and the consequences for species composed of populations that may be locally adapted.

Key-words: biophysical model, energy budget, energy use and costs, grasshopper, metabolic rate, phenotype, population dynamics, thermal tolerance

Introduction

Ecologists have long called for using individual ecologies to understand population dynamics (Schoener 1986; Kingsolver 1989; Koehl 1989; Lawton 1991). Linking individual ecologies to population dynamics requires addressing three primary questions (*sensu* Kingsolver 1989): (i) how do the organismal phenotypes interact with environmental conditions to determine the physiological experience of organisms? (ii) how do these physiological experiences constrain individual ecologies including

behaviour and rates of energy use and acquisition? and (iii) how do these behavioural and energetic implications determine population dynamics? The Metabolic Theory of Ecology (hereafter MTE, Brown *et al.* 2004) has renewed interest within the last decade in using energetics to scale across levels of ecological organization. The MTE defines metabolism to encompass the acquisition and processing of energy from the environment and the allocation of this energy to survival, growth and reproduction (Brown *et al.* 2004). Studies of clinal variation have reveal biogeographical and evolutionary consequences of individual energetics (Angilletta, Sears & Steury 2004; Karl & Fischer 2008; Ellers & Driessen 2011).

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We illustrate this integration from individual energetics to abundance and distribution using a case study: grasshopper communities along a 2000 m elevation gradient near Boulder, CO. The grasshopper communities were initially surveyed by Gordon Alexander between the 1930s and the 1960s. Recent resurveys have found that the extent and even direction of phenological shifts in response to recent climate change have varied between species and along the gradient (Nufio *et al.* 2010). Why have some populations and species exhibited more pronounced responses to recent climate change than others? Can contrasting metabolic constraints resulting from phenotypic differences account for differential responses to recent climate change between species and along the gradient?

Idiosyncratic responses, particularly species shifting their distributions to different extents and in different directions, have frequently been observed in response to past climate change across a variety of taxa (Williams & Jackson 2007). Yet, we are largely unable to account for or accurately predict these individualistic responses. Efforts to use species traits to predict responses to recent climate change generally predict only a small, but significant, amount of variation (Buckley & Kingsolver 2013). One potential explanation is that the interaction between a species' phenotype and environmental conditions has distinct energetic and demographic implications. Here, we investigate this explanation by documenting clinal variation in grasshopper traits and climates and exploring the ecological implications of this variation. By combining data on phenotypic clines with weather and climate data along an elevation gradient, we develop biophysical and energetic models to explore population and species differences in body temperature, activity and energy balance. We also review approaches for characterizing organism–environment interactions and their impacts on individual ecologies (challenges 1 and 2 introduced above) and illustrate these approaches with our grasshopper case study. We conclude by discussing techniques for translating this information into population dynamics (challenge 3).

CLINAL VARIATION AND ITS ENERGETIC IMPLICATIONS

Studying phenotypic variation across elevation and other environmental gradients can identify traits that may determine energetics and fitness in a given environment (Chown, Gaston & Robinson 2004; Helmuth, Kingsolver & Carrington 2005; Gaston *et al.* 2009; Kingsolver 2009). Clinal variation linked to thermal environments has been widely observed across taxa (Angilletta, Niewiarowski & Navas 2002; Blanckenhorn & Demont 2004; Gotthard 2004). Significant clinal variation along elevation gradients has been particularly well documented for insects. Gradients in colour influence solar absorbance and body temperatures and thermal tolerances tend to match environmental temperatures. A well-documented form of insect clinal variation is the temperature-size rule,

wherein cold temperatures delay development and result in larger body sizes (Whitman 2008). High-elevation insects typically respond to the reduced and variable temperatures and short growing seasons by reducing the number of developmental stages, generations or developmental thresholds (Hodkinson 2005).

Phenotypic traits including size and shape, coloration, behavioural posture and microhabitat selection determine how environmental conditions translate into body temperatures. Environmental factors such as radiation intensities and wind speeds influence body temperatures in addition to air and surface temperatures. Biophysical models enable the integration of environmental conditions and species traits to predict body temperatures. Biophysical models are heat budgets that balance energy input from solar radiation against the sum of thermal radiation, convection and conduction (Porter & Gates 1969; Gates 1980; Campbell & Norman 2000). The translation between environmental and body temperatures is complicated by behavioural thermoregulation, which can effectively buffer changes in environmental temperature (Kearney, Shine & Porter 2009).

Energy acquisition by ectothermic animals is constrained by their ability to locomote in order to gather resources and their ability to process the gathered resources via handling and assimilation. These processes are highly dependent on body temperatures. Rates of locomotion, feeding, assimilation and other aspects of performance form a humped-shaped function of temperature (i.e. a thermal performance curve) (Huey & Kingsolver 1989). These curves underlie many strategies to address the energetic implications of phenotypes. Activity time, which can be estimated by comparing thermal limits for locomotion to body temperatures, has frequently been used to quantify metabolic constraints (Kearney & Porter 2004; Buckley 2008; Sinervo *et al.* 2010).

Temperature also affects rates of energy use. In ectotherms, body temperature exerts an exponential effect on metabolic rates, with individuals with warmer body temperatures requiring disproportionately more energy per unit time (Gillooly *et al.* 2001). The metabolic impacts of recent climate warming on ectotherms are estimated to be equivalent in tropical and temperate regions despite the greater magnitude of warming in temperate regions. The equivalency is due to the exponential temperature dependency of metabolic rate occurring at higher temperatures in the tropics (Dillon, Wang & Huey 2010). Rates of energy acquisition and use can be compared to estimate the amount of discretionary energy available to organisms for growth and reproduction.

CASE STUDY: GRASSHOPPERS ALONG AN ALPINE ELEVATION GRADIENT

Our focal taxa, grasshoppers, exemplify how phenotypes vary along elevation gradients and influence energetics and demography. Grasshoppers tend to reverse the temperature-size rule, perhaps due to other constraints on size

such as food availability (Whitman 2008). Their thermal conditions have been found to affect digestive efficiency (Harrison & Fewell 1995) and life-history traits such as clutch and egg sizes (Dearn 1977; Hassall *et al.* 2006). In one of our focal species (*Melanoplus sanguinipes*), both metabolic rates (Rourke 2000) and thermoregulatory behaviours (Samietz, Salser & Dingle 2005) vary among populations along an elevation gradient in California. High-elevation populations of *M. sanguinipes*, which experience an abbreviated growing season, exhibit accelerated juvenile development and a reduced number of days to first reproduction (Dingle, Mousseau & Scott 1990). There is a higher incidence of diapause, and diapause occurs at a later developmental stage in these populations. Clinal variation in diapause may indicate adaptation to environmental uncertainty, whereas variation in development rates may indicate adaptation to season length (Dingle, Mousseau & Scott 1990).

Many grasshopper species, especially at higher elevations, have evolved shorter wings, leading to a reduction in flight capacity and dispersal distances. Short-winged and flightless species in mountain regions show greater genetic differentiation among geographical populations and a greater potential for local adaptation (Knowles 2000; Knowles & Otte 2000). We examine four focal species that are expected to differ in their exposure to climate change and their potential for local adaptation. *Melanoplus dodgei* and *Aeropedellus clavatus* are short-winged species with limited dispersal among sites along the elevational gradient, increasing their potential for local adaptation. *Camnula pellucida* and *M. sanguinipes* are long-winged species that are occasionally collected as accidentals at sites along the gradient where juveniles are not collected. These latter species thus have a higher dispersal capacity and a greater potential for gene flow across populations. All four of these species occur from the upper foothills to the subalpine, while *M. dodgei*, *A. clavatus* and occasionally *M. sanguinipes* occur in the alpine.

Abundance changes over the past 50 years have varied among species and along the elevation gradient (Fig. S1, Supporting information). The fastest developing species (*A. clavatus* and *M. dodgei*) have advanced their phenology (Fig. S1, Supporting information). The slowest developing species (*C. pellucida*) has advanced phenology at high elevation but delayed phenology at lower elevation. The species with intermediate phenology (*M. sanguinipes*) has delayed phenology.

The three grasshopper genera are phylogenetically distinct and likely established in North America following a complex history of dispersal events (Contreras & Chapco 2006). *Melanoplus sanguinipes* is broadly distributed, while the clade containing *M. dodgei* diversified in the Rocky Mountains following multiple dispersal events [with the split between melanopline genera occurring $\sim 10^6$ ya (Knowles & Otte 2000)]. Given these phylogenetic distinctions and our small number of focal species, we do not account for evolutionary history in our analyses.

In this study, we examine phenotypic variation among populations and species across four sites along the 40th N parallel in Boulder County, CO: Eldorado (1740 m), Bettaso Preserve (1980 m), A1 (2185 m), B1 (2591 m), C1 (3048) and D1 (3749 m). The habitats at these sites are grassy clearings associated with upper prairie, foothill, montane, subalpine and alpine life zones, respectively. First, we document clinal variation in body size, thermal tolerance and metabolic rate for the four focal grasshopper species. Second, we develop a simple biophysical model that can be used to integrate phenotypic and weather data in order to predict patterns of body temperatures for each species along the elevational gradient. Finally, we examine the implications of the clinal variation for rates of energy use and the potential duration of activity along the elevation gradient.

Materials and methods

THERMAL TOLERANCES AND METABOLIC RATE

We assessed thermal tolerance and metabolic rate for each grasshopper as described below. Between 8 and 25 individuals were measured for each population (mean $n = 13$, median $n = 12$). We first measured preferred body temperatures (PBT) using a thermal gradient constructed on an aluminium sheet ($0.125'' \times 24'' \times 48''$). We placed one end in an ice bath and the other on a hotplate (Springate & Thomas 2005), which created a temperature gradient spanning *c.* 5–50 °C. Grasshoppers were placed within the 5-cm-wide lanes created by corrugated plastic dividers that ran the long way across the thermal gradient. A clear acrylic lid was then placed above the gradient with holes for circulation and thermocouple measurements, and the grasshoppers were allowed to acclimate for 30 min. We then used an Extech type K thermocouple to monitor the thermal gradient and record the temperatures associated with the position of grasshoppers every 10 min over a 50-min period (following Forsman 2000; Springate & Thomas 2005). During the acclimation period, the grasshopper moved throughout the thermal gradient before reducing activity. Most grasshoppers spent the duration of the observation period resting in one position.

The relationship between metabolic rate and temperature for each population was measured using stop flow respirometry as follows. Grasshoppers were placed into 60-mL syringes and stored in dark incubators at 20, 30 and 40 °C. Grasshoppers were allowed to acclimate for 1 h, and then, the syringes were flushed with CO₂ and H₂O free air for 1 min at a flow rate of 100 mL min⁻¹. Water was removed with Drierite and CO₂ was removed with soda lime using a syringe scrubber. The syringes were then sealed at a volume of 50 mL using a Luer Loc and placed in a dark chamber. After one hour, a 35-mL volume of air was injected from each syringe into a Foxbox Gas Analysis System (Sable Systems) for analysis of CO₂ and O₂ concentrations. Rates of CO₂ and O₂ consumption were calculated using the relationships in Lighton (2008). Closed respirometry techniques analogous to ours have frequently been used to measure the temperature dependence of metabolic rates, but we note the rate estimates can be effected by grasshopper activity (Irlich *et al.* 2009).

Following metabolic rate measurements, we measured both critical thermal minima and critical thermal maxima, CT_{\min} and CT_{\max} , which were defined as the lower and upper temperatures at which the grasshoppers were no longer able to right themselves. For these measurements, grasshoppers were placed individually into 50-mL centrifuge tubes, which were slowly ($\sim 0.2\text{ }^{\circ}\text{C min}^{-1}$) cooled or heated in a water bath. Given that warming rates may influence estimates of critical thermal limits, we chose an intermediate rate (Chown *et al.* 2009). We waited an hour after the cooling to commence warming. We measured body mass (g), body and femur length (mm), and width (mm).

BIOPHYSICAL MODEL

We introduce our biophysical model as an overview of how phenotypes and environmental conditions interact to determine body temperatures. We use an energy budget to describe the flow of energy between the grasshopper and the environment: $Q_s = Q_t + Q_c + Q_{\text{cond}}$. Here, Q_s is the total input of heat due to solar radiation. Q_t describes the flux of thermal radiative heat due to both incoming thermal radiation (ground and sky) and that emitted by the grasshopper. Q_c is flux of heat between the grasshopper and the surrounding fluid (air) via convection. Q_{cond} is the flux of heat between the grasshopper's body and the solid surfaces with which the grasshopper's body is in contact via conduction. We omit evaporative heat loss as it should be negligible for the grasshopper (Anderson, Tracy & Abramsky 1979).

The solar radiative heat flux is estimated as the sum of direct ($Q_{s,\text{dir}}$), diffuse ($Q_{s,\text{dif}}$) and reflected ($Q_{s,\text{ref}}$) components (Kingsolver 1983):

$$\begin{aligned} Q_s &= Q_{s,\text{dir}} + Q_{s,\text{dif}} + Q_{s,\text{ref}} \\ Q_s &= \alpha A_{s,\text{dir}} H_{s,\text{dir}} / \cos(z) + \alpha A_{s,\text{ref}} H_{s,\text{dif}} + \alpha r_g A_{s,\text{ref}} H_{s,\text{ttl}} \end{aligned} \quad \text{eqn 1}$$

Each component is calculated as the product of the solar absorptivity of the grasshopper [we assume $\alpha = 0.7$, (Anderson, Tracy & Abramsky 1979)], the horizontal flux of solar radiation ($H_{s,\text{dir}}$, $H_{s,\text{dif}}$ and $H_{s,\text{ttl}}$ for the direct, diffuse and total fluxes, respectively) and the silhouette area of the grasshopper exposed to solar radiation ($A_{s,\text{dir}}$, $A_{s,\text{dif}}$ and $A_{s,\text{ttl}}$ for the direct, diffuse and total surface areas, respectively). The direct radiation is adjusted for the zenith angle (z , degrees), which is the angle of the sun away from vertical.

We calculate the surface area by approximating the body of a female grasshopper as a rotational ellipsoid (Samietz, Salsler & Dingle 2005). The major axis is equal to the grasshopper's length. We calculate the semi-minor axis (half of the grasshopper's width) as $a = (0.365 + 0.241 \cdot 1000 L) / 1000$ using a regression from Lactin & Johnson (1998). If $e = \sqrt{1 - a^2/c^2}$, surface area can be calculated as follows:

$$A = 2\pi a^2 + \frac{2\pi ac}{e \arcsin(e)}. \quad \text{eqn 2}$$

The ratio of silhouette area to surface of a grasshopper is a linear function of zenith angle: $A_s/A = 0.19 - 0.00173z$. Thus, $A_{s,\text{dir}} = A_{s,\text{ref}} = (0.19 - 0.00173z)A$. We partitioned the observed total radiation ($H_{s,\text{ttl}}$) into diffuse ($H_{s,\text{dif}}$) and direct ($H_{s,\text{dir}}$) components using the polynomial function of a clearness index, k_t , developed by Erbs, Klein & Duffie (1982).

We estimate thermal radiative flux as the sum of radiation from the sky and ground. We assume that one half of the

grasshopper's body is subject to atmospheric radiation and the other half is subject to thermal radiation from the ground surface. Thermal radiation is calculated using the Stefan–Boltzmann law, which states that radiative flux is proportional to the fourth power of the absolute temperature of a body. Here, T_b is the absolute body temperature, T_g is the absolute ground surface temperature and T_{sky} is the equivalent black body sky temperature [$0.0552 \cdot (T_a + 273)^{1.5}$, (Swinbank 1963)]. The Stefan–Boltzmann constant (σ) characterizes the proportionality of this relationship. The thermal emissivity (ϵ) accounts for incomplete absorption or emission of thermal radiation, but in this case, we assume that both the grasshopper and ground are perfect black bodies ($\epsilon = 1$). We account for the thermal radiative heat-transfer surface area ($A_t = A$). The relationship is thus:

$$Q_t = 0.5A_t \in \sigma (T_b^4 - T_{\text{sky}}^4) + 0.5A_t \in \sigma (T_b^4 - T_g^4). \quad \text{eqn 3}$$

Convective heat flux is estimated as the product of the convective heat-transfer coefficient in turbulent air (h_{cs}), the grasshopper's surface area exposed to convective heat flux ($A_c = A$) and the temperature difference between the grasshopper's body temperature (T_b) and air temperature (T_a):

$$Q_c = h_{\text{cs}} A_c (T_b - T_a). \quad \text{eqn 4}$$

We calculate h_{cs} from the convective heat-transfer coefficient as $h_{\text{cs}} = h_c(-0.007z/L + 1.71)$ where $z = 0.001$ m is the height above the ground. We use an empirically derived relationship for grasshoppers to estimate the heat-transfer coefficient, h_c ($\text{Wm}^{-2}\text{C}^{-1}$) (Lactin & Johnson 1998): $h_c = \text{Nu} \cdot K_f / L$ where the thermal conductivity of fluid, $K_f = 0.024 + 0.00007(T_a + 273)$ $\text{Wm}^{-1}\text{K}^{-1}$.

We use an empirical relationship from Anderson, Tracy & Abramsky (1979) to estimate the Nusselt number, N_u , as $N_u = 0.41 \text{Re}^{0.5}$ where Re is the Reynolds number. $\text{Re} = uL/\nu$, where u is wind speed (m s^{-1}) and ν is the kinematic viscosity of air ($\text{m}^2 \text{s}^{-1}$) ($\nu = 15.68 \times 10^{-6}$ at 300 K).

The rate of conduction is a function of the body area in contact with the substrate and the temperature differential between the body and the surface:

$$Q_{\text{cond}} = h_{\text{cut}} A_{\text{cond}} (T_b - T_g) / T \quad \text{eqn 5}$$

where h_{cut} is the thermal conductivity of the grasshopper cuticle (approximated as $0.15 \text{ W m}^{-1} \text{ K}^{-1}$; value for hornets; Galushko *et al.* 2005); A_{cond} is the surface area of the grasshopper in contact with the substrate; and T is the cuticle thickness (approximated as 6×10^{-5} m; Galushko *et al.* 2005). We only model conductance through the cuticle as we assume that the interior of the grasshopper is well mixed.

WEATHER DATA

We recorded (shaded) air and soil temperatures (Pace PT907 30k ohm thermistor, $\pm 0.15\text{ }^{\circ}\text{C}$), radiation (Pace SRS-100 Silicon Photodiode, 400–1100 nm, $\pm 5\%$ accuracy) and windspeed (anemometer, 0.9–78 m s^{-1} range, $\pm 5\%$ accuracy) averaged over 3-min intervals at our four focal sites using a Pace XR5 datalogger (Pace Scientific, Mooresville, NC, USA). We used these weather data to estimate grasshopper body temperatures, meta-

bolic rates and the potential for activity at 3-min intervals. These estimates were then averaged between sunrise and sunset across July for each site.

We additionally monitored the body temperatures of grasshopper physical models placed on the ground in representative vegetation. We constructed the physical models by placing thermistors into the thorax and abdomen of previously frozen grasshoppers, which were then dried and coated with clear epoxy. We monitored the temperatures of live and dead grasshoppers (by inserting a thin, type k thermocouple) along with our physical model in a variety of weather conditions to confirm that our physical model provides an accurate estimate of grasshopper body temperatures. We used the grab-and-stab method with a Type K thermocouple to detect the effect of behavioural thermoregulation on the relationship between ambient and air temperature.

Results

CLINAL VARIATION IN MASS, THERMAL TOLERANCE AND METABOLIC RATE

Species ($F = 24.5$, $P < 10^{-15}$), elevation ($F = 6.1$, $P < 10^{-15}$) and sex ($F = 77.4$, $P < 10^{-15}$) are significant determinants of body mass in an ANOVA ($F_{5,211} = 33.2$, $R^2 = 0.44$, $P < 10^{-15}$, Fig. 1). Grasshopper body mass declines with elevation (estimate $\pm 95\%CI = -7.4 \times 10^{-15} \pm 3.5 \times 10^{-4}$) and males are significantly smaller than females. The decline in body mass with elevation does not vary significantly among species. Indeed, all pairwise interactions between species, sex and elevation are non-significant and were thus omitted from the ANOVA.

Interspecific differences exist in both overall thermal tolerances and preferences and in the variation of these metrics along the elevation gradient (Fig. 2, Table 1). The preferred body temperatures (PBT, mean of observed temperatures in thermal gradient) and critical thermal minima (CT_{min}) of the two more dispersive species, *C. pellucida*

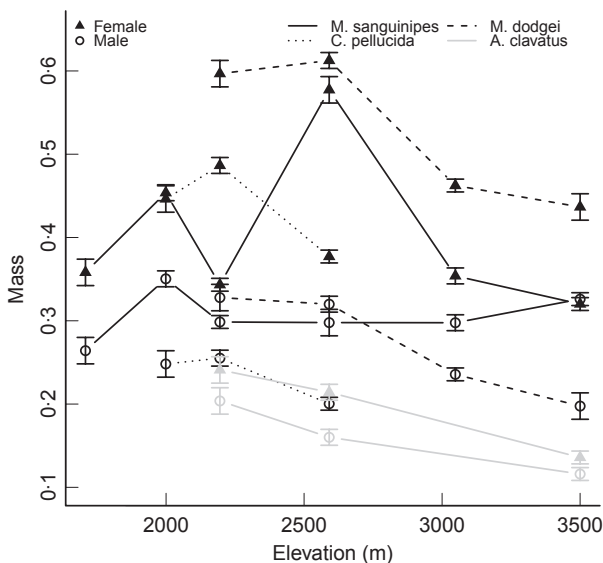


Fig. 1. Mass (mean \pm SE) generally declines with elevation for both male and female grasshoppers of each focal species.

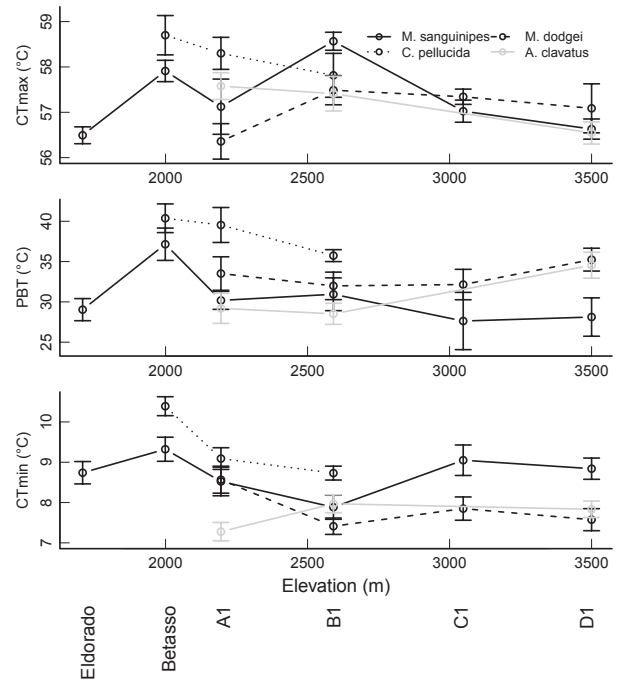


Fig. 2. Critical thermal limits (CT_{max} , CT_{min}) and preferred body temperatures (PBT) (means \pm SE) exhibit only limited variation along the elevation gradient for the four focal species.

Table 1. ANOVA models for critical thermal minima (CT_{min}) and maxima (CT_{max}) and preferred body temperatures (PBT)

	CT_{min} $F_{d.f., 205}$	PBT $F_{d.f., 151}$	CT_{max} $F_{d.f., 204}$
Species	24.7***	12.9***	5.7***
Elevation (m)	0.5	0.1	0.5
Mass (g)	0.01	4.3*	1.3
Species : elevation	4.9**	4.5**	2.4

Significant levels are depicted ($P < 0.1$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$).

and *M. sanguinipes*, are significantly higher than those of the other species. PBT increases significantly with mass. Although there is no significant main effect of elevation, there is a significant interaction between species and elevation. The PBTs of *C. pellucida* and *M. sanguinipes* decline more steeply with elevation than do the PBTs of other species. The CT_{min} of *C. pellucida* also declines more steeply with elevation. The critical thermal maxima (CT_{max}) of *M. dodgei* was significantly lower than that of the other species and exhibited less of a tendency to decline along the elevation gradient than the other species. We omitted sex and interactions with mass from the ANOVAs as they were not significant in any of the models. We confirmed the appropriateness of these omissions using stepwise model selection.

Resting metabolic rate (B) is expected to scale with mass (M ,g) and body temperature (T_b ,K) as $B \propto M^x e^{-E/kT_b}$, where x is the scaling coefficient, E is the apparent activation energy of biochemical reactions and k is the Boltzmann

constant ($k = 8.62 \times 10^{-5} \text{ eV K}^{-1}$) (Gillooly *et al.* 2001). We linearize the equation to estimate the mass, temperature and elevation (m, h) dependence of metabolic rate:

$$\ln(B) = b_0 + b_1 \ln(M) + b_2(1/kT_b) + b_3h. \quad \text{eqn 6}$$

We first fit the expression for resting metabolic rate (B , mL $\text{CO}_2 \text{ h}^{-1}$) for all species together in a single ANOVA to best estimate the scaling coefficients (Table 2). B varies significantly among species ($F = 16.8$, $P < 10^{-10}$) but not with sex ($F = 2.8$, $P = 0.1$). We estimated a steep scaling coefficient (b_1 estimate \pm 95% CI = 0.90 ± 0.07) between the natural log of metabolic rate and the natural log of body mass. B increases significantly with increasing temperature ($b_2 = -0.48 \pm 0.02$). Notably for understanding species' responses to the elevation gradient, we found that B increases slightly but significantly with elevation ($b_3 = 8.68 \times 10^{-5} \pm 0.002$). We did not detect significant interactions in the ANOVA that alter these conclusions. Temperature, elevation and species remain significant when controlling for individual as a random variable in a repeated measure ANOVA.

We used the scaling coefficient estimated above ($b_1 = 0.90$) to mass-correct the metabolic rate data in Fig. 3. Mass-corrected metabolic rate (B_m , mL $\text{CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) increases modestly up the elevation gradient. We next fitted the expression for resting metabolic rate (B) for each species independently. We found that B increases significantly with elevation for all species but only the two *Melanoplus* species exhibit significant increases in B with elevation (Table 2). Sex was not a significant effect for any of the species, so it was dropped from the ANOVAs.

BODY TEMPERATURES AND RATES OF ENERGY ACQUISITION AND USE

We validated our biophysical model by comparing the body temperatures predicted by the model to that measured for grasshopper physical models. We found that the model estimated body temperatures well when parameterized with soil temperature (Fig. 4). We used our biophysical model to estimate female body temperature,

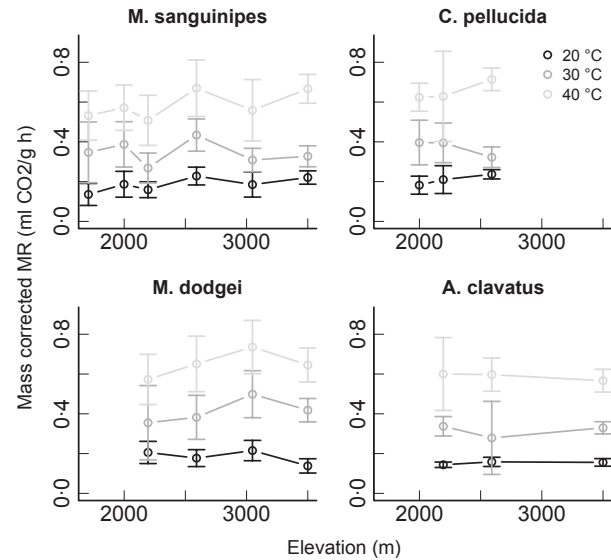


Fig. 3. Mass-corrected metabolic rates (B_m , mL $\text{CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) (means \pm SE) increase substantially with temperature but only modestly with elevation.

T_e , at 3-min intervals based on soil temperature, wind-speed and radiation data during daylight for July 2011 and accounting for altitudinal variation in mass and length. Body temperatures are similar between species across the elevation gradient with slight variation corresponding to body size: the largest species, *M. dodgei*, has slightly higher T_e s, whereas the smallest species, *A. clavatus*, has slightly lower T_e s. Body temperatures decline with elevation until reaching the highest site (C1), where high levels of radiation can elevate body temperatures (Figs 5a and S2, Supporting information).

We use species-specific fits to our metabolic rate equation above to estimate rates of energy use along the elevation gradient. Although mass-specific metabolic rates increase with elevation, this effect is overwhelmed by the decline in mass and T_e at higher elevations. Thus, rates of energy use generally decline with elevation and are highest for the largest species (Fig. 5b). However, rates of energy

Table 2. ANOVA models fitting metabolic rate for all species combined and each species independently. Parameter estimates are provided along with 95% confidence intervals

	b_1		b_2		b_3		Full ANOVA		
	Estimate	F	Estimate	F	Estimate	F	F	P	r^2
All species	0.90 ± 0.07	1682.3***	0.48 ± 0.02	2254.5***	$8.68 \times 10^{-5} \pm 0.002$	21.2***	$F_{[7,642]} = 573$	$<10^{-15}$	0.86
<i>Aeropedellus clavatus</i>	0.84 ± 0.10	290.1***	0.54 ± 0.02	1533.3***	$3.95 \times 10^{-4} \pm 7.1 \times 10^{-5}$	1.2	$F_{[3,139]} = 608$	$<10^{-15}$	0.93
<i>Cammula pellucida</i>	0.90 ± 0.13	197.7***	0.43 ± 0.04	351.3***	$4.99 \times 10^{-4} \pm 1.9 \times 10^{-4}$	0.3	$F_{[3,101]} = 183$	$<10^{-15}$	0.84
<i>Melanoplus dodgei</i>	0.98 ± 0.10	353.6***	0.48 ± 0.04	470.7***	$1.24 \times 10^{-4} \pm 1.1 \times 10^{-4}$	4.6*	$F_{[3,173]} = 276$	$<10^{-15}$	0.83
<i>Melanoplus sanguinipes</i>	0.85 ± 0.11	210.3***	0.47 ± 0.03	627.9***	$1.08 \times 10^{-4} \pm 6.3 \times 10^{-5}$	11.2**	$F_{[3,283]} = 221$	$<10^{-15}$	0.79

Significant levels are depicted (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

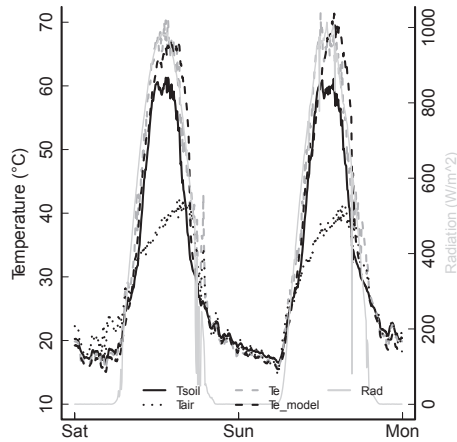


Fig. 4. The biophysical model predicts reasonably well the body temperature of a *Melanoplus sanguinipes* grasshopper physical model over 2 days in Eldorado. The input for the biophysical model is soil temperature and radiation data. We additionally depict air temperature.

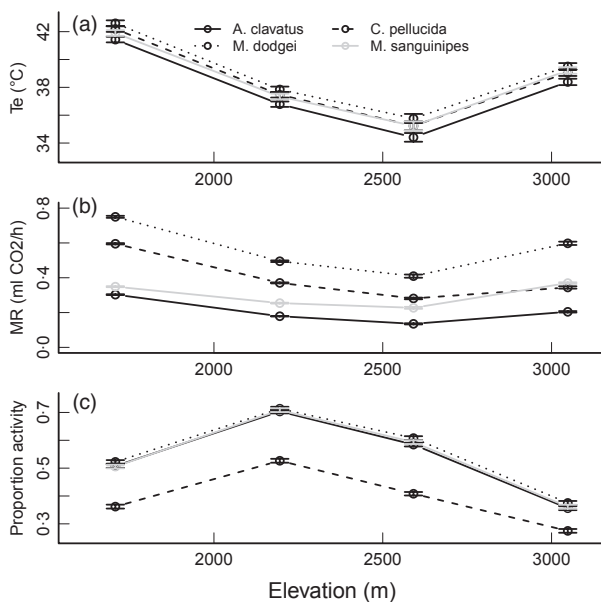


Fig. 5. The (a) operative environmental temperatures (T_e , °C) predicted by the biophysical model, (b) metabolic rates ($\text{mL CO}_2 \text{ h}^{-1}$) accounting for T_e and mass, and (c) the proportion of time that falls within the grasshopper's thermal tolerance range. Data (means \pm SE) are averaged between sunrise and sunset during August 2011.

use rise at the highest site due to higher values of T_e . We next estimate the proportion of daylight hours that are available to the grasshoppers for activity, a quantity that closely corresponds to the ability of ectotherms to acquire resources (Fig. 5c). We assume that grasshoppers can be active when their body temperatures fall within the 20% and 80% quantiles of the body temperatures observed within the thermal gradient. We bracket the potential body temperatures by assuming that the grasshopper can seek shade to avoid overheating. Comparing ambient temperature to grasshopper body temperature reveals an

approximately linear relationship at the low elevation site (Fig. S3, Supporting information). This suggests that the influence of behavioural regulation on this relationship is modest, at least at low elevation.

The activity limits are similar across species with the exception of the thermally warm adapted *C. pellucida* (*A. clavatus*: 22.9–37.2 °C, *C. pellucida*: 35.0–43.1 °C, *M. sanguinipes*: 23.3–37.5 °C, *M. dodgei*: 24.9–40.2 °C). Quantile regressions confirm that the lower ($t = 3.8$, $P < 10^{-3}$) and upper ($t = 6.6$, $P < 10^{-15}$) thermal limits are higher for *C. pellucida* than the other species. We estimate that activity durations are low at the lowest elevation site due to overheating. Activity times then decline with elevation among the higher elevation sites (C1, Fig. 5c). *Camnula pellucida* experiences much more restricted activity time than the other species.

Discussion

Significant clinal variation is characteristic of insects along elevation gradients (Hodkinson 2005), and in this study, we detected a decline in grasshopper mass with elevation. This variation in mass influences metabolic rates and has been broadly observed to influence grasshopper physiology, behaviour and fitness (Whitman 2008). We detect only modest clinal variation in thermal tolerances. Differences in thermal tolerance are thus unlikely to account for the differences in responses to climate change along the gradient. We find that the more dispersive species, *C. pellucida* and *M. sanguinipes*, have significantly higher CT_{max} and PBT, consistent with much of their range spanning hot, low elevation areas. Contrary to our expectations, CT_{max} and PBT of these species also decline more rapidly along the elevation gradient. The less dispersive *M. dodgei* exhibits lower CT_{min} and a lesser decline in CT_{min} along the elevation gradient. Our populations are less separated geographically than populations elsewhere that have been found to exhibit local adaptation (Dingle, Mousseau & Scott 1990). Gene flow may be sufficient to hinder local adaptation of either the less or more dispersive species. However, plasticity may obscure phenotypic differences between field-collected populations. Common garden experiments will improve our ability to detect genetic differences.

Previous research suggests that mass-specific metabolic rates tend to increase with elevation, potentially to counter shorter growing seasons and decreased performance in cooler temperatures (Chappell 1983; Rourke 2000). Mass-specific metabolic rates do increase along our focal elevation gradient, but the increase is modest. We find that metabolic rate increases with mass more rapidly than the $\frac{3}{4}$ exponent expected by metabolic theory (Brown *et al.* 2004). This finding is consistent with observations for other grasshopper species. Indeed, a scaling coefficient of 1.06 was estimated for adults of 32 Orthoptera species (Fielding & DeFoliart 2008).

Using our data on clinal variation to estimate rates of energy use and acquisition reveals shifting metabolic

constraints along the elevation gradient. Metabolic rates decline along the gradient due to decreasing body size. The proportion of time that the grasshoppers can be active remains roughly constant before declining at the highest elevations (Fig. 5). Trends are similar between species with the exception that *C. pellucida*, a warm adapted grasshopper, exhibits decreased activity time with elevation. Although our analysis provides initial insight into potential drivers of differential responses to climate change between species and along the elevation gradient, a fuller understanding would be afforded by translating the energetic implications of phenotypes into demographic impacts.

SCALING FROM ENERGETICS TO POPULATION DYNAMICS

Our analyses have focused on quantifying how phenotypes influence rates of energy use and activity time. A logical next step in our analysis, which we are currently pursuing, is to address how these energetic implications determine rates of survival and fecundity, and ultimately population dynamics. Predicted differences in population dynamics between phenotypes can then be compared to observed responses to recent climate change. We review approaches to quantifying the fitness consequences of phenotypes that focus on the behaviour of individuals, an individual's energy allocation, or characterizing the influence of phenotypes on the components of population dynamics.

Fully understanding demography requires considering the energy balance across the entire life cycle. Future work rearing grasshoppers from egg (Alexander & Hilliard 1964) or juvenile stages (Belovsky & Slade 1995) in cages along the elevation gradient and documenting development rates and body size will inform our understanding of the life-cycle energy budget. Approaches to modelling the energy budget include MTE, which has recently been extended to model ontogenetic growth by partitioning energy gain through metabolism to growth and maintenance (Zuo *et al.* 2012). A test of the ontogenetic growth model for *Manduca* caterpillars found ontogenetic shifts in metabolic scaling parameters and high assimilation rates contrary to the model, but a general form of the model did reflect larval growth, metabolism and development observations (Sears *et al.* 2012). A complementary framework based in energy allocation is dynamic energy budget (DEB) theory (Maino *et al.* 2014). DEB models partition an organism's mass into structure and a reserve. Energy is assimilated proportional to surface area and energy is retained for structural maintenance proportional to volume. A fixed fraction of acquired energy is allocated to growth and to maintenance metabolism, and the remainder is partitioned to development towards and maintenance of maturity and reproduction (Kearney *et al.* 2010; Kooijman 2010). Biological rates depend on the states of the organism (e.g. age, size, sex, nutritional status) and of its environment (e.g. food density, temperature) (Kooijman 2010). Energy budget models including DEBs can yield predictions of popu-

lation growth rates (r_{\max}) as well as fitness components including age at maturity and clutch frequency (Kearney 2012). New strategies for parameterization are enabling the application of this framework to organisms with more complex life histories (e.g., lizards, Kearney 2012). DEB models have been used to drive individual-based models (IBMs) (Martin *et al.* 2012).

Individual-based models estimate population dynamics by aggregating individuals with variable traits. The growth, survival and reproduction of each individual are functions of the organism's phenotype. The behaviours determining energy acquisition are often modelled explicitly (Grimm & Railsback 2005). One example, IBM examined the potential for migration timing to evolve in response to climate change and its implications for the persistence of Canadian sockeye salmon (Reed *et al.* 2011). IBMs have also been developed to model grasshopper population dynamics (Fielding 2004), and some of the models include temperature-dependent development (Carter *et al.* 1998) or respiration (Hilbert 1995). While they can be computationally intense and rely on deriving accurate descriptions of the influence of phenotypes on fitness components, IBMs provide a powerful framework for investigating the population-level implications of individual variation.

Alternative energy-budgeting approaches are based on empirical allocation data. For example, an approach developed for lizards (Dunham, Grant & Overall 1989; O'Connor, Sieg & Dunham 2006) more explicitly includes physiological constraints on activity and acquisition. Analogous to DEBs, an allocation rule is used to partition acquired energy for growth, maintenance, storage and reproduction. The models can be, but seldom are, parameterized to predict population dynamics (but see Adolph & Porter 1993). The models rely on appropriately quantifying thermal tolerances and the temperature dependence of performance and assimilation rates.

Assuming that individual foraging optimizes an ecological quantity related to survival or reproduction provides an additional way to link models of the temperature dependence of individual behaviour (see also Houston & McNamara 2014) to population dynamics (Buckley *et al.* 2010). More generally, Dell, Pawar & Savage (2014) provide a framework for estimating the temperature dependence of consumer-resource interactions derived from MTE.

Thermal constraints on survival, development and activity have been applied to predict the population dynamics of insects (Kingsolver 1989). For example, oviposition rates were estimated for grasshoppers based on laboratory estimates of temperature-dependent development time and compared to field observations (Samietz & Kohler 1998). Related energy budget models quantify the temperature dependence of grasshopper development and oviposition (Rodell 1977). Temperature-dependent rates of development and survival have been incorporated in matrix population models based on transition probabilities between stages (Hardman & Mukerji 1982). They are also incorporated in bioclimatic niche models (e.g. CLIMEX),

which include thermal constraints but do not directly assess energetics (Olfert & Weiss 2006). The tight link between grasshopper phenotypes and energetic responses to environmental conditions enables developing approaches to scale from energetics to population dynamics.

Conclusions

Scaling up from metabolic constraints on individuals provides a viable pathway to predicting a species' abundance and distribution. Biophysical models can be used to understand how an organism's phenotype interacts with environmental conditions to determine body temperatures. Body temperatures can be compared to measurements of thermal tolerance to estimate activity times. These estimates of activity time correspond closely to the amount of energy that can be acquired by foraging and metabolic rates can be used to estimate energetic costs. These energetic metrics can be translated into population dynamics by identifying constraints on energy or time that govern survival or fecundity. Frameworks for modelling population dynamics include individual-based and energy budget models.

Can scaling from individual traits to population dynamics provide insight into why organisms – including the grasshoppers in our case study – have responded individually to recent climate change? We have not yet identified differential metabolic constraints between grasshopper species than can account for intra- and interspecific differences in phenological and abundance shifts. We hope that integrating our data on thermal tolerances and metabolic rate into a population dynamic model might better account for these differences. Several related approaches for modelling metabolic constraints have begun to account for individualistic responses to climate change (Buckley & Kingsolver 2013). Attempts to use energetics to scale across levels of ecological organization, reinvigorated by the MTE, offer promise in understanding constraints on abundance and distribution in both current environments and those anticipated as climate change progresses.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Changes in abundance and first appearance date since 1959–1960.

Fig. S2. Ambient temperatures and radiation at the study sites.

Fig. S3. Comparison of grasshopper ambient and body temperature.