

Beyond average: an experimental test of temperature variability on the population dynamics of *Tribolium confusum*

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Abstract The relationship between ectotherm ecology and climatic conditions has been mainly evaluated in terms of average conditions. Average temperature is the more common climatic variable used in physiological and population studies, and its effect on individual and population-level processes is well understood. However, the intrinsic variability of thermal conditions calls attention to the potential effects that this variability could have in ecological systems. Regarding this point, two hypotheses are proposed. From the allocation principle, it may be inferred that if temperature variability is high enough to induce stress in the organisms, then this extra-cost should reduce the energetic budget for reproduction, which will be reflected in population parameters. Moreover, a mathematical property of non-linear functions, Jensen's inequality, indicates that, in concave functions, like the temperature–reproduction performance function, variability reduces the expected value of the output variable, and again modifies population parameters. To test these hypotheses, experimental cultures of *Tribolium confusum* under two different thermal variability regimens were carried out. With these data, we fitted a simple population dynamics model to evaluate the predictions of our hypothesis. The results show that thermal variability reduces the maximum reproductive rate of the population but no other parameters such as carrying capacity or the nonlinear factor in a nonlinear version of the Ricker model, which confirms our hypotheses. This result has important consequences, such as the paradoxical increase in

population variability under a decrease in thermal variability and the necessary incorporation of climatic variability to evaluate the net effect of climate change on the dynamics of natural populations.

Keywords Allocation principle · Jensen's inequality · Population growth rate · Population variability · Thermal variability

Introduction

Levels of ecological organization or hierarchies provide one of the central themes around which ecologists attempt to understand patterns of distribution (Lawton 1991). Mechanistic explanations for these patterns should link adjacent levels in the ecological hierarchy through the understanding and integration of physiology, ecology and evolutionary biology (Spicer and Gaston 1999). Understanding and explaining the selective pressures underlying differences in individual performance and demographic parameters within and across species emerge as a major topic among ecologists (Metcalf and Pavard 2007).

Because environmental temperature varies in time and space at different time-scales, organisms are continually challenged to maintain homeostasis (Johnston and Bennett 1996), and therefore the study of thermal physiology and population ecology has the potential to provide a mechanistic bridge for linking individuals, demography and population dynamics patterns (Crozier and Dwyer 2006). Special attention has been paid to the link between the ecological physiology of insects and their observed population dynamics (Davidson and Andrewartha 1948; Andrewartha and Birch 1954; Chown and Gaston 1999; Crozier and Dwyer 2006), and how physiological processes

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constrain their distribution and abundance (Uvarov 1931; Davidson and Andrewartha 1948; Andrewartha and Birch 1954; Martinat 1987; Huey and Berrigan 2001; Sinclair et al. 2003; Crozier and Dwyer 2006).

Theoretical models (Katz et al. 2005) as well as empirical data (Easterling et al. 2000; Solomon et al. 2008) have concluded that climate change impacts on temperature variability. Nevertheless, most current analyses of global climatic changes have focused on mean values, paying less attention to the role of climate variability. In this regard, experimental studies testing not only the effect of increases in mean temperature but also changes in temperature variability on phenotypic traits may be important at different evolutionary, ecological, and physiological scales (Travis and Futuyma 1993). Currently, most of the research on thermal variability has been focused on the effect on life-history traits like developmental time (Worner 1992; Ragland and Kingsolver 2008), hatching success (Ji et al. 2007) or some phenotypic characteristics of the progeny (Pétavy et al. 2004; Ji et al. 2007; Folguera et al. 2009), but there are a few examples concerning the influence of climatic variability on parameters commonly used in population dynamics studies like carrying capacity or the per capita population growth rate (Orcutt and Porter 1983; Martin and Huey 2008).

Consequently, a logical next step of research is to understand the role of temperature variability on population dynamics of insects. Two common ideas present in the literature are useful to achieve this objective: First, from the principle of allocation (Cody 1966; Levins 1968) it is inferred that organisms inhabiting environments with variable temperature could have higher metabolic costs than those living in stable environments. For example, due to the metabolic costs of acclimation, the reproductive dynamics may decrease and population parameters like the r_m may also decrease. However, another useful concept, Jensen's inequality (Jensen 1906), points out that thermal variability could positively or negatively affect population parameters.

Jensen's inequality is a mathematical property of non-linear functions (Ruel and Ayres 1999), this states that, for a sample of the variable x with average \bar{x} and $y = f(x)$ being a nonlinear function of x , then $\overline{f(x)} > f(\bar{x})$ if $f(x)$ is accelerating (2nd derivative is positive), and $\overline{f(x)} < f(\bar{x})$ if $f(x)$ is decelerating (2nd derivative is negative). According to this mathematical law and the dome-shaped relationship between ambient temperature (T_a) and r_m (Huey and Berrigan 2001; Frazier et al. 2006; Martin and Huey 2008) (Fig. 1), it is possible to infer that, close to the maximum of the $T_a - r_m$ function (the decelerating part of the function; Fig. 1), the more variable is T_a , the lower r_m will be. On the other hand, in the accelerating part of the function, the more variable is T_a , the higher r_m will be.

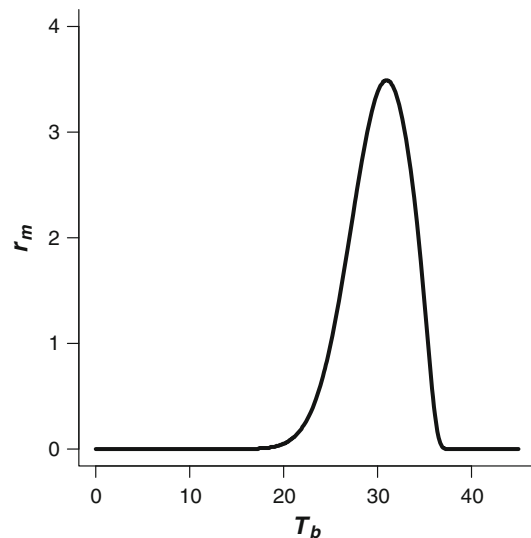


Fig. 1 Example of performance curve of r_m as a function of body temperature (T_b) for *T. confusum*. The curve was parametrized using the equation of Frazier et al. (2006) and data about r_m , T_m and thermal tolerance from Howe (1965) using a lunar-month time-base. Notice the asymmetry of the curve and the concave shape around the maximum

In this study, we examined the influence of T_a variability on the population dynamics of insects. Because we attempted to understand the role of physiological performance in population ecology, our experiments were designed to determine how animals' fitness changes under different physiological costs. First, we used laboratory cultures of *Tribolium confusum* (Coleoptera: Tenebrionidae) maintained at the same average temperature but under different levels of variability. Second, we used classical models of population dynamics to evaluate the previous predictions and other potential consequences of thermal variability on population parameters of insects in particular and ectotherms in general.

Materials and methods

Experimental methods

To evaluate the effect of thermal variability, we cultured *T. confusum* under 24°C and two regimens of variability: ± 0 and $\pm 8^\circ\text{C}$; the regimen of $24 \pm 8^\circ\text{C}$ corresponding to a step-change between 16 and 32°C in the day and night, respectively. We chose 24 and $\pm 8^\circ\text{C}$ because this average temperature is inside the range of tolerance for this species (Park 1934, 1954; Park and Frank 1948). The photoperiod was 12:12 h. This design allowed us to test variability without exceeding the tolerance limits or the optimum of the species (Howe 1965) and so avoid the effect of the asymmetry of the performance curve (Martin and Huey

2008). Another reason to use this design is because this amplitude approximately represents the daily thermal variability during the species reproductive season (spring and summer; Estay et al. 2009a). Pairs of *T. confusum* were cultured in bottles with 12 g of standard medium of wheat flour and dried brewer's yeast (Desharnais and Costantino 1982). In a first step, individuals were sexed as pupae and were maintained separately until they became adults. With adults, four different densities were used and initially established using the discrete design of Utida (1941) and Royama (1992): 2, 4, 8, and 16 individuals per bottle with a sex ratio 1:1. Each density was replicated between 4 and 8 times. After 1 month, the progeny of each population (bottle) was counted. With these data, we were able to fit a simple population dynamics model to evaluate differences between treatments.

Statistical analysis

Given that populations were maintained with a continuous supply of food and without natural enemies, they are expected to be dominated by a first order feedback. Hence, we used a simple model of intra-specific competition, Ricker's (1958) equation, to represent the reproductive function. This model, based in a difference equation, has been used successfully in the modeling of this and other insect species (Estay et al. 2009a, b).

Ricker's equation is:

$$r = r_m \left(1 - \left(\frac{N_{t-1}}{K} \right)^Q \right) \quad (1)$$

where N_{t-1} is the abundance at time $t-1$; r is the realized per capita growth rate $r = \ln(N_t/N_{t-1})$; r_m is the maximum per capita growth rate estimated for the species; K is the equilibrium density; and Q is a nonlinearity factor (Berryman 1999).

The parameter r_m was estimated using cubic splines to avoid convergence problems. This estimation was used to fit the models. We fitted the model to the data belonging to each treatment and compared the estimated parameters (r_m , K and Q) through a 95% confidence interval obtained by bootstrap.

Results

Consistent with our predictions, significant differences in r_m between the treatments (Table 1; Fig. 2) were observed. Comparing the 95% confidence intervals for each parameter in Table 1, no overlap in r_m between the estimated values of each treatment was detected. The value of r_m at constant ($24 \pm 0^\circ\text{C}$) temperature treatment was 3.70

Table 1 Estimated parameters, confidence intervals and R^2 for a Ricker model of population dynamics fitted to experimental data of *Tribolium confusum* growing at two different thermal variability regimens

Parameter	Estimated	95% CI	R^2
24 ± 0°C			
r_m	3.70	3.32–4.08	0.75
K	34.45	26.00–56.68	
Q	0.80	0.58–1.06	
24 ± 8°C			
r_m	2.73	2.19–3.09	0.63
K	38.92	27.30–82.44	
Q	1.04	0.65–1.62	

Significant differences are shown in bold

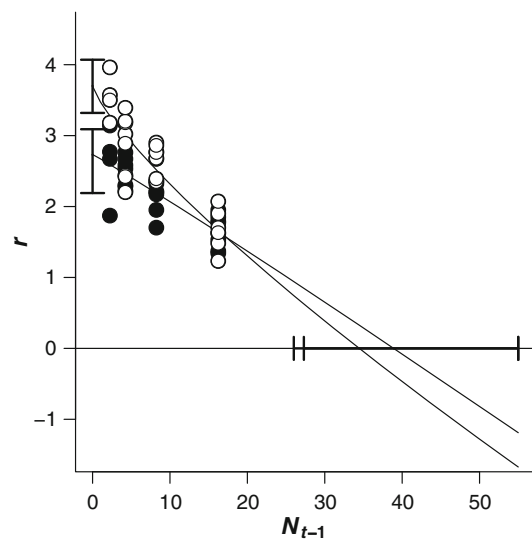


Fig. 2 Estimated reproductive functions of *Tribolium confusum* growing at $24 \pm 0^\circ\text{C}$ (open circles) and $24 \pm 8^\circ\text{C}$ (closed circles). N is the population density, r the realized per capita growth rate $\ln(N_t/N_{t-1})$. Solid lines are the estimated functions. 95% confidence intervals for r_m (intercept in the y axis) and K (intercept in the x axis) are shown

(3.32–4.08), one point higher than in the variable ($24 \pm 8^\circ\text{C}$) treatment 2.73 (2.19–3.09). Parameters K and Q remained without significant differences between treatments (Table 1).

Discussion

In spite of the well-known role of climate on insect population dynamics (Saldana et al. 2007; Lima et al. 2008; Estay et al. 2009a), the wide temporal and spatial range of available thermal conditions and the thermoregulatory homeostasis of animals under climate change conditions may play a major role in population and evolutionary

ecology. In other words, physiological maintenance, growth and reproduction in a given time period is dependent on thermal conditions; thus, its impact on the dynamic state-dependent physiology should be extremely important in determining the organism's population ecology and evolutionary success in a warming world.

Our results supported our hypotheses about the expected change in r_m due to an increase in thermal variability. Indeed, in our experiment, the maximum per capita growth rate (r_m) is significantly lower in the treatment with variable temperature ($24 \pm 8^\circ\text{C}$) than in the treatment with constant temperature. Although this result could be counterintuitive, since the optimal range of temperature for *T. confusum* is between 30 and 33°C (Howe 1965; White 1995), it would be expected that populations living half the day at their optimal temperature range have a higher reproductive rate than those living in a constant, outside the optimum, lower temperature or at least compensate for the half day living in a lower temperature (16°C) and have a similar r_m . However, consistent with our results, inhabiting a variable temperature environment represents an extra cost for the beetles. These costs could be related to the stress of living in a variable environment (Pétavy et al. 2004). According to the allocation principle, the energetic costs in which individuals may incur due to thermal stress—defined as an environmental factor that affects the physiological homeostasis with negative consequences on fitness—would reduce the amount of resources/energy allocated to reproduction and maintenance.

Nevertheless, the exact effect of thermal variability depends not only on the characteristics of the focal environment but also on the physiological and behavioral traits of the focal species. Different effects of thermal variability have been detected previously in other morphological or life-history traits. For example, Orcutt and Porter (1983) found a slightly positive effect of thermal variability on r_m using *Daphnia parvula*. This result could be attributed to the range of experimental temperatures used (perhaps in the accelerating part of the function $T_a - r_m$) or to some traits of *Daphnia* that overcome the stress of variable temperature.

However, even without invoking the allocation principle, Jensen's inequality predicts this situation due to the concave performance curve of r_m against temperature (Ruel and Ayres 1999). In fact, the strong reduction in r_m might be the combined effect of intrinsic mathematical properties of concave function and the trade-offs among different energy demanding biological processes.

On the other hand, the detrimental effect of thermal variability on r_m has an interesting consequence on the dynamic behavior of *Tribolium* populations. It has been demonstrated previously that r_m controls the population dynamics in the logistic model (May 1974, 1976). Certainly,

a higher value in this parameter is related to a higher instability in population dynamics. According to Solomon et al. (2008), at the global scale, the daily temperature range would be reduced in the near future as a result of the expected increase in minimum daily temperatures, therefore r_m should increase in our *Tribolium*'s system. This leads us to the paradoxical situation that a reduction in daily thermal amplitude (Solomon et al. 2008) could eventually increase population variability. This result calls the attention to the difficulties of predicting the effect of climate change on the population dynamics among ectotherms. Although most authors predict a general positive effect of global warming on population density of ectotherms at high latitude (Porter et al. 1991; Cammell and Knight 1992; Cannon 1998; Crozier and Dwyer 2006; Estay et al. 2009a) and a negative one for tropical species (Deutsch et al. 2008), the role of climate variability (positive or negative) needs to be clarified in order to estimate the net effect of climate change on the dynamics of natural populations.

Within the worldwide current concern about the consequences of global warming, the scientific literature is full of articles dealing with the responses of insect populations to changes in average temperature, precipitation, or CO_2 concentration (Elias 1991; Porter et al. 1991; Cammell and Knight 1992; Harrington and Woiod 1995; Harrington et al. 1995, 2007; Cannon 1998; Whittaker 1999; Volney and Fleming 2000; Bale et al. 2002; Keith et al. 2008; Dukes et al. 2009; Hering et al. 2009). Nevertheless, the expected responses of populations to changes in temperature variability are poorly understood. Our results, even though the expected reduction in daily thermal variability could be less drastic than in our experimental design and considering the particularities of our very simple biological systems, are useful to clarify the potential consequences of thermal variability in future studies dealing with individual performance, population dynamics and climate forcing, and to stress the increasing necessity of incorporating climate variability in the predictions of the effects of climate change on ecosystems.

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