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Global change biology

Thermal tolerance, acclimatory capacity and vulnerability to global climate change

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Despite evidence that organismal distributions are shifting in response to recent climatic warming, we have little information on direct links between species' physiology and vulnerability to climate change. We demonstrate a positive relationship between upper thermal tolerance and its acclimatory ability in a well-defined clade of closely related European diving beetles. We predict that species with the lowest tolerance to high temperatures will be most at risk from the adverse effects of future warming, since they have both low absolute thermal tolerance and poor acclimatory ability. Upper thermal tolerance is also positively related to species' geographical range size, meaning that species most at risk are already the most geographically restricted ones, being endemic to Mediterranean mountain systems. Our findings on the relationship between tolerance and acclimatory ability contrast with results from marine animals, suggesting that generalizations regarding thermal tolerance and responses to future rapid climate change may be premature.

Keywords: thermal tolerance; range size; rarity; climate change; diving beetle; ecophysiology

1. INTRODUCTION

Recently observed increases in global temperature have been associated with shifts in the geographical distribution of a range of terrestrial and aquatic organisms (e.g. Root *et al.* 2003), and although geographical variation in physiological traits has been investigated in many ectotherms (e.g. Addo-Bediako *et al.* 2000; Hoffmann *et al.* 2005; Ghalambor *et al.* 2006), there are few examples of direct causal links between environmental temperatures and changes in species' biogeography (e.g. Pörtner & Knust 2007). During periods of rapid climate change, taxa that are unable to shift their geographical ranges (Bradshaw & Holzapfel 2001; Balanya *et al.* 2006) are particularly at risk from extinction (Pounds *et al.* 2006), especially if they cannot compensate physiologically (Davis & Shaw 2001). Consequently, we need to improve our understanding of the physiological mechanisms underpinning thermal tolerance limits and the acclimatory capacity of those limits, if we are to predict the direct impact of climatic warming on biodiversity (Chown *et al.* 2004). Arguably, estimating population and ecosystem level effects of climate change merely on the basis of large-scale patterns, without an understanding of organismal physiological responses, can result in erroneous predictions (e.g. Helmuth *et al.* 2005).

Stillman (2003) recently proposed that species that have evolved the greatest absolute thermal tolerances have done so at the expense of maintaining the acclimatory ability of this tolerance. Such evolutionary trade-offs in thermal adaptation may set the limits of species' distribution (Pörtner *et al.* 2006). Stillman found that porcellanid crabs with the highest upper and lower thermal limits (UTL and LTL) have the lowest acclimatory capacities of these traits (ΔUTL and ΔLTL, respectively) and suggested that such taxa would therefore be most sensitive to further climatic changes. Stillman's 'hypothesis' may provide a general predictive framework for understanding the biological bases of responses to temperature changes, although we still need to know the extent to which his conclusion generalizes. Relationships between the measures of heat resistance and thermal acclimation have largely been documented in model organisms (Berrigan & Hoffmann 1998; Pörtner *et al.* 2006), and while acclimatory ability and thermal tolerance are key traits in physiological ecology, no study has specifically examined their interrelationships within a clade of closely related species.

Here we report the relationship between UTL, LTL (defined as lethal temperatures) and their relative acclimatory capacities across 13 congeneric, ecologically similar European diving beetles (*Deronectes* spp.; Coleoptera, Dytiscidae). *Deronectes* are found in fast-flowing streams at intermediate elevations across the Palaearctic, from Britain to western China, with greatest diversity around the Mediterranean, where many extant taxa appear to have originated in the Pleistocene (Ribera & Vogler 2004). Species' geographical ranges vary widely, from endemics known from single Mediterranean mountain systems, to those, such as *D. latus*, which occur over much of Europe (Fery & Brancucci 1997; Fery & Hosseinie 1998). Our study represents the first formal test of Stillman's findings and the first attempt to examine whether such evolutionary trade-offs in thermal adaptation occur more generally at an interspecific level, examining this within a well-defined, relatively diverse clade of ecologically similar species.

2. MATERIAL AND METHODS

Adult *Deronectes* were collected during spring and summer 2006 (table 1). Individuals of each species were collected as close as possible to the central point of their latitudinal ranges to avoid possible confounding effects of local adaptation in range edge populations (see Kirkpatrick & Barton 1997). Specimens were maintained in aquaria (volume: 5 l) containing aerated artificial pond water (APW, pH 7.5) in a 12 L : 12 D regime, and fed chironomid larvae. Each species was divided into two equal groups and kept at 14.5°C or 20.5°C, respectively, for 7 days (after Terblanche *et al.* 2006). These temperatures were chosen as representative seasonal temperatures within the range experienced by *Deronectes* during adult activity. After acclimation, individuals were further haphazardly assigned to two equal subgroups: one used to measure the UTL and the other the LTL of each species kept at 14.5°C or 20.5°C. UTL and LTLs were defined as individual lethal points (°C) at high and low temperatures (Chown & Nicolson 2004; see appendix 1 in the electronic supplementary material for details).

Any relationships present between species' mean thermal tolerance and acclimatory ability of thermal tolerance were detected separately using multiple regression tests, including body mass (bm).

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Table 1. Collection localities, number of individuals tested and geographical ranges for *Deronectes* species. Latitudinal range extent, LRE.

species	locality	*n*	*S* latitudinal limit	*N* latitudinal limit	LRE (°)
angusi	Pineda de la Sierra (Burgos, Spain)	26	42°00′	43°30′	1.5
aubei aubei	Sospel (Alpes Maritimes, France)	28	44°00′	48°00′	4
bicostatus	Rascafria (Madrid, Spain)	53	40°00′	43°00′	3
depressicollis	Riopar (Albacete, Spain)	57	37°00′	38°00′	1
fairmairei	Calaspara (Murcia, Spain)	36	31°00′	47°30′	16.5
hispanicus	Jimena de la Frontera (Málaga, Spain)	92	36°00′	44°30′	8.5
latus	Aylesbere (Devon, UK)	75	41°00′	69°00′	28
moestus	Francardo (Corsica, France)	48	37°00′	47°30′	10.5
opatrinus	Fuencaliente (Ciudad Real, Spain)	54	36°00′	45°30′	9.5
platynotus mazzoldi	Rila (Bulgaria)	30	40°00′	42°00′	2
platynotus platynotus	Zbirožský (Krivoklátsko, Czech Republic)	47	42°00′	50°30′	8.5
semirufus	Monti (Alpes Maritimes, France)	60	42°30′	45°30′	3
wewalkai	Rascafria (Madrid, Spain)	68	40°00′	41°00′	1

Also relationships between physiological variables and latitudinal range extent (LRE) were examined using a multiple regression test, including bm. Details on the statistical analyses are given in appendix 1 in the electronic supplementary material. All the analyses were conducted using JMP IN v. 5.1. Data met assumptions for normality (Shapiro–Wilk test, $W > 0.929$, $p > 0.326$), with the exception of LRE, which was normally distributed following log transformation. Transformed and untransformed data produced similar results, the latter being presented here. Assumption of homogeneity of variance, tested by analysing the relationships between residuals of the multiple regression and the physiological parameters used as independent variables, was met in all cases ($p > 0.05$). Where significant relationships were detected these were further assessed following phylogenetic transformation of data, based on mitochondrial COI-based phylogenies (Ribera *et al.* 2001; Ribera & Vogler 2004), using the CRUNCH algorithm of the CAIC software package (Purvis & Rambaut 1995).

3. RESULTS

Deronectes species with the highest UTLs also possess the greatest acclimatory capacity of this trait (figure 1*a*), a significant positive relationship being found between mean UTL and ΔUTL ($p=0.004$; table 2*a*). This relationship was also present after phylogenetic transformation of data ($\Delta UTL = 0.83 * UTL$, $R^2=0.69$, $F_{1,12}=24.98$, $p=0.0004$). In contrast, in *Deronectes* species, no relationship was detected between mean LTL and ΔLTL ($p=0.803$; table 2*b*). Mean UTL ranges from 42.6±0.2 s.e.°C in *D. semirufus* to 46.9±0.3 s.e.°C in *D. latus,* while mean LTL falls between −5.2±0.3 s.e.°C in *D. hispanicus* and −10.0±0.3 s.e.°C in *D. latus*. Acclimatory ability of UTL varied from −2.0 to +1.1°C, while ΔLTL varied between −2.0 to +1.4°C (see appendix 2 in the electronic supplementary material for details of acclimation). In all the cases, bm had no significant effect on the variables tested, with the exception of bm for ΔLTL ($p=0.035$; table 2*b*). A positive relationship exists between LRE and both mean UTL and mean LTL ($p=0.002$ and 0.034, respectively; table 2*c* and figure 1*c*); widespread species having higher tolerance to both high and low temperatures. These relationships were also present after phylogenetic transformation of data ($p=0.008$ and 0.009, respectively; $LRE = -0.961 + 6.41 * UTL - 3.333 * LTL + 2.517 * bm$, $R^2=0.742$, $F_{1,12}=7.657$, $p=0.0098$. In contrast, species' bm does not significantly relate to LRE (minimum $p=0.301$; table 2*c*). ΔUTL and ΔLTL were removed from the model prior to analysis (see appendix 1 in the electronic supplementary material).

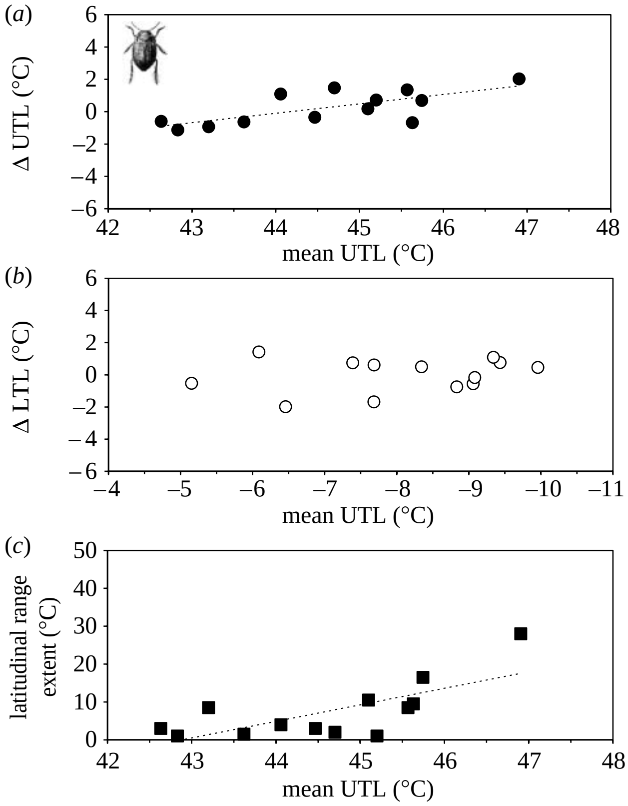

Figure 1. Relationships between (*a*) upper thermal limit (UTL, °C) and its acclimatory ability (ΔUTL, °C), (*b*) lower thermal limit (LTL, °C) and its acclimatory ability (ΔLTL, °C) and (*c*) UTL (°C) and LRE (degrees latitude). Circles/squares represent individual species of *Deronectes*. Dotted lines represent significant relationships between studied variables. Plots show raw data.

4. DISCUSSION

While our study does not refute Stillman's conclusions, we found no evolutionary trade-off between thermal tolerance and acclimatory capacity as he had

Table 2. Multiple regression tests of (*a*) mean UTL at 20.5°C and body mass (bm) on ΔUTL, (*b*) mean LTL at 14.5°C and bm on ΔLTL, (*c*) mean UTL at 20.5°C, mean LTL at 14.5°C and bm on LRE. (Degrees of freedom (d.f.), sum of square (SS), mean of square (MS), *F*-ratio and *p*-value (*p*), model R^2.)

	source	d.f.	SS	MS	*F*-ratio	*p*-value	R^2
(*a*)							
	model	2	7.564	3.782	6.937	0.013	0.581
	mean UTL at 20.5°C	1	7.390		13.554	0.004	
	bm	1	0.975		1.788	0.211	
	residual	10	5.452	0.545			
	total	12	13.017				
	predicted equation: $\Delta UTL = -26.51 + 0.63 *$ mean UTL at 20.5°C $- 0.18 *$ bm						
(*b*)							
	model	2	5.306	2.653	3.383	0.076	0.400
	mean LTL at 14.5°C	1	0.052		0.066	0.803	
	bm	1	4.690		5.980	0.035	
	residual	10	7.843	0.784			
	total	12	13.149				
	predicted equation: $\Delta LTL = 3.63 + 0.05 *$ mean LTL at 14.5°C $- 0.12 *$ bm						
(*c*)							
	model	3	513.217	171.072	7.455	0.008	0.713
	mean UTL at 20.5°C	1	419.762		18.294	0.002	
	mean LTL at 14.5°C	1	142.217		6.198	0.034	
	bm	1	27.667		1.206	0.301	
	residual	9	206.514	22.946			
	total	12	719.731				
	predicted equation: $LRE = -237.02 + 4.83 *$ mean UTL at 20.5°C $\pm 2.66 *$ mean LTL at 14.5°C $+ 1.03 *$ bm						

found in marine crabs. Instead, a positive coevolution seems to have occurred between UTL and ΔUTL in these diving beetles, perhaps related to the different mechanisms that may underlie UTLs in insects and crustaceans (Chown & Nicolson 2004; Klok *et al.* 2004). Also in contrast to Stillman's findings, LTL and its acclimatory capacity have apparently evolved independently in diving beetles. Overall, our results suggest a difference between evolutionary physiological trends in these two groups of arthropod (Stillman 2003).

In porcellanid crabs, Stillman predicted that species with greater thermal limits would be most vulnerable to increased warming since they had the most limited acclimatory capacity and already live close to their UTLs. In contrast, in this genus of beetles at least, species with the lowest tolerance to high temperatures will be most vulnerable to increasing temperatures since upper thermal tolerance predicts acclimatory capacity: species with the least ability to cope with high temperatures also have the least ability to acclimate to them. It is worth noting that these taxa already have the most restricted global distribution; species' mean UTL, together with LTL, being a good predictor of LRE. Phenotypic plasticity (here measured as thermal tolerance acclimatory ability) did not strongly relate to species' LRE. While we have not considered seasonal and developmental plasticity in this study (e.g. Hoffmann *et al.* 2005; Terblanche & Chown 2006; Terblanche *et al.* 2006), it would appear that in these diving beetles a species' thermal tolerance and phenotypic plasticity are equally good predictors of responses to climatic changes. Such a finding differs from other documented cases that suggest that phenotypic plasticity may be more important than tolerance *per se* in determining responses to changes (Seebacher *et al.* 2005). In this group of insects, restricted endemic species would seem to be most at risk from continued global warming, simply on the basis of their thermal physiology. In this context, if we also consider the effects of increased warming on habitat availability in Mediterranean mountain systems (Wilson *et al.* 2005), such taxa may be considered as doubly threatened in the future.

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