

RESPONSES TO GLOBAL CLIMATE CHANGE

Upper thermal limits in terrestrial ectotherms: how constrained are they?

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Summary

1. Terrestrial ectotherms are likely to face increased periods of heat stress as mean temperatures and temperature variability increase over the next few decades. Here, we consider the extent to which changes in upper thermal limits, through plasticity or evolution, might be constrained, and we survey insect and reptile data to identify groups likely to be particularly susceptible to thermal stress.

2. Plastic changes increase thermal limits in many terrestrial ectotherms, but tend to have less effect on upper limits than lower limits.

3. Although comparisons across insect species have normally not taken into account the potential for plastic responses, mid-latitude species seem most prone to experience heat stress now and into the future, consistent with data from lizards and other groups.

4. Evolutionary adaptive potential has only been measured for some species; there is likely to be genetic variation for heat responses in populations, but selection and heritability experiments suggest that upper thermal limits may not increase much.

5. Although related species can differ by several degrees in their upper thermal limits, there is strong phylogenetic signal for upper limits. If these reflect evolutionary constraints, substantial molecular changes may be required to increase upper thermal limits.

6. Findings point to many terrestrial ectotherms having a limited potential to change their thermal limits particularly within the context of an average predicted temperature increase of 2–4 °C for mid-latitude populations over the next few decades.

Key-words: adaptation, comparative analysis, evolution, hardening, insects, plasticity, upper thermal limit

Introduction

Compared with the range of temperatures measured on earth, the thermal limits to life are narrow. Some organisms, typically members of the Archaea and Bacteria that live in unusual environments (Price & Sowers 2004; Cavicchioli 2006; Pikuta, Hoover & Tang 2007), are capable of routine metabolism at extreme temperatures. Resting stages in several metazoans are also able to survive temperature extremes, such as the anhydrobiotic larvae of the midge *Polypedilum vanderplancki* (−270 to 106 °C; Watanabe *et al.* 2002). However, for most metazoans, the range of temperatures that can be endured and over which

activity takes place is relatively small. Over the full extent of geological time, the trend also seems to have been one of initial low temperature growth optima (*c.* 20 °C) in the Last Universal Common Ancestor, with an increase in the ancestors of the bacterial (*c.* 69 °C) and archaeal (*c.* 66 °C) domains, but a subsequent return to lower temperature optima in many clades, perhaps reflecting the history of the planet's thermal regime (Boussau *et al.* 2008).

In metazoans, lower thermal limits for survival and activity (excluding encysted or anhydrobiotic stages) are exceptionally variable, ranging in insects, for example, from *c.* −70 °C in an Arctic beetle (Miller 1982) to about 17 °C in the case of activity of some tropical species (Terblanche *et al.* 2007). Upper thermal tolerance limits for metazoans are somewhat narrower. The top end of the

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range is in the region of 47 °C, possibly reflecting an oxygen limitation mechanism of thermal tolerance together with the thermal sensitivity of macromolecular structures (Feder & Hofmann 1999; Pörtner 2002; Robertson 2004), whereas stenothermal Antarctic invertebrates and fish seem incapable of surviving temperatures of greater than about 15 °C for any significant period, and may be incapable of routine functioning at temperatures of more than 2–3 °C (Podrabsky & Somero 2006; Barnes, Peck & Morley 2010; Bilyk & DeVries 2011). Much of the variation in upper and lower thermal limits to activity and survival is related to features both of the organisms and the environments to which they are typically exposed. Whilst at first such relationships might seem self-evident, they include various subtleties such as phylogenetic signal in thermal tolerance traits (Clusella Trullas, Blackburn & Chown 2011; Kellermann *et al.* 2012), variation in tolerances and behavioural regulation among life stages (Bowler & Terblanche 2008; Marais & Chown 2008), the influence of the predictability of environmental variation (Sinclair, Addo-Bediako & Chown 2003; Chown & Terblanche 2007) and the effects of environmental modifiers such as snow cover (Irwin & Lee 2003).

Differences between marine and terrestrial species appear especially pronounced, with the former tending to have coupled upper and lower limits such that a change at the one end of the range (as a consequence of plastic changes or evolutionary adaptation) is usually accompanied by a change at the other, likely owing to the significance in these species of oxygen limitation as the main mechanism determining limits to functioning (Pörtner 2002, 2010). Although this mechanism is thought also to extend to terrestrial ectotherms (Pörtner 2002), which would imply similarly coupled upper and lower thermal tolerances, several lines of evidence suggest that this may not be the case. A comparison of upper and lower thermal limits of marine and terrestrial ectotherms has indicated that these limits decline with increasing latitude at the same rate in marine species, whereas in terrestrial species the rate of decline in upper limits is an order of magnitude slower than in lower limits (Sunday, Bates & Dulvy 2011). The terrestrial pattern of reduced latitudinal variation in upper limits is also pronounced in insects (Addo-Bediako, Chown & Gaston 2000; Overgaard *et al.* 2011), although limits can vary latitudinally within and among species (Hoffmann, Anderson & Hallas 2002; Sgrò *et al.* 2010). Moreover, some notable exceptions exist, such as the apparently low heat coma temperature of an ice crawler, *Grylloblatta* sp. (*c.* 15–20 °C; Morrissey & Edwards 1979). In insects, upper limits also tend to vary much less with acclimation or acclimatization than do lower limits, and the responses are often decoupled in laboratory selection experiments (Hoffmann *et al.* 1997; Chown 2001; Alford, Blackburn & Bale 2012).

If upper thermal limits are constrained to a relatively narrow range, rising global temperatures may spell problems for terrestrial ectotherms, and particularly tropical

and subtropical species. Several studies have suggested that low-latitude ectotherms may have a narrow thermal safety margin (Deutsch *et al.* 2008; Huey *et al.* 2009, 2012; Clusella Trullas, Blackburn & Chown 2011; Duarte *et al.* 2012), making extinction both plausible and imminent. At least one investigation has also shown that such temperature-driven, climate change-related extinctions may well be underway (Sinervo *et al.* 2010). However, concerns have been raised about the generality of these scenarios and particularly the extent to which risks associated with temperature increases may be restricted to low-latitude areas only (Chown *et al.* 2010; Hoffmann 2010; Clusella Trullas, Blackburn & Chown 2011; Kingsolver *et al.* 2011). More generally, much of the discussion of species responses to climate change has not taken into consideration the extent to which upper thermal tolerance traits might evolve (Kearney *et al.* 2009; Hoffmann 2010; Eliason *et al.* 2011; Hoffmann & Sgrò 2011; Kingsolver *et al.* 2011). If upper limits are relatively constrained, then rising temperatures, especially the substantial increases now being predicted (up to 4 °C on average at the end of the century, Betts *et al.* 2011), are likely to be responsible for widespread population changes and possibly many extinctions. However, if scope exists for responses via evolution, plasticity, epigenetic mechanisms that act across generations, and/or for other mechanisms that might release further genetic variation to accelerate responses (Rutherford & Lindquist 1998; Sgrò, Wegener & Hoffmann 2010; Specchia *et al.* 2010), then the risks to ectotherms might be lower than currently estimated. Here we explore these questions, assuming that if fundamental limits to upper thermal limits exist, we might expect (i) a muted spatial signature in thermal limits; (ii) deep phylogenetic signal and constraint for these traits; (iii) relatively fixed acclimation responses; (iv) low to zero heritability reflecting a low additive genetic variance and (v) substantial genome rearrangement to deal with extreme thermal environments. We deal briefly also with the question of measuring thermal responses because measurement protocol can at times have a pronounced effect on estimated thermal limits (Terblanche *et al.* 2011).

Measuring thermal responses

The accurate measurement of thermal responses and variation therein have been widely discussed, both recently (Hazell & Bale 2011; Rezende, Tejedo & Santos 2011; Terblanche *et al.* 2011; Overgaard, Kristensen & Sørensen 2012) and in the past (Mellanby 1939; Lutterschmidt & Hutchison 1997). Much of the discussion has centred around the life stages at which thermal responses should be measured (Hoffmann 2010); the relevance of measurements on different fitness components including survival, sterility, mating and others (Baust & Rojas 1985; Bale 1987; Denlinger & Yocum 1998); the rate of temperature change in thermal assays (Terblanche *et al.* 2007; Chown *et al.* 2009; Ribeiro, Camacho & Navas 2012); the ecological relevance of traits that might be easy to measure in the

laboratory (Hoffmann *et al.* 1997; Mitchell & Hoffmann 2010) and the ability of measures to capture plastic responses and maternal effects (Loeschcke & Hoffmann 2007; Nyamukondiwa & Terblanche 2010). In measuring upper thermal limits within and across species, conflicts often arise between ease of measurement and ecological reality. Ideally, thermal limits should be measured on sensitive life stages across multiple fitness traits and generations under controlled conditions that are relevant to field conditions, but these are unrealistic targets for species with long generation times that cannot be reared easily. When considering the effects of climate change on biodiversity, the species of interest may be threatened, have small population sizes, and have specific habitat requirements, making them less than amenable to rigorous testing. Even when species are not threatened, it should be acknowledged that most species in an assemblage are rare. For example, across a range of spatial extents, it is fairly typical that <10% of the species make up at least half of the individuals in an assemblage (Gaston 2011). Therefore, assays are almost always likely to be imperfect with limitations that need to be acknowledged even if they cannot be addressed.

In assessing thermal limits, a useful distinction can be made between conditions that can be tolerated for a short period and conditions that are required for continuous growth and development (Hoffmann, Sørensen & Loeschcke 2003; Chown & Nicolson 2004). Typically, extreme temperatures can be tolerated for a short period of time depending on rapid hardening and an organism's thermal developmental history. Continuous development is usually only possible at lower temperatures, which can also depend on the developmental history of an organism. Short-term thermal exposures are difficult to characterize because they involve uncommon events. Ready illustrations of the rarity of such events are available for both aquatic and terrestrial species. For example, upper thermal limits for the intertidal limpet, *Lottia gigantea*, were only exceeded on three occasions over 5 years and then only on some surfaces (Denny *et al.* 2009). Similarly, in the terrestrial slug, *Deroceras panormitanum*, lower lethal temperatures were exceeded on only a few occasions over a 6-year period at the high elevation range limit of the species on Marion Island, but sufficiently often to constitute a range barrier (Lee *et al.* 2009). Extreme temperatures experienced by organisms can vary depending on microhabitat and other factors such as wind speed and humidity. For instance in intertidal zones, models and measures of mussel body temperature indicate that upper thermal temperature risk can be reduced by increased wind speed and changes in the timing of low tide as well as wave splash and solar radiation (Helmuth & Hofmann 2001). Similarly, wind speed and solar radiation have pronounced impacts on the body temperature of terrestrial species, as has long been apparent to biophysical ecologists (Porter *et al.* 2000).

A challenge in measuring thermal responses is to make them relevant to field conditions now and into the future.

There has been much debate recently about whether measures of thermal response variation within and between species represent an artefact of confounding stresses or other factors (Rezende, Tejedo & Santos 2011; Terblanche *et al.* 2011). The empirical data point to rather complex interactions between heat stress and factors such as food and desiccation (Terblanche *et al.* 2007; Overgaard, Kristensen & Sørensen 2012; Ribeiro, Camacho & Navas 2012), and a key issue is to determine which conditions (internal to the organism and external in the environment) are most relevant to those experienced under stressful field conditions (and likely to be experienced in the future). With the exception of some mark release studies examining the ability of *Drosophila* and parasitoids to locate resources (Thomson, Robinson & Hoffmann 2001; Loeschcke & Hoffmann 2007), experimental studies have rarely considered the effects of plastic and genetic variation under field conditions.

Plasticity

Resistance to short periods of heat stress has some degree of plasticity depending on prior thermal conditions experienced at the immature and adult phases, although much less than resistance to low temperatures, at least in *Drosophila* (Kristensen *et al.* 2008). Perhaps the most well characterized of the plastic effects on heat resistance involves hardening within a life cycle stage. Short periods of exposure to non-lethal but warm conditions tend to increase subsequent resistance of terrestrial ectotherms to heat (Bährndorff *et al.* 2009; Fischer *et al.* 2010; Sobek *et al.* 2011). The effects of hardening may be enhanced by repeated exposures to a non-lethal temperature (Krebs & Loeschcke 1994), and much of this response is likely to be mediated by heat shock protein genes that are upregulated following exposure to a non-lethal stress (Dahlggaard *et al.* 1998; Benoit *et al.* 2011). Short exposures also influence other components of thermal performance, such as temperature-related induction of sterility in males (Jørgensen, Sørensen & Bundgaard 2006).

As well as being influenced by short-term hardening exposures, heat stress resistance is also influenced by developmental temperature, generally increasing as organisms are raised under warmer conditions (Hoffmann, Sørensen & Loeschcke 2003; Fischer *et al.* 2010). Developmental effects may extend across a generation because conditions in the parental generation influence resistance of the offspring generation (Wang & Kang 2005). Heat resistance can also be influenced by nutrition. In *Drosophila melanogaster*, high protein diets tend to increase resistance levels compared with diets rich in carbohydrates, in contrast to their effects on some measures of cold resistance (Andersen *et al.* 2010). Nutritional variation may have an impact on the thermal environment sought out by individuals; when faced with chronic limits to the supply of nutrients, locusts select lower body temperatures than those that have more regular nutrient access and in doing so improve

nutrient use efficiency, but with slower growth as an outcome (Coggan, Clissold & Simpson 2011). Such regulation probably extends to the landscape scale in a variety of species. For example, in Nearctic *Papilio*, host preference is substantially influenced by the thermal conditions likely to be faced by individuals and their probability of encountering conditions that are lethal to the larval, but not pupal stages (Scriber 2002); in low temperature areas, hosts that maximize growth rate must be selected to avoid late season freezing of the larvae. Nevertheless as in the case of hardening, developmental effects on heat resistance tend to be smaller than for cold resistance; across several *Drosophila* species, developmental temperatures altered cold limits by 2–4 °C, but heat limits by <1 °C (Overgaard *et al.* 2011). Such a pattern has been generally noted for insects (Chown 2001; Chown & Nicolson 2004).

A challenge is to assess the likely importance of hardening and acclimation under field conditions. Attempts have been made to simulate thermal changes in the field and link these to the expression of plasticity (Kelty & Lee 2001). Repeat collections of flies from the same environment, but exposed to different thermal conditions also point to the likely importance of hardening and other forms of plasticity (Overgaard & Sørensen 2008). With sufficient information on the microenvironments experienced by ectotherms at different developmental stages and on the timing of heat stress events, it should be possible to predict times and locations when plastic responses influence upper thermal limits.

Phenotypic variation through space and time

Several studies have suggested that phenotypic variation in upper thermal limits (both upper lethal temperature and critical thermal maximum) is less spatially variable than lower lethal limits at a range of scales. In insects, these have included intraspecific investigations of *Drosophila melanogaster* (Hoffmann, Anderson & Hallas 2002),

D. birchii (Griffiths, Schiffer & Hoffmann 2005) and *Glossina pallidipes* (Terblanche *et al.* 2006); intra- and interspecific studies of weevils (Klok & Chown 2003) and interspecific studies of dung beetles (Gaston & Chown 1999), *Drosophila* spp., (Kimura 2004) and water beetles (Calosi *et al.* 2010). In some groups, such as in a genus of water beetles, variation for the upper lethal limits is much less marked than for lower limits (Calosi *et al.* 2008). Among amphibians, a shallower latitudinal decline in thermal maxima than minima has been noted for amphibians both in the United States and in Australia (Brattstrom 1968, 1970; Snyder & Weathers 1975; John-Adler, Morin & Lawler 1988). In reptiles, the range of critical thermal maxima (CT_{max}) for lizards and snake species is lower than that of critical thermal minima (CT_{min}), when examined interspecifically across several geographic regions or latitudes (Spellerberg 1972; Van Berkum 1988).

For insects considered at the broadest scale, there appears to be much less variation overall, and much less spatial variation, in upper than lower limits (Addo-Bediako, Chown & Gaston 2000). Using a macrophysiological approach and based on the original data set from Addo-Bediako, Chown & Gaston (2000), we recompiled information on upper and lower lethal temperatures and critical thermal minima and maxima for insects (see Supporting Information, further information available on request) and applied a rigorous analysis incorporating phylogenetic relatedness to investigate variation overall and spatial variation in these traits. These issues were also considered in squamate reptiles based on a similarly compiled data set (Clusella Trullas, Blackburn & Chown 2011). In the insects, significantly less variation is found in upper than lower thermal limits, although the difference in variation is smaller in critical thermal limits that reflect activity, and not significant (Table 1). Spatially, a similar pattern is clear, with both measures of high temperature tolerance varying less with mean annual temperature (Table 2) or with latitude (Fig. 1) than those

Table 1. Summary statistics for measures of upper and lower activity (critical thermal limits) and lethal limits for insects and squamate reptiles obtained from the literature

Measure	<i>n</i>	Mean	SD	Minimum	Maximum	Range	C.V.
Insects							
Critical thermal minimum	75	3.1	5.4	−5.6	17.0	22.6	1.9
Critical thermal maximum	173	43.0	4.9	30.2	56.6	26.4	1.5
Levene's test $F_{(1,246)} = 0.17$, $P = 0.68$							
Lower lethal temperature	189	−11.7	12.0	−70.0	8.3	78.3	4.6
Upper lethal temperature	119	39.3	7.1	26.4	56.0	29.6	2.3
Levene's test $F_{(1,306)} = 4.44$, $P < 0.05$							
Lizards and snakes							
Critical thermal minimum	130	6.8	3.4	1	15.4	14.4	1.2
Critical thermal maximum	238	41.5	3.1	33.1	51.0	17.9	1.0
Levene's test $F_{(1,366)} = 4.47$, $P < 0.05$							

The coefficient of variation (C.V.) was obtained following the conversion of the temperature values to Kelvin (°C + 273.15) to make all variables positive, so avoiding problems associated with a C.V. that includes zero or negative values. The outcome of Levene's test for homogeneity of variances is shown in each case.

Table 2. Results of the phylogenetic generalized least-squares (PGLS, Star = no phylogeny, Prop = proportional branch length phylogeny, with signal indicated by λ) analyses adjusting for phylogenetic effects on the relationship between measures of temperature limits and mean annual temperature in insects and squamate reptiles

Response variable	Phylogeny	λ	AIC	Slope \pm SE	Intercept \pm SE	<i>n</i>	<i>t</i>	<i>P</i>
Insects								
CT _{min}	Star	0	408.6	0.44 \pm 0.05	-1.73 \pm 0.65	75	9.6	0.0001
	Prop	0.80	395.6	0.29 \pm 0.05	1.06 \pm 2.01			<0.05
CT _{max}	Star	0	1010.1	0.27 \pm 0.04	38.68 \pm 0.77	173	6.3	0.0001
	Prop	0.86	919.35	0.23 \pm 0.04	38.95 \pm 2.35			<0.05
LLT	Star	0	1415.8	0.80 \pm 0.11	-19.92 \pm 1.33	189	7.5	0.0001
	Prop	0.15	1410.6	0.69 \pm 0.11	-19.54 \pm 2.31			<0.05
ULT	Star	0	799.7	0.25 \pm 0.08	35.60 \pm 1.34	119	3.1	0.003
	Prop	1	692.2	0.25 \pm 0.06	36.87 \pm 3.08			<0.05
Lizards + Snakes								
CT _{min}	Star	0	654.4	0.28 \pm 0.04	2.49 \pm 0.68	130	6.9	0.0001
	Prop	0.90	614.7	0.2 \pm 0.04	4.07 \pm 1.6			0.0001
CT _{max}	Star	0	1211.7	-0.09 \pm 0.04	43.14 \pm 0.70	237	-2.6	0.01
	Prop	0.93	1043.7	-0.01 \pm 0.02	42.19 \pm 1.47			>0.05

The number of species is given by *n* and model fit by the Akaike Information Criterion (AIC). For insects, both lethal and sub-lethal measures were used, and the slopes of the critical values differ significantly (ANCOVA interaction term $F_{(1,244)} = 105.2$, $P = 0.015$), as do those of the lethal temperatures (ANCOVA interaction term $F_{(1,304)} = 1200.1$, $P = 0.00002$).

of low temperature tolerance, both including and excluding phylogenetic relatedness to ensure species comparisons are independent [including relatedness tends to result in an improved fit (lower Akaike Information Criterion or AIC)]. In squamate reptiles, variation in CT_{min} and CT_{max} is similar, although a significant difference exists between them, with less variation in CT_{max} (Table 1). At global scales, and after adjusting for non-independence associated with phylogenetic relationships, the CT_{max} of reptiles is not related to mean annual temperature while CT_{min} decreases significantly (Fig. 2).

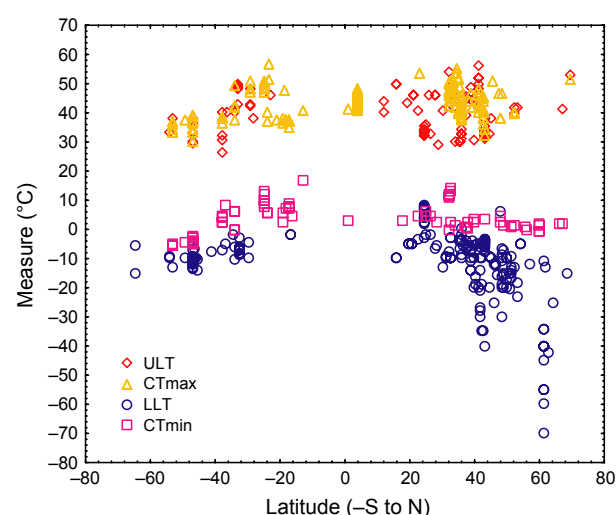


Fig. 1. Variation across latitude of upper (ULT) and lower (LLT) lethal temperatures and critical thermal maxima (CT_{max}) and minima (CT_{min}) in insects, obtained by compilation of values from the literature following the methods of Addo-Bediako, Chown & Gaston (2000). The source data are available in the Supporting Information.

These data are in keeping with less comprehensive previous investigations of the taxa in question (Huey *et al.* 2009; Sunday, Bates & Dulvy 2011) and provide support for what Gaston *et al.* (2009) termed Brett's rule (less geographic variation for upper than lower lethal limits), which was originally proposed for fish (Brett 1956). However, the data also show that substantial variation exists among taxonomic groups, and comprehensive interspecific analyses using similar methods are rare for any group of organisms. Perhaps best assessed in this respect is the genus *Drosophila*, where information on spatial variation among species based on the range position and size is growing. For example, intraspecific data on stress tolerance across a fairly wide latitudinal range is available for *D. melanogaster* (Hoffmann, Anderson & Hallas 2002; Sgrò *et al.* 2010), and interspecific studies of geographic variation in tolerance traits are accumulating for a variety of species (Kimura 2004; Kellermann *et al.* 2012). Several studies now point to fundamental differences in the mean of traits and the extent to which such means change through evolution, which might be associated with geographic range size rather than with geographic range position (Griffiths, Schiffer & Hoffmann 2005; Kellermann *et al.* 2009b).

Plasticity in upper tolerance traits tends to be narrower than plasticity in lower tolerance traits, at least for insects (Chown 2001; Chown & Nicolson 2004; Alford, Blackburn & Bale 2012). A similar pattern may hold in reptiles; an acclimation response ratio, incorporating effects of variation among acclimation temperatures in different studies, suggests that the magnitude of response is significantly larger for CT_{min} than for CT_{max} (CT_{min}: 0.23 \pm 0.11 °C (mean \pm SD; range, 0.09–0.49); CT_{max}: 0.12 \pm 0.08 °C (0.02–0.34), $F_{(1,45)} = 15.17$, $P < 0.001$, Clusella-Trullas, unpublished data). From the perspective of short-term (acclimation or acclimatization) responses to thermal

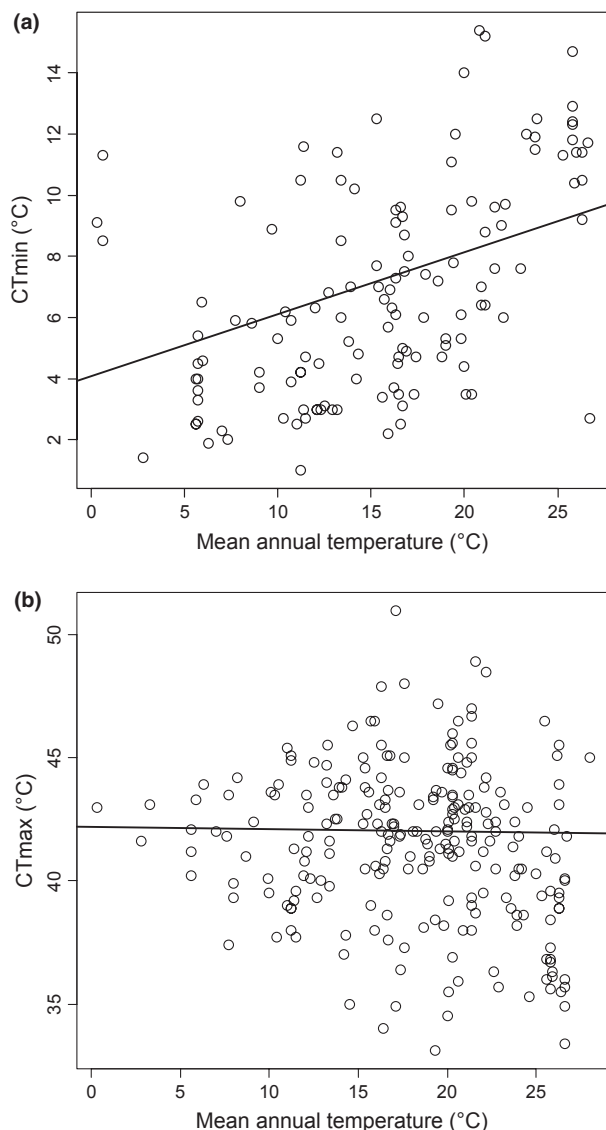


Fig. 2. The relationship between mean annual temperature (obtained from Hijmans *et al.* 2005) and (a) critical thermal minima (CT_{min}) and (b) critical thermal maxima (CT_{max}) in squamate reptiles. Data on which these figures are based are drawn from Clusella Trullas, Blackburn & Chown (2011).

variation, it has long been assumed that tropical (lowland) species should show much less phenotypic plasticity than temperate (lowland) species (see review in Ghalambor *et al.* 2006). Nonetheless, plasticity in thermal tolerance does not vary in a clear fashion with range position (latitude). Patterns established for anurans both in the United States and in Australia (Brattstrom 1968, 1970) and for a wide range of organisms (Angilletta 2009) suggest that a positive relationship between plasticity and latitude is uncommon. By contrast, investigations of amphibians (Brattstrom 1968, 1970) and several genera of water beetles (Calosi *et al.* 2008, 2010) indicate that acclimation capacity might be much more strongly related to variation in geographic range size (Brattstrom's rule – Gaston *et al.* 2009). Once again, though, few studies have considered a

monophyletic unit of animals across a wide range of latitudes. In comparisons of *Drosophila* species where tight environmental control is possible, a recent comparison of tropical and more widespread species suggests no association between the latitudinal range of a species and its acclimation ability (Overgaard *et al.* 2011).

The available data for ectotherms, and notably holometabolous insects that vary significantly in their life stages, tend to focus on adult rather than juvenile stages. Demographic effects of thermal extremes (or indeed any stressful event) may play out at any life stage (see discussion in Chown & Terblanche 2007; Hoffmann 2010), but investigations of variation among stages and its ecological significance are limited (reviewed in Bowler & Terblanche 2008; Kingsolver *et al.* 2011). Forecasts for the impacts of climate change are increasingly recognizing the significance of extreme events (see review by Chown *et al.* 2010), and unanticipated extremes may be especially important from a population dynamics perspective for sensitive life stages (Chown & Nicolson 2004; Harmon, Moran & Ives 2009). If areas with high mean annual temperatures or high warm quarters (in the terminology of Hijmans *et al.* 2005) are also subject to greater extremes (see discussion in Katz & Brown 1992), then the available thermal tolerance data make clear that impacts on populations might span a fairly wide range of latitudes and might be especially significant for range-restricted species. Initial investigations suggest that warming tolerance (CT_{max} minus habitat temperature) is especially constrained for tropical species (Deutsch *et al.* 2008; Huey *et al.* 2009). However, subsequent work on squamate reptiles has shown that a broader range of species might be particularly susceptible, especially those from latitudes between 20 and 40 °C (most commonly below the subtropical high where many large deserts are also found; Clusella Trullas, Blackburn & Chown 2011; Fig. 3a). A similar pattern is evident in insects, whether maximum temperature of the warmest month or mean temperature of the warmest quarter is used as a proxy for habitat temperature (Fig. 3b,c), although more data are needed for species living close to the equator. Thermal extremes may therefore pose the most significant threats for species from these latitudes. How these play out will depend on the way in which ectotherms are able to make behavioural adjustments to use microclimates to avoid temperatures that exceed their performance limits. Thus, a negative thermal safety margin presently either suggests that the population originally measured is proceeding to extinction (Sinervo *et al.* 2010), or that behavioural adjustments, enabling differential microclimate use, may be providing some respite.

Phylogenetic signal and constraints

Evolutionary constraints may lead to phylogenetic signal for thermal responses (i.e. related species sharing similar thermal responses). If species cannot easily evolve, their thermal niche will be constrained and dictate the

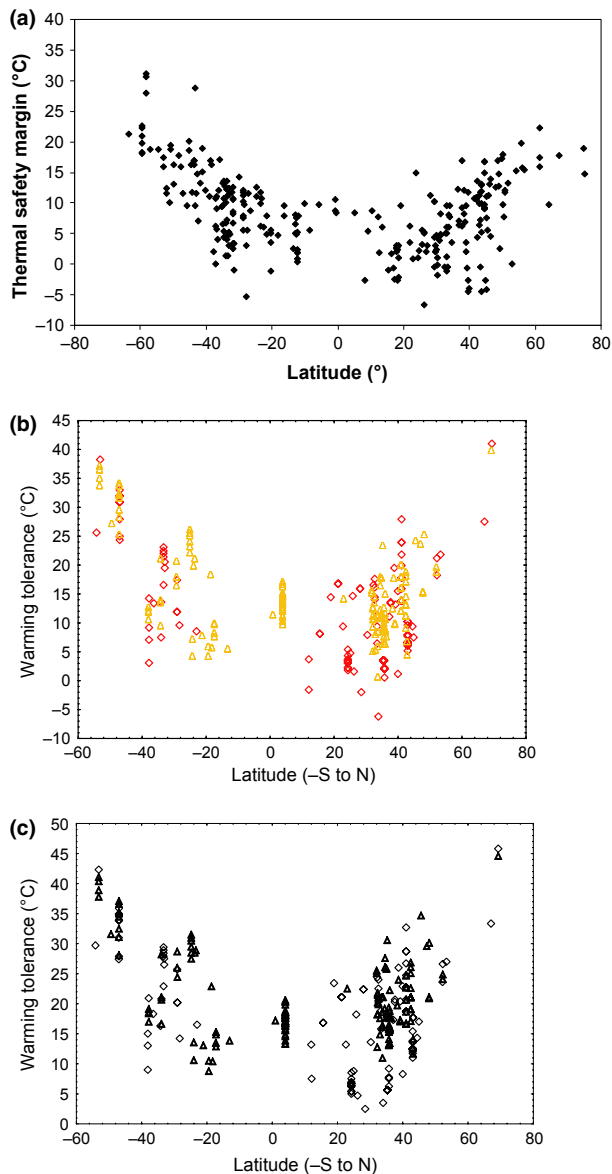


Fig. 3. Thermal safety margin or warming tolerance for squamate reptiles and insects. (a) Thermal safety margin for squamate reptiles calculated as the difference between the optimal temperature (here actually preferred temperature) and mean temperature of the warmest quarter (taken from Hijmans *et al.* 2005), based on Clusella Trullas, Blackburn & Chown (2011). Warming tolerance for insects calculated as the differences between upper lethal temperature (diamonds) or critical thermal maximum (triangles) and either (b) maximum temperature of the warmest month or (c) mean temperature of the warmest quarter, taken from Hijmans *et al.* (2005).

environments in which they can persist. Phylogenetic signal is generally clear both for the squamate reptiles and the insects (see the lambda values, a measure of phylogenetic signal, in Table 2). However, phylogenetic signal can also be present for two other reasons: similar selection pressures and similar environmental effects (Hansen, Pienaar & Orzack 2008; Losos 2008). Phylogenetic signal may reflect the fact that related species are exposed to similar

selection because they tend to occur in the same environments; evolutionary adaptation will then ensure that they end up with similar phenotypes because the opportunity for selection to produce similar phenotypes will be greater for related than for unrelated species. In this case, phylogenetic signal may not reflect a constraint. Apparent phylogenetic signal may also arise from plasticity. If related species are found in close proximity, they may be exposed to similar conditions which can result in a similar thermal phenotype owing to plastic responses to the same environment.

Several approaches exist for attempting to separate these factors to identify evolutionary constraints within phylogenies (or niche conservatism) from signal (Cooper, Jetz & Freckleton 2010). One approach is to look for very strong phylogenetic signal – so strong that the similarity among related species exceeds than expected under models of evolution that include only drift. However, many cases where evolution might still be acting to provide constraints would then be excluded. Another approach is to consider the spatial context wherein species exist and control for this in making comparisons (Freckleton & Jetz 2009); given that spatial proximity of species is a proxy for the environmental similarity species are likely to experience, this approach may help to identify both the opportunity for selection and for environmentally related effects that can produce signal in the absence of constraints. Nevertheless, this approach may still only capture part of the environmental differences and selection opportunities of closely related species for thermal responses. Species in the same location can differ markedly in the level of thermal stress they experience, so spatial proximity may not accurately reflect the similarity of selection (Helmuth & Hofmann 2001). Moreover, this approach does not capture past changes in species distributions, including recent expansions and contractions.

For upper thermal limits, there are only a few instances where attempts have been made to identify phylogenetic signal. In fact, as mentioned above, most of the focus has been on using phylogenetic information to ensure that comparisons between species tolerance limits and environmental variables are independent of phylogenetic relatedness. For instance, upper thermal tolerance limits of porcelain crabs in the genus *Petrolisthes* are related to their local microhabitat distribution; species from the upper intertidal zones typically have lower thermal maxima than those from the lower intertidal or subtidal zones where a much narrower range of temperatures is experienced (Stillman & Somero 1996, 2000). A comparative analysis of 20 species indicated that the association between microhabitat distribution and upper thermal limits persisted even when phylogenetic relatedness was corrected and also that high intertidal species with greater thermal tolerance were not necessarily restricted to one part of the phylogeny of this genus (Stillman & Somero 2000). In a comparison of 32 species of *Liolaemus* lizards, Labra, Pienaar & Hansen (2009) also detected no association between upper thermal

limits and thermal environmental conditions, and no evidence of a phylogenetic signal for this trait or for the preferred temperature of lizards, which was correlated to their thermal environments. However, in a large comparative analysis of almost 100 *Drosophila* species reared in a common environment, phylogenetic constraints were separated from phylogenetic signal likely to arise from common selection pressures. In this case, there was a strong phylogenetic constraint for upper thermal limits but no evidence of common selection pressures influencing phylogenetic signal owing to spatially associated species distributions (V. Kellermann, unpublished data). An increased understanding of phylogenetic constraints should emerge as the molecular evolution of key genes and pathways involved in establishing thermal limits is dissected (Bettencourt & Feder 2001; Hoffmann & Willi 2008; Patarnello *et al.* 2011).

Heritable variation in resistance

GENERAL ISSUES

The measurement of heritable variation within populations for physiological traits is possible if large numbers of individuals differing in relatedness can be measured in the same assay. Usually, individuals are reared across multiple generations under the same controlled environmental conditions to minimize environmental effects and control for age. In terrestrial insects, selection experiments where populations are exposed in specific assays (Bublii & Loeschcke 2005) or moved into new environments (Gibbs 1999; Rand *et al.* 2010) are also increasingly being used to investigate heritable variation in physiological traits, with the added benefit that these experiments can directly assess the potential changes in trait means in populations.

Heritable variation and selection responses are normally measured by some estimate of heritability (degree of phenotypic variation in a trait that is genetic) or evolvability (extent to which the mean in a trait can be shifted under selection, as determined by estimates of genetic variation and mean values). The merits of these different measures have been widely debated (Hansen, Pelabon & Houle 2011); particularly when presenting information comparing traits and species that differ substantially in means, both measures can be useful and are often presented, and changes in the genetic variance of a trait can be clearly distinguished from changes in the environmental variance. Because heritable variation is specific to the way a trait is measured, any estimates of heritable variation need to be interpreted within the context of the measurement approach used. Thus, while a variety of measurements are used to assess 'heat resistance' of small ectotherms, these assays may be measuring different traits with unclear relevance to natural conditions (Terblanche *et al.* 2011). For instance, heritable variation in resistance in adult *Drosophila* has been measured as knockdown under constant or

ramping temperatures in a long tube where flies fall down a series of baffles (Gilchrist, Huey & Partridge 1997) or in small vials (Hoffmann *et al.* 1997), or as mortality following constant or ramping heat exposure (Mitchell & Hoffmann 2010).

DROSOPHILA DATA

Most data on genetic variation in heat resistance come from *Drosophila* studies (Hoffmann 2010). In *Drosophila melanogaster* and *D. simulans* adults, knockdown in a baffled tube shows heritable variation leading to a selection response in one of the species under ramping and constant conditions, although the response does not change resistance beyond a few generations even when fly populations are held at a large size (Gilchrist, Huey & Partridge 1997; Hoffmann *et al.* 1997; Bublii & Loeschcke 2005). Heritable variation has also been detected at the larval stage (Krebs & Feder 1997) and in other *Drosophila* species (Sambucetti, Scannapieco & Norry 2010) as well as from population comparisons (Sarup & Loeschcke 2010; Sgrò *et al.* 2010), which may depend on the conditions used for rearing and testing flies (Sarup & Loeschcke 2010; Sgrò *et al.* 2010). However, studies in *D. melanogaster* under temperature ramping for knockdown in small vials point to a low heritability associated with a sharp reduction in additive genetic variance (Mitchell & Hoffmann 2010).

The detection of genetic variation for upper thermal limits is likely to depend on the way these limits are measured, which may reflect exposure to multiple stressors (Rezende, Tejedo & Santos 2011) or other factors (Terblanche *et al.* 2011) influencing the environmental variance (and therefore heritability, though not necessarily the genetic variance of a trait). Selection on this variation has most likely contributed to population differentiation as reflected by latitudinal clinal patterns under constant and ramping temperature stress that can be linked to climatic conditions (Parkash, Sharma & Kalra 2010; Sgrò *et al.* 2010; Sisodia & Singh 2010). The genetic basis of population differences can be quite complex and depend on environmental context. For instance, *D. buzzatii* from lowland populations show increased genetically based knockdown resistance to heat that matches their evening activity period (Sørensen & Loeschcke 2002) suggesting a clock-related adaptation.

There is some information about the genetic basis of variation in heat resistance in *Drosophila*. Overexpression and RNAi studies have shown the involvement of specific genes in mortality assays for genes such as Hsp22 (Bhole, Allikian & Tower 2004), Hsp70 (Krebs & Feder 1998) and apolipoprotein D (Muffat, Walker & Benzer 2008), while genes controlling other aspects of heat responses have also been characterized (Bettencourt *et al.* 2009). In some studies, natural variation in heat shock gene expression has been related to resistance, such as Hsp40 expression (Carmel *et al.* 2011) and Hsp70 expression (Krebs & Feder 1997), but this is not always the case as Hsp70 is essential for survival under extreme heat shock, but variation in

expression of Hsp70 does not necessarily correlate with adult survival (Jensen *et al.* 2010). Comparisons of gene expression patterns in selected lines point to many genes affected by selection whose actions are unresolved. For example, phototransduction genes are altered by selection but their role in heat shock resistance is unclear (Nielsen *et al.* 2006). Much remains to be discovered about the genes and genetic interactions involved in heat resistance as new candidates continue to emerge for further testing (Norry *et al.* 2008; Rand *et al.* 2010).

One complication in characterizing the genetic basis of upper thermal limits is that different measures of heat resistance are likely to be to some extent genetically independent. Selection for resistance to knockdown under heat leads to only partially correlated responses to heat resistance as scored through mortality (Hoffmann *et al.* 1997; Bublly & Loeschke 2005). It has been argued that a lack of a correlated selection response may reflect low statistical power (Santos *et al.* 2011), but this seems unlikely because even when traits reflecting other measures of heat resistance do not show a correlated selection response, they can differ among replicate selected (or control) lines. Heat resistance variation and thermal preference are also independent in *D. subobscura* (Dolgova *et al.* 2010), as are flight and survival under heat stress (Fasolo & Krebs 2004) as well as sterility and survival (Vollmer *et al.* 2004). Some genes affecting different components of heat resistance have been identified, such as heat shock factor (hsf) implicated in knockdown but not other heat resistance measures (Sørensen, Loeschke & Kristensen 2009).

These *Drosophila* data point to heritable variation for heat resistance measured in specific assays, with some notable exceptions particularly under thermal ramping where the genetic variance may be reduced. Patterns established with one measure of heat resistance may not extrapolate to other measures owing to a different genetic basis. The extent to which ecologically relevant thermal responses can evolve remains unclear, and comparative studies of heritable variation are needed to test whether species with particularly low upper thermal limits might have a limited adaptive capacity (c.f. Kellermann *et al.* 2009a).

NON-DROSOPHILA DATA

There are few estimates of heritable variation for terrestrial ectotherms other than *Drosophila*. Variation in heat resistance has been described among strains of biocontrol agents screened for their suitability in different environmental conditions. The insect-feeding nematode, *Heterorhabditis bacteriophora*, when collected from different geographic regions, showed substantial variation in lethal levels of heat exposure ranging from 33.3 to 40.1 °C when nematodes were not acclimated (Mukuka *et al.* 2010). There was little association between strain rankings when acclimated and non-acclimated nematodes were compared, and also no association between geographic origin and the mean tem-

perature of the location where they were collected. In the absence of heritable variation, heat stress may be countered by allochronic changes in populations. For instance, the ability of populations of the lepidopteran *Thaumetopoea pityocampa* to tolerate high temperatures differed by 6 °C depending on the timing of their development (Santos *et al.* 2011). Heritable variation for upper thermal limits have also been described for several pest species, including variation among clones of the peach aphid, *Myzus persicae* (Alford, Blackburn & Bale 2012).

Most of the other data on heritable variation for upper thermal limits come from aquatic organisms, and we briefly summarize this information. Heat resistance has been estimated in two species of fish; for mosquito fish (*Gambusia holbrooki*), the heritability for time until death was estimated at around 30% (Meffe *et al.* 1995), while for least killifish (*Heteronuria formosa*) there are contradictory estimates of 18–46% based on parent offspring regression (Doyle, Leberg & Klerks 2011) and temperature at death and an estimate of near 0 based on a lack of selection response (Baer & Travis 2000). Genetic variation for thermal responses has been considered in corals because of the potential for coral bleaching under increasing water temperatures and also owing to acidification (Pandolfi *et al.* 2011). Colonies of the coral *Acropora millepora* differ in their response to heat as measured by their ability to maintain photosynthesis and generate protective pigments, and there was also heritable variation in the ability of symbionts to sustain coral growth under warm conditions (Csaszar *et al.* 2010). These findings point to the potential for adaptive evolutionary changes in the corals that might act to reduce coral bleaching. The persistence of some coral reefs under past periods of warming also suggest resilience in some reef systems (Pandolfi *et al.* 2011), and there are some populations persisting already under warmer conditions such as in the Arabian Gulf which may provide genotypes for future adaptation (Riegl *et al.* 2011). Differences in thermal responses have also been documented among clones of other marine organisms such as the bryozoan *Celleporella hyaline* (Pistevos *et al.* 2011). In some marine species, there may be very little geographic variation in thermal tolerance, as in the case of early immature stages of the sea urchin *Strongylocentrotus purpuratus* collected from Oregon to Mexico (Hammond & Hofmann 2010), whereas in others like immature stages of marine snails (*Nucella* spp.), there is evidence for strong latitudinal variation (Zippay & Hofmann 2010).

At this stage, there have been no comparisons of evolutionary adaptation in CT_{max} across clades of terrestrial ectotherms akin to comparisons for cold or desiccation responses (c.f. Kellermann *et al.* 2009a). However, in a selection experiment on 12 species of phytoplankton strains where temperature was increased through a number of generations and adaptation most likely involved new mutations, some species adapted rapidly whereas others had a very limited adaptive capacity (Huertas *et al.* 2011). Those that successfully adapted tended to be from

continental water bodies that fluctuated in temperature, whereas species from open and coastal waters adapted to a much more limited extent. As in the case of the *Drosophila* data, these patterns point to potential limits to selection responses depending on the ecology of species.

Responses to extreme environments

Despite the evidence for comparatively limited variation in heat resistance, its plasticity and its evolvability, examples exist of species that have either overcome heat resistance barriers, or have entirely lost the ability to do so, resulting in very different thermal tolerances. In insects, for example, the highest tolerances, of non-encysted stages, are known from several thermophilic ants, including *Melophorus bagoti* from Australia ($CT_{max} = 56.7^\circ C$), *Cataglyphis bombycinus* from Tunisia ($CT_{max} = 53.6^\circ C$) and *Ocymyrmex velox* ($CT_{max} = 54.1^\circ C$) from Namibia (Christian & Morton 1992; Wehner & Wehner 2011). These limits and the foraging temperatures at which the ants are active are much higher than those found for most other ant and insect species. It is thought that the thermophilic taxa avoid competition from the less heat-tolerant species and are able to make use of resources in the form other arthropods that have succumbed to heat and/or desiccation stress (Wehner & Wehner 2011). Clearly, this represents an evolved response, although the shift may have taken place in a common ancestor of the genera given the known thermophily of both *Cataglyphis* and *Ocymyrmex* (see further data in Marsh 1985; Cerdá, Retana & Cros 1998). What mechanisms underlie this high temperature tolerance are not known, although continual synthesis of heat shock proteins is a likely candidate (Gehring & Wehner 1995). The substantial fitness costs of Hsp expression (Feder & Hofmann 1999) might explain why such high temperature tolerances are uncommon in other species, but phylogenetic constraints at the molecular level might also be involved.

Loss of thermal tolerance has been suggested only for a single insect species, the ice crawler *Grylloblatta* sp., which is incapable of tolerating temperatures greater than $15\text{--}20^\circ C$ (Morrissey & Edwards 1979), although experiments of the kind typically undertaken for assessing critical limits were not used to determine thermal tolerance in the species. Even one of the only insect species found on Antarctica, the midge *Belgica antarctica*, is capable of 80% survival (of larvae) of a 3-h exposure to $30^\circ C$ (Benoit *et al.* 2009). Little is known about the extent to which tolerance ability might be lost or the rates and reasons for these losses, although DNA decay might be a significant contributor (Hoffmann & Willi 2008).

High temperatures facilitating evolutionary change?

There has been intermittent interest in the past few decades in whether environmental conditions can trigger cross-gen-

eration effects that help in adaptation. Perhaps the simplest cross-generation effect is where exposure to heat stress in one generation influences responses to heat in the ensuing generation. This may be short term, as in the case of maternal effects that last a generation, or longer term, such as when inherited cytoplasmic factors are involved, or when stress triggers evolutionary change by affecting the expression of genetic variability.

Large maternal effects for heat resistance exist for field-collected *Drosophila simulans* (Jenkins & Hoffmann 1994), resulting in offspring reflecting their mothers in terms of heat resistance more closely than their fathers. This pattern is likely to be adaptive if offspring experience similar warm conditions to their mothers. Maternal effects triggered by environmental temperature are also well known for life-history traits and these can increase offspring fitness (Ghalambor *et al.* 2007) although their effects are often not clear (Stelgenga & Fischer 2007). For instance in a marine bryozoan (*Bugula neritina*), warm temperatures result in females producing smaller and more variable offspring with an increased dispersal ability and higher fitness (Burgess & Marshall 2011). Maternal effects that persist across generations (i.e. cytoplasmic effects) are known for *Drosophila* (Stephanou & Alahiotis 1983) but have rarely been studied in other organisms.

Apart from generating maternal effects, stressful conditions can also generate evolutionary changes by triggering the expression of genetic variation that can then be selected (Mittelman & Wilson 2010). This might occur because stressful conditions influence recombination/mutation/transposition rates, influence the expression of canalized traits and/or affect the environmental/genetic variance (Hoffmann & Parsons 1991; Hauser *et al.* 2011). Whether high temperatures can influence these processes is unclear. In *Drosophila* experiments, high culture temperatures have been associated with an increased expression of genetic variation in some life-history traits but not necessarily morphological traits (Sgrò & Hoffmann 1998; Petavy *et al.* 2006). As far as we are aware, the rate of adaptation to stressful conditions has not been shown to be enhanced by heat exposure in ectotherms, although heat stress may enhance the expression of genetic variants contributing to loss of fitness following inbreeding (Chen & Wagner 2012).

In contrast, in plants, epigenetic mechanisms are thought to represent a stress response mechanism that can increase mutation/recombination/transposition rates as well as directly influence offspring fitness under stressful conditions. Various studies on *Arabidopsis* have shown that heat stress increases recombination and transposition rates with potentially long-term consequences on rates of adaptation (Hauser *et al.* 2011). In addition, heat stress causes methylation and generates increased resistance in progeny when these are untreated, although it is lost in later generations (Boyko *et al.* 2010). These types of effects may be mediated via DNA methylation or other mechanisms associated with gene silencing.

Maternal effects represent a type of phenotypic plasticity that might enhance or retard evolutionary rates (Kirkpatrick & Lande 1989). Plastic responses involving acclimation may reduce selection pressures and slow rates of evolution if the acclimation response is successful. Obviously, plasticity is in itself potentially genetically variable and contributes to the selection response. There is evidence for differences in acclimation ability for high temperature tolerance among populations although the effects may be small (Sgrò *et al.* 2010). Whether maternal effects themselves enhance evolutionary rates depends on several factors including the predictability of environments across generations and direction of the maternal effects (Kirkpatrick & Lande 1989). For high temperature responses, there are few empirical data to directly test effects on evolutionary rates.

Thermal stresses can also indirectly influence rates of evolutionary change through affecting population size and patterns of fragmentation. As populations become reduced in size, adaptive changes become less likely as a consequence of a loss of genetic variation, and a decrease in the likelihood that adaptive mutations will occur (Lynch & Lande 1993; Bell & Collins 2008), and fragmentation may also decrease speciation rates (Birand, Vose & Gavrilits 2012). *Drosophila* experiments with small populations indicate a reduced adaptive response under heat stress (Willi & Hoffmann 2009).

Upper thermal limits and climate change

The data for terrestrial ectotherms discussed previously point to species from mid-latitudes in particular being closest to their thermal maxima. Moreover, although data are still quite scanty, species may have only a limited capacity to deal with changes in upper thermal limits. Under an expected 2–4 °C warming scenario (IPCC 2007), mid-latitude populations near limits are likely to face the threat of extinction because they cannot adapt to new environmental conditions. Plastic changes seem set, at least so far as data from the insects suggest, to cover at most in the order of 2–4 °C (Hoffmann, Sørensen & Loeschke 2003; Chown *et al.* 2009; Allen, Clusella-Trullas & Chown 2012), which will provide little scope for ectotherms to deal with substantial heat stress (bearing in mind that global forecasts of 2–4 °C increase in temperature imply much larger increases for continental areas), depending on the nature thereof. Adaptive changes are possible and will potentially increase heat resistance to some extent, but selection limits may be reached quite quickly and the nature of the heat stress in populations (particularly whether it occurs in combination with other stresses) may be critical.

However, much more information is needed on the upper thermal limits of species, particularly under the types of stressful conditions that species are likely to experience in the field given the availability of microhabitats of varying temperatures and other conditions. Most

research on upper thermal limits has defined these in terms of exposures to constant or rising temperatures under laboratory conditions, yet under climate change, thermal stress is likely to occur in combination with other environmental changes. Typically, ectotherms tested in the laboratory are well fed and free from other stresses including disease. In contrast, in nature, thermally stressful periods are expected to often coincide with periods of other stresses. These might include a potential reduction in food supply resulting from asynchrony in the emergence of predators and their prey or plant growth and herbivore activity (Visser *et al.* 1998). Competitive interactions from invading species will also often alter under climate change (Schweiger *et al.* 2010). In aquatic environments, rising or extreme temperatures may be exacerbated by low flow regimes owing to drought and by an associated decline in oxygen availability. Although the evidence for oxygen limitation of thermal tolerance (Pörtner 2002, 2010) is at best equivocal for terrestrial insects (Klok & Chown 2003; Lighton 2007; Stevens *et al.* 2010), evidence is mounting that it may have a significant role for aquatic species or for species with aquatic life stages (Verberk & Bilton 2011). When multiple environmental factors change, the effects can be complex to predict because they do not act independently (Padmanabha, Lord & Lounibos 2011).

There is almost no information on how thermal limits are influenced by combinations of stressors. Changes in the conditions that organisms experience during thermal stress could lead to quite unpredictable upper thermal limits (Terblanche *et al.* 2011; Overgaard, Kristensen & Sørensen 2012). Moreover, thermal stress can influence susceptibility to other selective agents; tropical *Bicyclus anynana* butterflies lose immune function as measured by phenoloxidase (PO) activity and haemocyte numbers when exposed to warm conditions, and the effects are particularly marked when adults have a limited food supply (Karl *et al.* 2011). On the other hand, thermal stress in nature can also be buffered through behaviour and movement as well as seasonal timing. In the absence of physiological adaptation to stressful conditions, adaptive changes in these strategies may help organisms to withstand stressful conditions.

Nevertheless, if the evolution of upper thermal limits is tightly constrained, it is perhaps inevitable that lineages with high upper thermal limits will expand their range at the cost of species with limited potential to acclimate and adapt. Still, more data are needed on all aspects of upper thermal limits. We are starting to build a picture of regions where species are close to their upper limits, and mid-latitude species may be most prone to experience heat stress even though temperature changes may be largest at higher latitudes. However, many aspects of adaptive responses including heritable variation, phylogenetic constraints and adaptive geographic variation have so far been explored for a very narrow range of species and under a limited set of experimental conditions.

Acknowledgements

Elrike Marais compiled the databases of insect thermal tolerance and assisted with the preparation of the Supporting Information. AAH is supported by a Laureate Fellowship from the Australian Research Council.

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Received 1 April 2012; accepted 1 June 2012
Handling Editor: Charles Fox

Supporting Information

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

Table S1. Critical thermal maximum data for insects.

Table S2. Critical thermal minimum data for insects.

Table S3. Upper lethal temperature data for insects.

Table S4. Lower lethal temperatures data for insects.

Table S5. Supercooling point data and an indication of freezing tolerance (FT) or freeze avoidance (FA) for insects.

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