

*Research*

# Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation

Raymond B. Huey<sup>1,\*</sup>, Michael R. Kearney<sup>2</sup>, Andrew Krockenberger<sup>3</sup>,  
Joseph A. M. Holtum<sup>4</sup>, Mellissa Jess<sup>5</sup> and Stephen E. Williams<sup>4</sup>

<sup>1</sup>*Department of Biology, University of Washington, Seattle, WA, USA*

<sup>2</sup>*Department of Zoology, The University of Melbourne, Victoria 3010, Australia*

<sup>3</sup>*School of Marine and Tropical Biology, James Cook University, Cairns, Queensland 4870, Australia*

<sup>4</sup>*School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia*

<sup>5</sup>*Reef and Rainforest Research Centre, 51 The Esplanade, Cairns, Queensland 4870, Australia*

A recently developed integrative framework proposes that the vulnerability of a species to environmental change depends on the species' *exposure* and *sensitivity* to environmental change, its *resilience* to perturbations and its potential to *adapt* to change. These vulnerability criteria require behavioural, physiological and genetic data. With this information in hand, biologists can predict organisms most at risk from environmental change. Biologists and managers can then target organisms and habitats most at risk. Unfortunately, the required data (e.g. optimal physiological temperatures) are rarely available. Here, we evaluate the reliability of potential proxies (e.g. critical temperatures) that are often available for some groups. Several proxies for ectotherms are promising, but analogous ones for endotherms are lacking. We also develop a simple graphical model of how behavioural thermoregulation, acclimation and adaptation may interact to influence vulnerability over time. After considering this model together with the proxies available for physiological sensitivity to climate change, we conclude that ectotherms sharing vulnerability traits seem concentrated in lowland tropical forests. Their vulnerability may be exacerbated by negative biotic interactions. Whether tropical forest (or other) species can adapt to warming environments is unclear, as genetic and selective data are scant. Nevertheless, the prospects for tropical forest ectotherms appear grim.

**Keywords:** climate change; ectotherms; endotherms; temperature; thermoregulation; tropics

## 1. INTRODUCTION

Climate warming presents major challenges to organisms [1,2]. Consequently, biologists are endeavouring to develop robust ways to evaluate the differential vulnerability of organisms to climate change [3–10] and then to evaluate and implement management strategies tailored for species judged most at risk [11].

Attempts to evaluate vulnerability and to develop management strategies should be based on relevant biological foundations. Williams *et al.* [5] developed an integrative framework for assessing traits that promote vulnerability. They proposed that the vulnerability of a species depends on its *sensitivity* to environmental change, its *exposure* to that change, its *resilience* or ability to recover from perturbations and its potential to *adapt* to change. That framework is appealing, but implementing it will be challenging

because each of these vulnerability traits requires extensive biological information.

Here, we address implementation of that model. We begin by reviewing how and why the above factors influence organismal vulnerability [5]. Then we outline the biological data necessary to evaluate each factor. However, because such data are rarely available, we suggest and evaluate 'quick-and-dirty' proxies. We focus on terrestrial organisms, especially 'dry-skinned' ectotherms such as lizards or insects, for which the critical data (natural history, physiology, behaviour) are relatively rich. We do not discuss aquatic organisms, for which temperature impacts are complicated by interactions with O<sub>2</sub>, CO<sub>2</sub> and salinity [12–14], intertidal organisms, which live in rapidly fluctuating environments and sometimes have few options for behavioural thermoregulation [14–17], and 'wet-skinned' organisms such as amphibians, where temperature impacts are complicated by sensitivity to moisture [18] and to fungal infections [19].

Many aspects of climate are changing in diverse environments, but we focus on the direct effects of increased air temperature ( $T_a$ ) on the thermal biology

\* Author for correspondence ([hueyrb@uw.edu](mailto:hueyrb@uw.edu)).

One contribution of 13 to a Theme Issue 'Conservation physiology: integrating physiological mechanisms with ecology and evolution to predict responses of organisms to environmental change'.

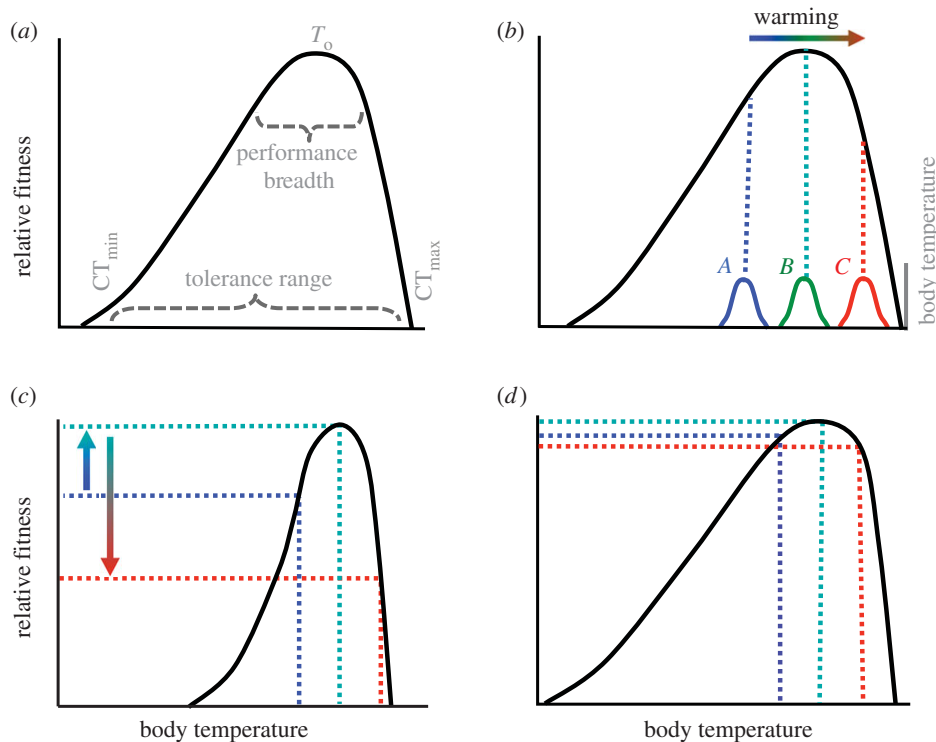


Figure 1. (a) Thermal fitness (performance) curve for a hypothetical ectotherm, with key descriptive parameters  $CT_{\min}$ ,  $CT_{\max}$ , tolerance range, performance breadth and optimal temperature ( $T_o$ ) identified (adapted from Huey [48]). (b) With climate warming, realized  $T_b$  distributions can shift higher. If warming results in  $T_b$  that are closer to  $T_o$  of a species (for example  $T_b$  shift from A to B), then warming should enhance fitness; but if warming raises  $T_b$  above  $T_o$  (e.g. if  $T_b$  shifts from B to C), fitness will be reduced (see text). (c,d) Step increases in  $T_b$  distributions from warming can have much bigger effects on (c) thermal specialists than on (d) thermal generalists.

of terrestrial animals, especially ectotherms. Changes in environmental temperature are the most direct and predictable outcome of increased greenhouse gas emissions [2]. Such changes can alter body temperatures ( $T_b$ ) of ectotherms, and thus their physiological performance and vulnerability [8,10,20–24], or heat loads on endotherms [25–28], and thus their energy and water balances.

An organism's vulnerability also depends on factors other than temperature (e.g. disease, food, rainfall, cloud cover,  $CO_2$  and  $O_2$ ) as well as on additional stressors (e.g. habitat destruction and fragmentation, fire, pollutants, invasive species) that can interact with climate warming [7,29–39]. Furthermore, no organism is an ecological island; and so its vulnerability will also depend on how climate change alters its interactions with competitors, predators, parasites, diseases and mutualists [9,17,40–45]. Despite these complexities, attempts to understand an organism's vulnerability to climate warming must build from a robust understanding of its sensitivity and response to temperature.

## 2. PHYSIOLOGICAL SENSITIVITY

### (a) *Physiological traits dictating sensitivity*

A thermal 'performance' or 'fitness' curve serves as a convenient descriptor of how a change in body temperature ( $T_b$ ) influences physiological sensitivity and fitness of ectotherms [22,46,47]. Very low and high  $T_b$  reduce an ectotherm's performance and can be lethal in the extreme: these endpoint  $T_b$  are called

the 'critical temperatures' (figure 1a;  $CT_{\max}$ ,  $CT_{\min}$ ). Within those critical limits, performance reaches a maximum at an optimal temperature region ( $T_o$ ), and then typically plummets at higher  $T_b$  [46,49,50]. Thermal performance curves can, however, shift somewhat depending on the trait, acclimation and time of temperature exposure [48,51–53].

An organism's integrated performance or fitness over some time interval depends on its performance curve, weighted by the  $T_b$  it experiences during that interval [22,50,54–56]. Thus, the physiological impact of warming depends primarily on an organism's field  $T_b$  (at the commencement of warming) relative to its  $T_o$ . If pre-warming  $T_b$  is less than  $T_o$  ('A' in figure 1b), then warming-induced increases in  $T_b$  will enhance fitness. If pre-warming  $T_b$  are similar to  $T_o$  ('B' in figure 1b), then modest warming will have little impact (at least initially); but if  $T_b$  rises significantly above  $T_o$  ('C' in figure 1b), then warming should cause catastrophic effects, because fitness drops rapidly at  $T_b$  greater than  $T_o$ .

Sensitivity to climate warming also depends on whether a species is a thermal generalist or specialist [6,47,49,54,57,58]. A given increase in  $T_b$  from warming will usually have a larger impact on a thermal specialist (figure 1c) than on a thermal generalist (figure 1d).

In contrast to ectotherms, most endotherms (birds and mammals) are homeothermic and use behavioural, morphological and, especially, physiological adjustments to maintain a high and relatively constant body temperature (approx. 35–40°C being the 'set-point') under diverse environmental conditions [59,60].

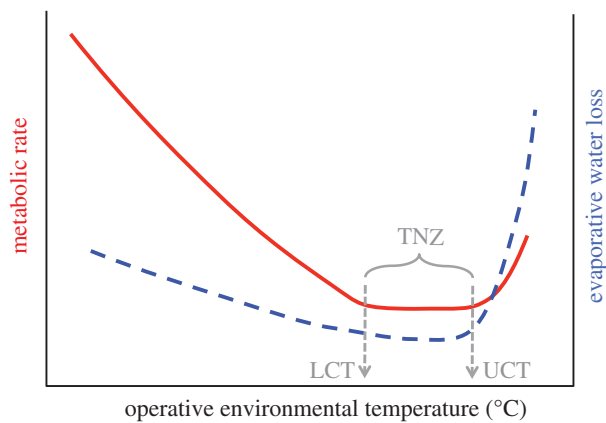


Figure 2. Effects of environmental temperature on rates of metabolic heat production (red) and of evaporative water loss (blue) of endotherms. At low environmental temperatures, energy expenditures and thus heat production are elevated to balance heat loss. At high ambient temperatures, rates of evaporative water loss are elevated to dump excess heat. Indicated are the thermal neutral zone (TNZ), and the lower (LCT) and upper (UCT) critical temperatures, beyond which metabolic rates increase.

Endotherms with body temperatures only a few degrees below or above the set-point temperature range can be physiologically stressed [28]. Most endotherms can be thus considered extreme thermal specialists (with respect to  $T_b$ ).

When exposed to changing environmental temperatures, endotherms typically defend body temperature (figure 2). For example, if environmental temperature falls below an endotherm's 'thermoneutral zone' (TNZ), a 'comfort zone' within which endotherms can maintain a low metabolic rate, endotherms increase metabolic heat to offset increased heat loss. But if environmental temperatures rise above the TNZ, endotherms usually defend their set-point temperature primarily by increasing rates of evaporative cooling (panting, sweating). Temperatures bounding the TNZ are called the 'lower critical temperature' (LCT) and 'upper critical temperature' (UCT). The width and position of the TNZ partly reflect measurement conditions, but mainly reflect the size, shape and pelage of the endotherm, and its ability to control heat loss through postural adjustments, fur or feather erection and altered blood flow [26,61].

Finally, thermal sensitivities of both ectotherms and endotherms can shift somewhat depending on its recent or anticipated environmental experience [62]. (Such phenotypic plasticity of physiology is often called 'acclimatization' (for natural shifts) or 'acclimation' (for shifts in laboratory studies).) In ectotherms, for example, recent exposure to elevated temperatures sometimes enhances thermal performance at higher temperatures ([63], but see [64,65]). Such 'beneficial' acclimation [64] can help buffer physiological impacts of climate change (figure 3a) [22,57,62,66,67] relative to the case of limited acclimation (figure 3b). Endotherms can also acclimatize, sometimes by changing insulation or posture [26]. They can also shift their 'set-point' body temperatures: torpor and hibernation are extreme cases.

### (b) Which organisms are physiologically sensitive to climate warming?

The above considerations suggest indicator traits that may predict species most vulnerable to climate warming: specifically, vulnerable species are likely to be thermal specialists, to be active at  $T_b$  that are near (or even above)  $T_o$  [6,9,68,69] and to have limited capacity to acclimatize to changing  $T_b$ . Where geographically do such organisms typically occur? In a seminal paper, Janzen [57] predicted that thermal specialists and species with limited acclimation capacity should occur in the lowland tropics because temperature variation (daily or seasonal) is relatively limited there.

Janzen's prediction was largely based on intuition, but has been supported subsequently by empirical studies on diverse ectotherms [6,37,70–75]. Indeed, tolerance ranges (figure 1a) increase with latitude in many taxa including frogs [76], insects [77,78] and lizards (figure 4) [37,68,79]. Interestingly, the increased tolerance range at high latitude consistently results from a much greater shift in  $CT_{min}$  than in  $CT_{max}$  [37,68,74,76,77,79], probably because minimum yearly (ambient) temperatures drop rapidly with latitude, whereas maximum yearly temperatures are relatively independent of latitude (except at extreme latitudes [37,72,77,80]).

Although the tolerance range ( $CT_{max} - CT_{min}$ ) is relatively narrow for most tropical ectotherms (figure 4), thermal performance breadth (figure 1a) for sprinting is surprisingly independent of latitude in lizards [79], at least at high performance levels (e.g. 85% of maximum). Whether this holds for other ectotherm performance traits needs to be determined.

Comparative levels of thermal specialization in endotherms are not as well described as those of ectotherms. The width of the TNZ (figure 2) is a potential index of endotherm thermal specialization; but we see two concerns here. First, laboratory measurements of TNZ are sensitive to the specific experimental conditions, which will differ from the field [26]. Second, TNZ itself is rarely measured. Even so, the width of the TNZ should be (roughly) inversely proportional to the LCT (figure 2) simply because the UCT (figure 2) appears much less variable than the LCT [81]. Hence, we focus our discussion on LCT.

In a pioneering paper, Scholander *et al.* [61] showed that the LCT of tropical mammals was much higher than that of non-tropical species (figure 5), primarily because they had less dense and less deep pelage. Thus TNZ is directly related to latitude, such that tropical species have a relatively narrow TNZ. Nevertheless, the impact of climate warming on endotherms in warm environments should be more sensitive to the UCT than to the LCT. However, because interspecific (or phenotypic) variation in UCT appears minor [81], endotherms may have limited capacity to shift UCT by physiological or morphological adjustments. Torpor may be an endotherm's primary way of dealing with stressfully warm environments [83], even in the tropics [84].

Janzen [57] also predicted that tropical organisms would have limited acclimatization capacities (figure 3b). Evidence for ectotherms is limited but is generally consistent with this expectation (reviewed in [72,75], but see

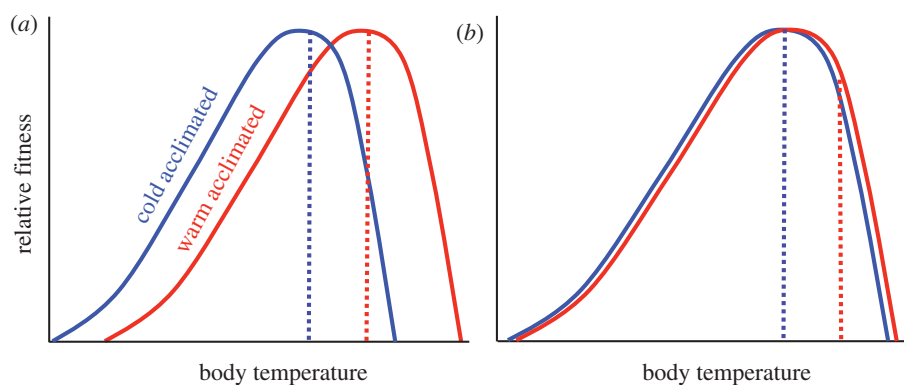


Figure 3. Acclimatization to low (blue dotted line) versus high (red dotted line)  $T_b$  (simulating an acute climate shift) sometimes induces a phenotypic shift in an ectotherm's thermal fitness curve. (a) Depicts an ectotherm with marked acclimatization capacities. Its elevated  $T_o$  (red) provides some physiological buffering against climate warming ('Beneficial Acclimation'). (b) Shows an ectotherm with a relatively limited response. If its  $T_b$  is elevated by climate warming (red dotted line), its performance will decline.

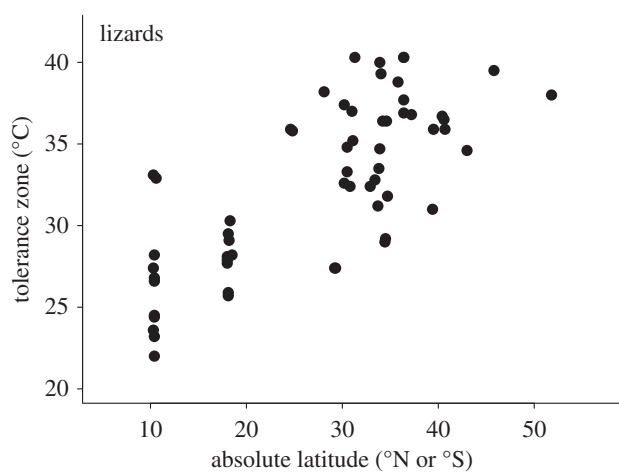


Figure 4. Tolerance zones ( $CT_{max} - CT_{min}$ ; see figure 1a) of lizards increase with absolute latitude. The increase is due primarily to a shift in  $CT_{min}$  (rather than  $CT_{max}$ ) with latitude (see text). Note: see Huey *et al.* [68] for a phylogenetic analyses.

[85]). One counterexample involves a tropical crocodile, in which sustained swimming speed showed perfect compensation for acclimation temperature [63]. In contrast, diving metabolic rate did not compensate adequately in another tropical crocodile [86]. Also, a recent study shows rapid cross-generation acclimation of aerobic scope to temperature by a tropical reef fish [87].

Comparative (latitudinal) evidence for endotherm acclimation capacities is even more scanty. One relevant index could be the magnitude of seasonal or environmental shifts in the position or width of TNZ [88,89], especially shifts of UCT. However, we know of no comprehensive review on this topic. Clearly, a comprehensive analysis and review of acclimatization responses of tropical versus temperate zone species (ectotherms and endotherms) to warming temperatures is needed.

### (c) Quantifying physiological traits and proxies

Ideally, one should measure the full thermal sensitivity (figure 1a) of fitness or of key functional traits (see fig. 6 in [47]) [48,90,91] of the ectotherm of interest.

Moreover, the particular performance traits selected should be tailored to the ecology of the species under study [46] but generally might include sprint speed, prey capture ability, development time, reproductive rate, growth rate or net energy gain [46,56,91,92]. Performance of such traits can be linked to survival and fitness [93–96], but establishing links among thermal performance curves, environmental variation and fitness is challenging [97]. For some species with short generation times, one can measure the thermal sensitivity of Darwinian fitness (e.g. intrinsic rate of population growth or net reproductive rate [51,98–102]), but the relevance of different fitness measures is demography-dependent [51].

Importantly, performance curves depend to some extent on experimental methodology [53]. This is apparent in estimates of  $CT_{max}$ , which can vary with heating rate [103–105] or with the specific index of  $CT_{max}$  [106,107]. Thus, caution is appropriate when compiling data from independent studies [37,68,108,109], though the biological signal is often large enough to swamp these issues, at least in some taxa [68,110].

Because measuring a full thermal performance curve of an ectotherm is often impractical, a search among available proxies (e.g. critical temperatures, figure 1a) might provide climate workers with robust clues as to the position and shape of a species' performance curve. The thermal dependence of sprint speed has been quantified for many lizards and thus offers an opportunity to evaluate the ability of several potential proxies to predict  $T_o$  for sprint speed [68]. We find that  $CT_{max}$ , mean  $T_b$  of lizards active in the field, and preferred body temperature in laboratory thermal gradients all predict  $T_o$ , at least roughly (figure 6a–c). However,  $CT_{min}$  and mean maximum daily temperature in summer do not (figure 6d,e). Nevertheless, considerable scatter is evident, even for the significant proxies (figure 6a–c); and this scatter may reflect phylogenetic influences [111], methodological differences [103] or experimental error. Therefore, these indices should be used with caution [112]. Furthermore, even significant relationships are not scaled 1:1 (figure 6a–c), and so regression approaches will be required to predict  $T_o$  from proxies.

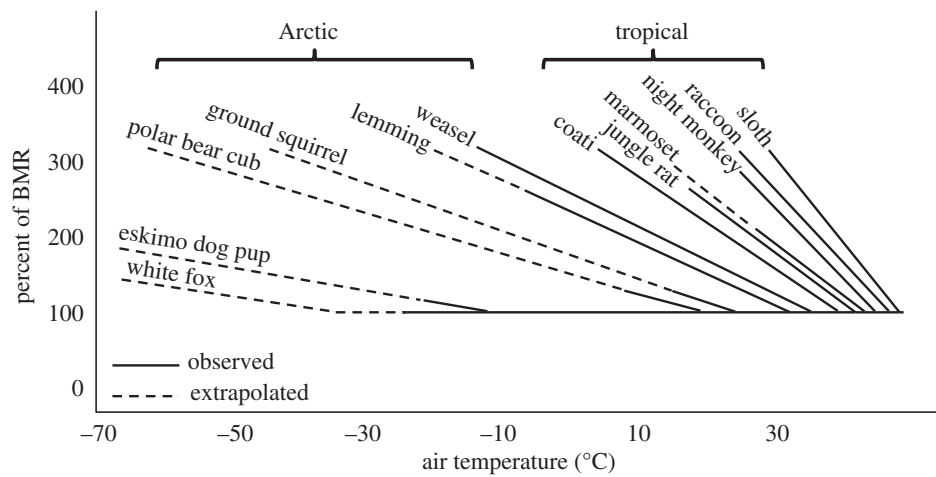


Figure 5. Metabolic rate as a percentage of basal metabolic rate (BMR) versus air temperature for Arctic and tropical mammals. Arctic mammals have relatively low LCTs, and thus relatively broad TNZs, assuming that UCTs are independent of latitude. Adapted from Porter & Kearney [26], which was based on the study of Scholander *et al.* [61,82].

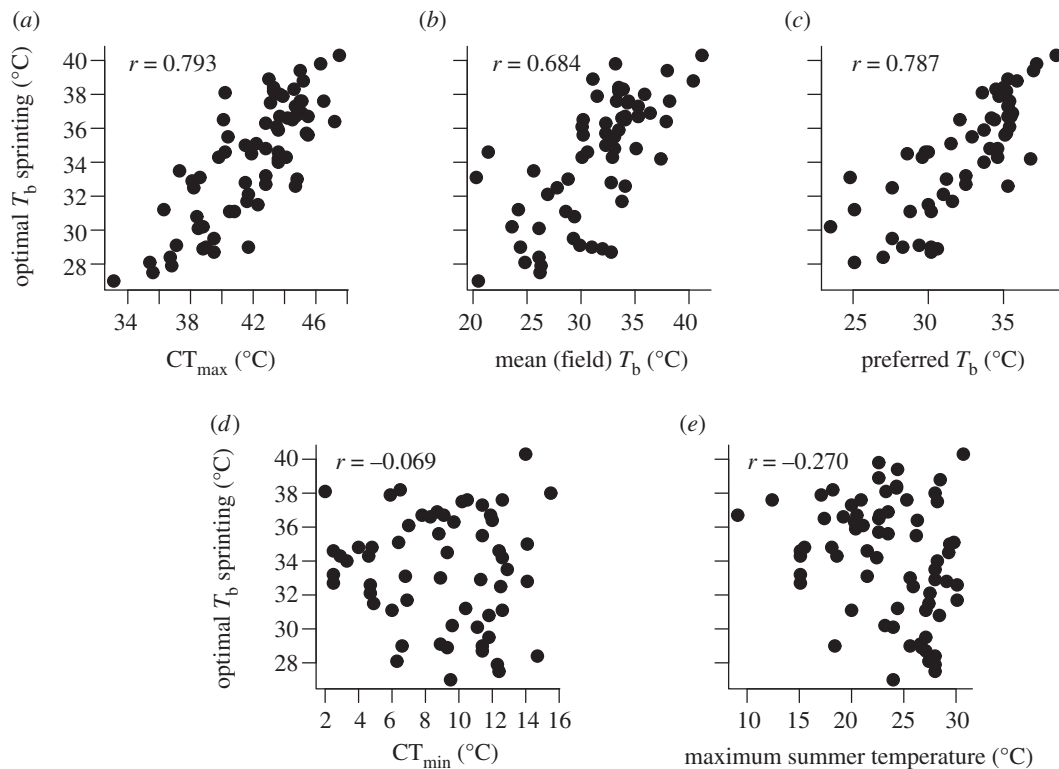


Figure 6. Potential proxies for optimal temperatures ( $T_o$ ) with lizard data as exemplars: (a)  $CT_{max}$ , (b) mean  $T_b$  (field), (c) preferred  $T_b$  in laboratory thermal gradients, (d)  $CT_{min}$  and (e) mean maximum daily temperature for the three warmest months.  $CT_{max}$ ,  $T_b$  and  $T_p$  predict  $T_o$  (a–c), but  $CT_{min}$  and maximum summer temperatures do not (d,e). Data source: Huey *et al.* [68].

The thermal dependence of metabolic rate also provides opportunities to quantify thermal endpoints. Metabolic rate increases exponentially with temperature, but eventually plateaus and then drops as an animal approaches a critical or mortal temperature [113]. Lighton & Turner [114] showed with ants that the temperature at which metabolic rate starts to drop correlates closely with the temperature at which locomotion ceased. Similarly, the upper temperature at which metabolic rate starts to drop has been used to index the onset of temperature stress in salamanders, and Bernardo & Spotila [115] argue that the magnitude of that drop is also a

physiologically meaningful index of vulnerability to warming.

For endotherms, potential proxies are currently less clear. Endotherms have high physiological capacities to buffer environmental variations [60], but are not immune to extreme heat waves [38,116,117], which may increase in frequency, intensity and duration as climate warms [118]. For endotherms facing such conditions, perhaps the UCT (figure 2)—or perhaps ambient temperature at the onset of panting—might be useful proxies of risk. However, we know of no recent comparative study that quantifies these temperatures as a function of latitude or climate.

Body size will undoubtedly affect endotherm vulnerability, but its roles are complex [26]. For example, large endotherms will have thermal inertia and greater reserves (e.g. fuel and water), and thus should have longer survival times during extreme heat waves [117]; but small endotherms may have more thermoregulatory opportunities (e.g. access to cool burrows or small patches of shade).

Diurnality is an obvious risk factor for endotherms, as day-active species may be potentially exposed to high heat loads as well as to water stress [117]. Because these stresses may force them to restrict activity times [119,120], their energy budgets may be constrained. As noted above, some endotherms can escape the heat by becoming torpid during warm spells [83,84], but only if they have access to cool retreats (e.g. deep burrows).

Overall, an evaluation of vulnerability proxies for endotherms requires further investigation. Perhaps the first step is developing a full mechanistic understanding of factors that increase endotherm vulnerability to warming [26,27].

#### **(d) Estimating relevant environmental temperatures**

Predictions of the physiological impacts of climate warming on physiology require reliable estimates of how the distribution of environmental temperatures will shift with warming. However, climate models [2] typically predict only mean annual air temperatures. Unfortunately, mean annual temperatures have limited physiological relevance because they eliminate within-site temperature variation (large in temperate zones) that drives physiological activity and performance [37,121–123]. Such metrics also completely obscure chronic or acute thermal events, which sometimes dominate selection [9,37,52,124,125].

Air temperatures have limited physiological relevance. ‘Operative body temperature’ ( $T_e$ ) is a more relevant index because  $T_e$  approximates the equilibrium  $T_b$  of an ectotherm at a given time and place.  $T_e$  can differ substantially from air temperature (especially for large organisms) because  $T_e$  is determined not only by air temperatures (convection) but also by radiation, conduction, evaporation and metabolism [121,126]. Fortunately, biophysical and climate models can be combined to predict  $T_e$  in the future [4,8,127].

$T_e$  of ectotherms can be estimated in two ways. First, one can construct physical models that approximate size, shape and colour of a given animal, implant a thermocouple and then measure  $T_e$  [121,126]. These models are typically hollow and equilibrate quickly, and the resulting  $T_e$  can be within 1°C of actual  $T_b$  at the same site [128,129]. (Note: adjustments need to be made for large ectotherms, which have substantial thermal inertia [130–132], and amphibians, which can have high rates of evaporative water loss [18,133]). Second, one can measure the key environmental variables (e.g. air temperature, wind speed, radiation) in a particular micro-environment, as well as animal properties (size, shape, reflectivity and behaviour), and then use a mathematical model to calculate  $T_e$  [26,121,134]. Given spatially explicit data on climate and terrain, one can

use these latter models to estimate  $T_e$  at any spot or time [8,127] or the distribution of  $T_e$  at a site [128]. These approaches are complementary: physical models are convenient for mapping microclimate variation on a fine scale [128,135], whereas mathematical models enable ‘what if’ simulations as well as an understanding of the physical basis of  $T_e$  [8,26,127].

Estimating environmental heat loads on endotherms is complicated because endotherms metabolically generate high internal-heat loads, have insulation and can achieve high rates of evaporative heat loss. To index thermal stresses on endotherms, biophysical ecologists [136] estimate ‘standard operative temperature’ ( $T_{es}$ ). As with  $T_e$ ,  $T_{es}$  can be calculated or approximated using physical models. Heated models are preferred [136,137], but even unheated ones can provide useful predictions of activity and behaviour [138]. Standardized heat-generating objects can be placed in different retreat-sites, such as tree hollows, to assess the interaction between insulation of the retreat-site and heat production by the organism [139]. Indeed, metabolic heat production can be sufficient to cause significant heat stress to endotherms inside well-insulated retreats [139,140].

#### **(e) Behavioural temperature regulation as a buffer**

In most terrestrial habitats, a range of potential  $T_e$  (or  $T_{es}$ ) exists at any time of day, and that range will shift over the day and seasons [121]. As has been known for decades [141,142], mobile animals can behaviourally exploit that thermal heterogeneity and thus control  $T_b$  within relatively narrow ranges. For example, they might move to a sunny spot (relatively high  $T_e$ ) early in the morning or late in the afternoon, bask and thus use solar radiation to drive  $T_b$  higher. Then they might move to shade at midday, avoiding solar radiation and taking advantage of convective cooling to keep their  $T_b$  from rising excessively. Regulation of time of activity, posture and retreat-site selection are classic methods of behavioural thermoregulation [142–145].

Behavioural thermoregulation can thus buffer the impact of climate warming [8,146,147]. However, behavioural thermoregulation is feasible only if the thermal environment is heterogeneous [8], as evaluated by the distribution of  $T_e$  [135,148,149]. If all accessible microhabitats have similar  $T_e$ , then microhabitat selection can have little or no impact on  $T_e$  and thus  $T_b$ . Thermal heterogeneity is limited at night and at all times beneath the canopy in heavily forested areas [128,150], except in clearings and in sun flecks. Not surprisingly, nocturnal and forest ectotherms must behaviourally control  $T_b$  primarily by regulating the time of activity (i.e. becoming active only when  $T_e$  are suitable). Thermal heterogeneity can also be limited even in very open habitats at midday, when most of the ground surface is fully exposed to solar radiation [8,135,144].

#### **(f) Complications from diverse life-cycle stages**

Terrestrial ectotherms typically have a sessile egg stage and mobile juvenile and adult stages. Many insects have more complex life cycles: their stages (eggs,

larvae, pupae, adults) can live in dramatically different habitats and can differ in vagility [125,151]. For instance, a butterfly may have a sessile egg phase on one host plant, a motile larval phase on the same plant, a sessile pupal phase in the soil and a flying adult phase. Each life-cycle stage may thus experience different thermal environments (especially if stages are non-overlapping in time [152]) and may even have quite different thermal sensitivities and behavioural options [125,151,153–157]. For such species, predictions of the impact of climate warming thus require consideration of the vulnerability of each life-cycle stage [52,125,158], especially on development [47].

Sessile stages (especially eggs) are incapable of behavioural buffering (but see [159]). Yet the thermal environment of embryos (e.g. eggs) can have a major effect on subsequent survival, development rates, adult size and morphology, physiological capacities, and even gender [22,127,160–163]. Although eggs cannot move, the mother's choice of the oviposition site may provide some buffering ([127,161,164–166], but see [167]). For example, a female can control the thermal conditions her eggs will experience simply by altering the depth of her nest or its shading [127,161,168,169], by changing season of laying [170,171] or by using buffered microhabitats such as termite mounds [172] or transpiring leaves [166]. Even so, females can only potentially choose from among the available temperatures, which may not be suitable [127,161]. Egg retention and viviparity can also enable a female to control the thermal environment of her embryos [173].

### (g) Genetic responses to climate warming

If climate warming increases  $T_b$ , such that performance and fitness is reduced ( $b$  to  $c$  in figure 1b), selection will favour genotypes that perform relatively well at higher temperatures [9,52,56,174–176]. If the selective response can keep pace with the change in  $T_b$ , overall fitness will not be affected dramatically by climate change [52,58,124,176–179]. Furthermore, gene exchange between genetically differentiated populations may enable persistence [10].

Modelling selection and the response to selection on thermal sensitivity is complex [9,52,56,58,67,177,179–181], but we can summarize factors that will be influential. The simple response to selection is characterized in the familiar 'breeder's equation' response = (selection differential)  $\times$  (heritability). Response will be relatively fast in species that have short generation times, pronounced heritable variation in thermal sensitivity, large population size, limited inbreeding and thermally specialized physiologies [58,67,180,181]. Unfortunately, the genetic architecture of ectotherm thermal sensitivity is largely unknown, but recent studies suggest that some lizards [9] and even some *Drosophila* [52] have limited capacity to keep pace with warming. We return to genetic issues below.

## 3. TEMPORAL RESPONSES TO CLIMATE WARMING

We are now in a position to evaluate the temporal pattern of the impact of global warming on an organism. We focus on a case in which an ectotherm initially lives

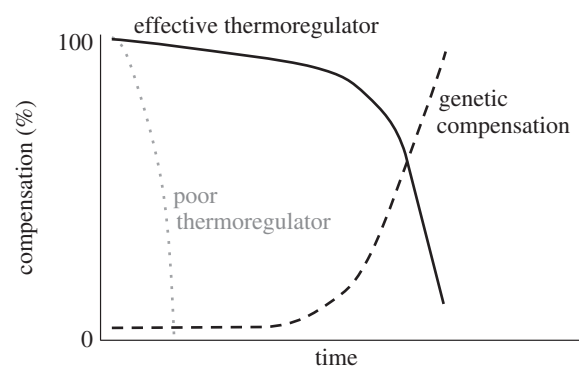


Figure 7. Consequences of differences in ability to compensate behaviourally (or via acclimatization) for climate warming. At the start, assume that mean  $T_c$  equals mean  $T_o$ , so that the thermal environment is ideal. If  $T_c$  increases from warming, a species with strong behavioural capacity to thermoregulate (black line) will not experience a marked shift in  $T_b$  (and thus no associated selection on thermal sensitivity) for some time. But if warming continues, the species will eventually exceed the limit of behavioural (or physiological) compensation and will then begin to rely on genetic compensatory changes (dashed line), or to go extinct. However, if a species has limited thermoregulatory capacity (dotted grey line), it will soon need to rely on genetic compensation to survive (note: the earlier onset of selection for genetic compensation is not depicted).

in an environment where most  $T_c$  are initially at or near  $T_o$  ('B' in figure 1b). Thus, any warming can potentially reduce performance and fitness.

Whether warming does reduce fitness depends in part on the organism's capacity for behavioural buffering and acclimatization, as noted above. An appreciation that behaviour can buffer environmental change traces to Charles Bogert ([182], see also [183]), and is called the 'Bogert Effect' [146]. Consider two extremes. If a species has well-developed capacity for behavioural thermoregulation (or for acclimatization) and if it lives in a thermally heterogeneous environment, then it can achieve  $T_b$  near  $T_o$  for an extended period of warming before reaching the limits of behavioural buffering (figure 7, black line). In other words, it evades the force of selection for some time. However, if warming continues, it will eventually reach the limits of behavioural buffering, and its  $T_b$  will rise significantly above  $T_o$ . Its survival will then depend on its capacity to respond to selection (black dashed line). Alternatively, if a species lives in a thermally homogeneous environment and thus has limited opportunities for behavioural compensation (figure 7, grey dotted line), its  $T_b$  will soon be forced above  $T_o$ . Consequently, it will rapidly experience selection for increased heat tolerance [151]. (Note: the impact of  $T_b$  shifts will also depend on an organism's acclimatization capacity [67] and on the availability of water, which provides a physiological buffer via evaporative cooling.)

We can also consider the temporal pattern of warming-induced changes in  $T_b$  for a species that is initially living in an environment in which  $T_c$  are generally less than  $T_o$  ('A' in figure 1b), as may apply to many high-latitude ectotherms [6,8,180]. As warming proceeds, a thermoregulating animal will generally select the warmest available microenvironments, and consequently its  $T_b$

and thus its fitness may increase as  $T_c$  increase [6,8]. But once  $T_c$  begin to exceed  $T_o$ , the animal will begin to pick the coolest microenvironments; thus behavioural buffering will reduce the rate of fitness decline relative to the rate of change in the thermal environment (figure 6) by the Bogert Effect. In other words, behaviour allows organisms living in cool environments not only to take advantage of the initial stages of warming, but then potentially to use behaviour to evade further warming.

What kinds of terrestrial animals have limited capacities for behavioural buffering? As noted above, these will be species living in thermally homogeneous environments. They are typically (below-canopy) forest species living in the lowland tropics. These ectotherms may be additionally vulnerable because they have limited acclimatization capacities [72], low heat tolerance [68,78,184] and already live in environments that are warm relative to  $T_o$  [6,47,68,123,185,186]. Their vulnerability will only be exacerbated if climate change induces a dieback of tropical forests [187].

The proposal that many tropical ectotherms are vulnerable to warming [6,8,9,47,68,123,186,188] has been challenged recently. For example, Hoffmann [52] and Clusella-Trullas *et al.* [37] have suggested that selection on heat tolerance is dominated by extreme events, which were supposedly ignored in prior studies [6,68] and which can sometimes be accentuated in mid-latitude areas [15,52]. We agree that extreme temperatures will sometimes be important, but demographic persistence may often be governed by warming-induced energetic limitations. Sinervo *et al.* [9] discovered that extinctions of lizard populations were correlated with spring warming, not summer warming. They proposed that spring warming led to a demographic collapse by reducing foraging time and energy gain of females during the critical breeding season, even though spring temperatures are far from extreme. Undoubtedly, both extreme events and demographic collapse are important; and further work should be focused on establishing their relative importance.

In a large comparative analysis, Clusella Trullas *et al.* [37] found that preferred body temperatures of reptiles have stronger correlations with rainfall than with air temperature variables. They suggested that increased tropical rainfall or cloud cover will mitigate the impact of warming on tropical ectotherms [37,39]. We agree but note that current predictions about rainfall have high uncertainty [187].

Third, all authors agree that ectotherms from mid-latitudes—not just ones from the tropics—are also vulnerable. In particular, mid-latitude desert species live in extreme environments [8,135], can have negative thermal safety margins (fig. 2 in [68]), be in negative energy balance [9] and are thus at risk of stress and extinction [8,21]. Indeed, lizard extinctions have already been observed at mid-latitude sites [9].

Predicting geographical patterns of ectotherm responses to climate change is difficult, as the number of involved biological factors—and the environmental uncertainties—is large. Extinctions will occur widely [9]. Even so, the total biotic impact of climate warming may probably be largest in the tropics, because that is where most ectotherms live [6,185].

#### (a) *Asymmetry of biotic interactions*

Our paper has thus far focused on impacts of warming on single species, but warming will also affect biotic interactions among species, greatly complicating predictions of warming impacts [17,44,45,124,189]. Importantly, the impact of climate warming may be decidedly asymmetric on warm- versus cold-adapted species. Consider a tropical locality with both forest-habitat and open-habitat lizards. Forest lizards typically encounter warm (but not hot)  $T_c$ , are usually thermoconformers (except species that use sun flecks) and typically have low  $T_o$  and  $CT_{max}$  relative to open-habitat species [68,184]. Prior to climate warming,  $T_c$  inside lowland forests can be ideal (i.e. near  $T_o$ ) for lowland forest species [48,148], but may be too cool for the open-habitat species, which have higher  $T_o$  [190]. Because thermoregulatory options are limited for forest species (above), climate warming will necessarily increase  $T_c$  and thus  $T_b$ : if so, heat stress is inevitable. However, that same rise in  $T_c$  will make the forest increasingly suitable for the open-habitat species. If warming continues, the open-habitat species will be able to invade the forest, at least at warm times of the year [68]. They may even begin to use the forest as a thermal refuge.

The forest species is thus likely to be in ‘double trouble’: warming will not only induce heat stress, but also induce increased biotic stress [68]. This combination could induce strong selection on thermal sensitivity of the forest species, but might nonetheless overwhelm their adaptive capacities. If so, tropical forest species are at amplified risk from warming.

These suggestions assume that forest structure and other environmental variables will be unaffected by warming, such that the rise in  $T_c$  beneath the canopy is driven only by  $T_a$ . However, climate warming may reduce plant productivity and growth by increasing respiratory costs relative to photosynthetic gains (but see [33,187,191,192]). If this causes canopies to open, solar radiation will penetrate and raise  $T_c$  even further [193]. Moreover, humidity will drop, adding novel water stress to the woes of forest animals, especially those that are moisture-sensitive [179,194]. The increasing threat of forest disturbance or clearing [34] and declines in rainfall and cloud cover [124,195] potentially add another synergistic threat to closed forest species by opening up the canopy, adding the cascading threat of drying and fire [29], reducing thermal buffering and refugia, and facilitating invasion by the open-habitat species.

A similar effect may occur for species arrayed along an altitudinal gradient. Warming may force some species to retreat uphill [115,196–200], which can lead to community disassembly, especially in the tropics [201]. However, shifts may depend on precipitation regimes as well [202]. As warm-adapted species move uphill, cold-adapted (thus high-altitude) species may be exposed to novel competitors as well as reduced range size, potentially increasing their extinction risk [9].

#### 4. CONCLUDING REMARKS

We have outlined some of the issues that are relevant to predictions as to whether climate warming will harm



or benefit organisms. Physiological information is fundamental here [4–6,24,39,124,203,204]: one needs to know whether a species is a thermal specialist or a thermal generalist, is warm versus cold-adapted, has marked acclimation capacities [67] or is sensitive to other physiological variables [37,52]. One also needs to know which stage of the life cycle (e.g. eggs versus adults) is most vulnerable [52,125,202]. Laboratory estimates of an organism's thermal sensitivity are useful in predicting phenotypic effects of warming (figure 1a), but some proxies for thermal sensitivity (e.g.  $CT_{max}$ , field  $T_b$ ) may sometimes be adequate (figure 6b). Information on operative temperatures (level and heterogeneity) is also needed to evaluate whether operative temperatures (at the initiation of warming) are at or below a species' thermal optimum [6] and whether spatial and temporal heterogeneity in operative temperatures will facilitate behavioural buffering [8]. We need more insight into whether selection is driven primarily by extreme events [37,52] or by chronic pressures [9]. Genetic information [67,124,179] will be necessary to anticipate whether species are genetically capable of keeping pace with shifting climates (a 'Red Queen' scenario), or whether they will increasingly lag behind (a 'moon-walk' scenario) and ultimately go extinct. Genetic approaches require estimates of selection differentials in nature and of heritabilities for fitness traits [22,58,67,177,178,181,205]. Unfortunately, those are rarely available [9,51,56,179,181], making current predictive attempts unreliable. We have much to learn and little time to work.

Our review reinforces the recent view [5,6,8,68,185,186,206] that tropical forest ectotherms are at risk from warming and that they may have limited genetic variation and thus not be able to adapt rapidly [52,207,208]. If this expectation is correct, then the ecological impact of climate warming will be devastating, because tropical forests are the centre of diversity of most terrestrial ectotherm taxa.

We do not deny that many organisms elsewhere also appear in trouble from warming [8,9,21,37,52,68,124]. In fact, many lizard populations outside the tropics may have already gone locally extinct from climate warming; and many more are projected to go extinct [9]. Behavioural buffering can help [8,146], but may only slow or delay the march towards extinction.

This paper emerged from a workshop ('Predicting climate change impacts on biodiversity: the way forward') held in Daintree, Queensland, Australia (17–21 November 2008). This workshop was organized by the Centre for Tropical Biodiversity and Climate Change at James Cook University and funded by the MTSRF. We thank other participants for ideas that emerged during discussions, B. Sinervo and S. Clusella-Trullas for comments, and C. Franklin and F. Seebacher for the opportunity to participate in this volume. R.B.H. was supported by NSF grant IBN-0416843. M.R.K. was supported by an ARC Australian Research Fellowship DP110101776.

## REFERENCES

- 1 Parmesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
- 2 IPCC. 2007 *Climate change 2007: the physical science basis*. Cambridge, UK: Cambridge University Press.
- 3 Bernardo, J., Ossola, R. J., Spotila, J. & Crandall, K. A. 2007 Interspecies physiological variation as a tool for cross-species assessments of global warming-induced endangerment: validation of an intrinsic determinant of macroecological and phylogeographic structure. *Biol. Lett.* **3**, 695–699. (doi:10.1098/rsbl.2007.0259)
- 4 Buckley, L. B. 2008 Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *Am. Nat.* **171**, E1–E19. (doi:10.1086/523949)
- 5 Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A. & Langham, G. 2008 Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* **6**, 2621–2626. (doi:10.1371/journal.pbio.0060325)
- 6 Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. & Martin, P. R. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)
- 7 Wake, D. B. & Vredenburg, V. T. 2008 Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc. Natl Acad. Sci. USA* **105**, 11 466–11 473. (doi:10.1073/pnas.0801921105)
- 8 Kearney, M., Shine, R. & Porter, W. P. 2009 The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proc. Natl Acad. Sci. USA* **106**, 3835–3840. (doi:10.1073/pnas.0808913106)
- 9 Sinervo, B. et al. 2010 Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899. (doi:10.1126/science.1184695)
- 10 Moritz, C., Langham, G., Kearney, M., Krockenberger, A., VanDerWal, J. & Williams, S. 2012 Integrating phylogeography and physiology reveals divergence of thermal traits between central and peripheral lineages of tropical rainforest lizards. *Phil. Trans. R. Soc. B* **367**, 1680–1687. (doi:10.1098/rstb.2012.0018)
- 11 Lee, T. M. & Jetz, W. 2008 Future battlegrounds for conservation under global change. *Proc. R. Soc. B* **275**, 1261–1270. (doi:10.1098/rspb.2007.1732)
- 12 Pörtner, H. O. & Kunst, R. 2007 Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95–97. (doi:10.1126/science.1135471)
- 13 Pörtner, H. O. & Farrell, A. P. 2008 Physiology and climate change. *Science* **322**, 690–692. (doi:10.1126/science.1163156)
- 14 Evans, T. G. & Hofmann, G. E. 2012 Defining the limits of physiological plasticity: how gene expression can assess and predict the consequences of ocean change. *Phil. Trans. R. Soc. B* **367**, 1733–1745. (doi:10.1098/rstb.2012.0019)
- 15 Helmuth, B., Harley, C. D. G., Halpin, P. M., O'Donnell, M., Hofmann, G. E. & Blanchete, C. A. 2002 Climate change and latitudinal patterns of intertidal thermal stress. *Science* **298**, 1015–1017. (doi:10.1126/science.1076814)
- 16 Huey, R. B., Carlson, M., Crozier, L., Frazier, M., Hamilton, H., Harley, H., Honag, A. & Kingsolver, J. G. 2002 Plants versus animals: do they deal with stress in different ways? *Integr. Comp. Biol.* **42**, 415–423. (doi:10.1093/icb/42.3.415)
- 17 Harley, C. D. G. 2011 Climate change, keystone predation, and biodiversity loss. *Science (Wash.)* **334**, 1124–1127. (doi:10.1126/science.1210199)
- 18 Tracy, C. R., Christian, K. A. & Tracy, C. R. 2010 Not just small, wet, and cold: interacting effects of body size, skin resistance, and microclimate on thermoregulation

- and arboreality in frogs. *Ecology* **91**, 1477–1484. (doi:10.1890/09-0839.1)
- 19 Blaustein, A. R., Gervasi, S. S., Johnson, P. T. J., Hoverman, J. T., Belden, L. K., Bradley, P. W. & Xie, G. Y. 2012 Ecophysiology meets conservation: understanding the role of disease in amphibian population declines. *Phil. Trans. R. Soc. B* **367**, 1688–1707. (doi:10.1098/rstb.2012.0011)
  - 20 Huey, R. B. 1991 Physiological consequences of habitat selection. *Am. Nat.* **137**, S91–S115. (doi:10.1086/285141)
  - 21 Dunham, A. E. 1993 Population responses to environmental change: physiologically structured models, operative environments, and population dynamics. In *Biotic interactions and global change* (eds P. M. Kareiva, J. G. Kingsolver & R. B. Huey), pp. 95–119. Sunderland, MA: Sinauer Associates.
  - 22 Angilletta Jr, M. J. 2009 *Thermal adaptation: a theoretical and empirical synthesis*. Oxford, UK: Oxford University Press.
  - 23 Sinervo, B. & Huey, R. B. 1990 Allometric engineering: an experimental test of the causes of interpopulation differences in performance. *Science* **248**, 1106–1109. (doi:10.1126/science.248.4959.1106)
  - 24 Seebacher, F. & Franklin, C. E. 2012 Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. *Phil. Trans. R. Soc. B* **367**, 1607–1614. (doi:10.1098/rstb.2012.0036)
  - 25 Porter, W. P., Budaraju, S., Stewart, W. E. & Ramankutty, N. 2000 Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. *Am. Zool.* **40**, 1175–1176. (doi:10.1093/icb/40.4.597)
  - 26 Porter, W. P. & Kearney, M. 2009 Size, shape and the thermal niche of endotherms. *Proc. Natl Acad. Sci. USA* **106**, 19 666–19 672. (doi:10.1073/pnas.0907321106)
  - 27 Kearney, M. R., Wintle, B. A. & Porter, W. P. 2010 Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conserv. Lett.* **3**, 203–213. (doi:10.1111/j.1755-263X.2010.00097.x)
  - 28 Angilletta, M. J., Cooper, B. S., Schuler, M. S. & Boyles, J. G. 2010 The evolution of thermal physiology in endotherms. *Front Biosci.* **E2**, 861–881. (doi:10.2741/E148)
  - 29 Laurance, W. F. & Williamson, G. B. 2001 Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conserv. Biol.* **15**, 1529–1535. (doi:10.1046/j.1523-1739.2001.01093.x)
  - 30 Travis, J. M. J. 2003 Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. R. Soc. Lond. B* **270**, 467–473. (doi:10.1098/rspb.2002.2246)
  - 31 Wright, S. J. 2005 Tropical forests in a changing environment. *Trends Ecol. Evol.* **20**, 553–560. (doi:10.1016/j.tree.2005.07.009)
  - 32 Pounds, J. A. *et al.* 2006 Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167. (doi:10.1038/nature04246)
  - 33 Lewis, S. L. 2006 Tropical forests and the changing earth system. *Phil. Trans. R. Soc. B* **361**, 195–210. (doi:10.1098/rstb.2005.1711)
  - 34 Malhi, Y., Roberts, J. T., Betts, R. A., Killeen, T. J. & Nobre, C. A. 2007 Climate change, deforestation, and the fate of the Amazon. *Science* **319**, 169–172. (doi:10.1126/science.1146961)
  - 35 Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. A. 2008 Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460. (doi:10.1016/j.tree.2008.03.011)
  - 36 Bonebrake, T. C. & Mastrandrea, M. D. 2010 Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. *Proc. Natl Acad. Sci. USA* **107**, 12 581–12 586. (doi:10.1073/pnas.0911841107)
  - 37 Clusella-Trullas, S., Blackburn, T. M. & Chown, S. L. 2011 Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *Am. Nat.* **177**, 738–751. (doi:10.1086/660021)
  - 38 Krockenberger, A. K., Edwards, W. & Kanowski, J. 2012 The limit to distribution of a rainforest marsupial folivore is consistent with thermal intolerance hypothesis. *Oecologia* **168**, 889–899.
  - 39 Chown, S. L. 2012 Trait-based approaches to conservation physiology: forecasting environmental change risks from the bottom up. *Phil. Trans. R. Soc. B* **367**, 1615–1627. (doi:10.1098/rstb.2011.0422)
  - 40 Ives, A. R. & Gilchrist, G. W. 1993 Climate change and ecological interactions. In *Biotic interactions and global change* (eds P. Kareiva, J. G. Kingsolver & R. B. Huey). Sunderland, MA: Sinauer Associates.
  - 41 Buckley, L. B. & Roughgarden, J. 2006 Climate, competition, and the coexistence of island lizards. *Funct. Ecol.* **20**, 315–322. (doi:10.1111/j.1365-2435.2006.01095.x)
  - 42 Lister, B. C. & Garcia, A. 1992 Seasonality, predation, and the behaviour of a tropical mainland anole. *J. Anim. Ecol.* **61**, 717–733. (doi:10.2307/5626)
  - 43 Pincebourde, S. & Casas, J. 2006 Multitrophic biophysical budgets: thermal ecology of an intimate herbivore insect–plant interaction. *Ecol. Monogr.* **76**, 175–194. (doi:10.1890/0012-9615(2006)076[0175:MBBTEO]2.0.CO;2)
  - 44 Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W. & Holt, R. D. 2010 A framework for community interactions under climate change. *Trends Ecol. Evol.* **25**, 325–331. (doi:10.1016/j.tree.2010.03.002)
  - 45 Adamo, S. A. & Lovett, M. M. E. 2011 Some like it hot: the effects of climate change on reproduction, immune function and disease resistance in the cricket *Gryllus texensis*. *J. Exp. Biol.* **214**, 1997–2004. (doi:10.1242/jeb.056531)
  - 46 Huey, R. B. & Stevenson, R. D. 1979 Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* **19**, 357–366. (doi:10.1093/icb/19.1.357)
  - 47 Amarasekare, P. & Savage, V. 2012 A framework for elucidating the temperature dependence of fitness. *Am. Nat.* **179**, 179–191. (doi:10.1086/663677)
  - 48 Huey, R. B. 1982 Temperature, physiology, and the ecology of reptiles. In *Biology of the Reptilia, physiology (C)*, vol. 12 (eds C. Gans & F. H. Pough), pp. 25–91. London, UK: Academic Press.
  - 49 Gilchrist, G. W. 1995 Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. *Am. Nat.* **146**, 252–270. (doi:10.1086/285797)
  - 50 Martin, T. L. & Huey, R. B. 2008 Why suboptimal is optimal: Jensen's inequality and ectotherm thermal preferences. *Am. Nat.* **171**, E102–E118. (doi:10.1086/527502)
  - 51 Huey, R. B. & Berrigan, D. 2001 Temperature, demography, and ectotherm fitness. *Am. Nat.* **158**, 204–210. (doi:10.1086/321314)
  - 52 Hoffmann, A. A. 2010 Physiological climatic limits in *Drosophila*: patterns and implications. *J. Exp. Biol.* **213**, 870–880. (doi:10.1242/jeb.037630)
  - 53 Schulte, P. M., Healy, T. M. & Fanguie, N. A. 2011 Thermal performance curves, phenotypic plasticity,

- and the time scales of temperature exposure. *Integr. Comp. Biol.* **51**, 691–702. (doi:10.1093/icb/icr097)
- 54 Huey, R. B. & Slatkin, M. 1976 Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* **51**, 363–384. (doi:10.1086/409470)
- 55 Tracy, C. R. & Christian, K. A. 1983 Ecological relations among space, time and thermal niche axes. *Ecology* **67**, 609–615. (doi:10.2307/1937684)
- 56 Kingsolver, J. G., Ragland, G. J. & Shlichta, J. G. 2004 Quantitative genetics of continuous reaction norms: thermal sensitivity of caterpillar growth rates. *Evolution* **58**, 1521–1529.
- 57 Janzen, D. H. 1967 Why mountain passes are higher in the tropics. *Am. Nat.* **101**, 233–249. (doi:10.1086/282487)
- 58 Huey, R. B. & Kingsolver, J. G. 1993 Evolution of resistance to high temperature in ectotherms. *Am. Nat.* **142**, S21–S46. (doi:10.1086/285521)
- 59 Scholander, P. F. 1955 Evolution of climatic adaptation in homeotherms. *Evolution* **9**, 15–26. (doi:10.2307/2405354)
- 60 Porter, W. P. & Gates, D. M. 1969 Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* **39**, 227–244. (doi:10.2307/1948545)
- 61 Scholander, P. F., Hock, R., Walters, V., Johnson, F. & Irving, L. 1950 Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.* **99**, 237–258. (doi:10.2307/1538741)
- 62 Somero, G. N. 2010 The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers’. *J. Exp. Biol.* **213**, 912–920. (doi:10.1242/jeb.037473)
- 63 Glanville, E. J. & Seebacher, F. 2006 Compensation for environmental change by complementary shifts of thermal sensitivity and thermoregulatory behaviour in an ectotherm. *J. Exp. Biol.* **209**, 4869–4877. (doi:10.1242/jeb.02585)
- 64 Leroi, A. M., Bennett, A. F. & Lenski, R. E. 1994 Temperature acclimation and competitive fitness: an experimental test of the beneficial acclimation assumption. *Proc. Natl Acad. Sci. USA* **91**, 1917–1921. (doi:10.1073/pnas.91.5.1917)
- 65 Huey, R. B., Berrigan, D., Gilchrist, G. W. & Herron, J. C. 1999 Testing the adaptive significance of acclimation: a strong inference approach. *Am. Zool.* **39**, 135–148. (doi:10.1093/icb/39.2.323)
- 66 Stillman, J. H. 2003 Acclimation capacity underlies susceptibility to climate change. *Science* **301**, 65. (doi:10.1126/science.1083073)
- 67 Chevin, L.-M., Lande, R. & Mace, G. M. 2010 Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* **8**, e1000357. (doi:10.1371/journal.pbio.1000357)
- 68 Huey, R. B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E. & Álvarez, H. J. 2009 Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B* **276**, 1939–1948. (doi:10.1098/rspb.2008.1957)
- 69 Beaumont, L. J., Pitman, A., Perkins, S., Zimmermann, N. E., Yoccoz, N. G. & Thuiller, W. 2011 Impacts of climate change on the world’s most exceptional ecoregions. *Proc. Natl Acad. Sci. USA* **108**, 2306–2311. (doi:10.1073/pnas.1007217108)
- 70 Wake, D. B. & Lynch, J. F. 1976 The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. *Natur. Hist. Mus. Los Angeles Co. Sci. Bull.* **25**, 1–65.
- 71 Huey, R. B. 1978 Latitudinal pattern of between-altitude faunal similarity: mountains might be ‘higher’ in the tropics. *Am. Nat.* **112**, 225–229. (doi:10.1086/283262)
- 72 Ghalambor, C. K., Huey, R. B., Martin, P. R., Tewksbury, J. J. & Wang, G. 2006 Are mountain passes higher in the tropics? Janzen’s hypothesis revisited. *Integr. Comp. Biol.* **46**, 5–17. (doi:10.1093/icb/icj003)
- 73 McCain, C. M. 2009 Vertebrate range sizes indicate that mountains may be ‘higher’ in the tropics. *Ecol. Lett.* **12**, 550–560. (doi:10.1111/j.1461-0248.2009.01308.x)
- 74 Sunday, J. M., Bates, A. E. & Dulvy, N. K. 2010 Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B* **278**, 1823–1830. (doi:10.1098/rspb.2010.1295)
- 75 Mitchell, K. A., Sgrò, C. M. & Hoffmann, A. A. 2011 Phenotypic plasticity in upper thermal limits is weakly related to *Drosophila* species distributions. *Funct. Ecol.* **25**, 661–670. (doi:10.1111/j.1365-2435.2010.01821.x)
- 76 Snyder, G. K. & Weathers, W. W. 1975 Temperature adaptations in amphibians. *Am. Nat.* **109**, 93–101. (doi:10.1086/282976)
- 77 Addo-Bediako, A., Chown, S. L. & Gaston, K. J. 2000 Thermal tolerance, climatic variability and latitude. *Proc. R. Soc. Lond. B* **267**, 739–745. (doi:10.1098/rspb.2000.1065)
- 78 Kimura, M. T. 2004 Cold and heat tolerance of *Drosophilid* flies with reference to their latitudinal distributions. *Oecologia* **140**, 442–449. (doi:10.1007/s00442-004-1605-4)
- 79 van Berkum, F. H. 1988 Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am. Nat.* **132**, 327–343. (doi:10.1086/284856)
- 80 Bradshaw, W. E. & Holzapfel, C. M. 2006 Evolutionary response to rapid climate change. *Science* **312**, 1477–1478. (doi:10.1126/science.1127000)
- 81 Vaughan, T. A., Ryan, J. M. & Czaplewski, N. J. 2011 *Mammalogy*. Sudbury, MA: Jones and Bartlett Publishers.
- 82 Scholander, P. F., Walters, V., Hock, R. & Irving, L. 1950 Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.* **99**, 225–236. (doi:10.2307/1538740)
- 83 Geiser, F. & Turbill, C. 2009 Hibernation and daily torpor minimize mammalian extinctions. *Naturewissenschaften* **96**, 1235–1240. (doi:10.1007/s00114-009-0583-0)
- 84 Geiser, F. & Stawski, C. 2011 Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. *Integr. Comp. Biol.* **51**, 337–348. (doi:10.1093/icb/icr042)
- 85 Overgaard, J., Kristensen, T. N., Mitchell, K. A. & Hoffmann, A. A. 2011 Thermal tolerance in widespread and tropical *Drosophila* species: does phenotypic plasticity increase with latitude? *Am. Nat.* **178**, S80–S96. (doi:10.1086/661780)
- 86 Campbell, H. A., Dwyer, R. G., Gordos, M. & Franklin, C. E. 2010 Diving through the thermal window: implications for a warming world. *Proc. R. Soc. B* **277**, 3837–3844. (doi:10.1098/rspb.2010.0902)
- 87 Donelson, J. M., Munday, P. L., McCormick, M. I. & Pitcher, C. R. 2012 Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nat. Clim. Change* **2**, 30–32. (doi:10.1038/nclimate1323)
- 88 Hart, J. S. 1957 Climatic and temperature induces changes in the energetics of homeotherms. *Rev. Can. Biol.* **16**, 133–174.
- 89 Dawson, W. R. & Carey, C. 1976 Seasonal acclimatization to temperature in Cardueline finches I. Insulative and metabolic adjustments. *J. Comp. Physiol.* **112**, 317–333.
- 90 Stevenson, R. D., Peterson, C. R. & Tsuji, J. S. 1985 The thermal dependence of locomotion, tongue

- flicking, digestion and oxygen consumption in the wandering garter snake. *Physiol. Zool.* **58**, 46–57.
- 91 Angilletta Jr, M. J., Hill, T. & Robson, M. A. 2002 Is physiological performance optimized by thermoregulatory behavior? A case study of the eastern fence lizard, *Sceloporus undulatus*. *J. Therm. Biol.* **27**, 199–204. (doi:10.1016/S0306-4565(01)00084-5)
- 92 Arnold, S. J. 1983 Morphology, performance and fitness. *Am. Zool.* **23**, 347–361.
- 93 Bennett, A. F. & Huey, R. B. 1990 Studying the evolution of physiological performance. In *Oxford surveys in evolutionary biology*, vol 7 (eds D. J. Futuyma & J. Antonovics), pp. 251–284. Oxford, UK: Oxford University Press.
- 94 Jayne, B. C. & Bennett, A. F. 1990 Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* **44**, 1204–1229. (doi:10.2307/2409283)
- 95 Calsbeek, R. & Irschick, D. J. 2007 The quick and the dead: correlational selection on morphology, performance, and habitat use in island lizards. *Evolution* **61**, 2493–2503. (doi:10.1111/j.1558-5646.2007.00206.x)
- 96 Irschick, D. J. & Garland Jr, T. 2001 Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu. Rev. Ecol. Syst.* **32**, 367–396. (doi:10.1146/annurev.ecolsys.32.081501.114048)
- 97 Kingsolver, J. G., Massie, K. R., Shlichta, J. G., Smith, M. H., Ragland, G. J. & Gomulkiewicz, R. 2007 Relating environmental variation to selection on reaction norms: an experimental test. *Am. Nat.* **169**, 163–174. (doi:10.1086/510631)
- 98 Carey, J. R. 1993 *Applied demography for biologists*. Oxford, UK: Oxford University Press.
- 99 Bennett, A. F., Lenski, R. E. & Mittler, J. E. 1992 Evolutionary adaptation to temperature. I. Fitness responses of *Escherichia coli* to changes in its thermal environment. *Evolution* **46**, 16–30. (doi:10.2307/2409801)
- 100 Frazier, M. R., Huey, R. B. & Berrigan, D. 2006 Thermodynamics constrains the evolution of insect population growth rates: ‘warmer is better’. *Am. Nat.* **168**, 512–520. (doi:10.1086/506977)
- 101 Knies, J. L., Kingsolver, J. G. & Burch, C. L. 2009 Hotter is higher and broader: adaptation to temperature in a population of bacteriophages. *Am. Nat.* **173**, 419–430. (doi:10.1086/597224)
- 102 Anderson, J. L., Albergotti, L., Ellebaracht, B., Huey, R. B. & Phillips, P. C. 2011 Does thermoregulatory behavior maximize reproductive fitness of natural isolates of *Caenorhabditis elegans*? *BMC Evol. Biol.* **22**, 257. (doi:10.1186/1471-2148-11-157)
- 103 Terblanche, J. S., Deere, J. A., Clusella Trullas, S., Janion, C. & Chown, S. L. 2007 Critical thermal limits depend on methodological context. *Proc. R. Soc. B* **274**, 2935–2942. (doi:10.1098/rspb.2007.0985)
- 104 Mitchell, K. A. & Hoffmann, A. A. 2010 Thermal ramping rate influences evolutionary potential and species differences for upper thermal limits in *Drosophila*. *Funct. Ecol.* **24**, 694–700. (doi:10.1111/j.1365-2435.2009.01666.x)
- 105 Rezende, E. L., Tejedo, M. & Santos, M. 2011 Estimating the adaptive potential of critical thermal limits: methodological problems and evolutionary implications. *Funct. Ecol.* **25**, 111–121. (doi:10.1111/j.1365-2435.2010.01778.x)
- 106 Berrigan, D. 2000 Correlations between measures of thermal stress resistance within and between species. *Oikos* **89**, 301–304. (doi:10.1034/j.1600-0706.2000.890211.x)
- 107 Folk, D. G., Hoekstra, L. A. & Gilchrist, G. W. 2007 Critical thermal maxima in knockdown-selected *Drosophila*: are thermal endpoints correlated? *J. Exp. Biol.* **219**, 2649–2656. (doi:10.1242/jeb.003350)
- 108 Chown, S. L., Jumbam, K. R., Sørensen, J. G. & Terblanche, J. S. 2009 Phenotypic variance, plasticity and heritability estimates of critical thermal limits depend on methodological context. *Funct. Ecol.* **23**, 133–140. (doi:10.1111/j.1365-2435.2008.01481.x)
- 109 Terblanche, J. S., Hoffmann, A. A., Mitchell, K. A., Rako, L., le Roux, P. C. & Chown, S. L. 2011 Ecologically relevant measures of tolerance to potentially lethal temperatures. *J. Exp. Biol.* **214**, 3613–3725. (doi:10.1242/jeb.061283)
- 110 Chown, S. L., Addo-Bediako, A. & Gaston, K. J. 2003 Physiological diversity: listening to the large-scale signal. *Funct. Ecol.* **17**, 562–572. (doi:10.1046/j.1365-2435.2003.07431.x)
- 111 Huey, R. B. 1987 Phylogeny, history, and the comparative method. In *New directions in ecological physiology* (eds M. E. Feder, A. F. Bennett, W. W. Burggren & R. B. Huey), pp. 76–98. Cambridge, UK: Cambridge University Press.
- 112 Chown, S. L. & Terblanche, J. S. 2007 Physiological diversity in insects: ecological and evolutionary contexts. *Adv. Insect Physiol.* **33**, 50–152. (doi:10.1016/S0065-2806(06)33002-0)
- 113 Pörtner, H. O. 2001 Climate change and temperature dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* **88**, 137–146. (doi:10.1007/s001140100216)
- 114 Lighton, J. R. B. & Turner, R. J. 2004 Thermolimit respirometry: an objective assessment of critical thermal maxima in two sympatric desert harvester ants, *Pogonomyrmex rugosus* and *P. californicus*. *J. Exp. Biol.* **207**, 1903–1913. (doi:10.1242/jeb.00970)
- 115 Bernardo, J. & Spotila, J. R. 2006 Physiological constraints on organismal response to global warming: mechanistic insights from clinally varying populations and implications for assessing endangerment. *Biol. Lett.* **2**, 135–139. (doi:10.1098/rsbl.2005.0417)
- 116 Welbergen, J. A., Klose, S. M., Marcus, N. & Eby, P. 2008 Climate change and the effects of temperature extremes on Australian flying-foxes. *Proc. R. Soc. B* **275**, 419–425. (doi:10.1098/rspb.2007.1385)
- 117 McKecknie, A. E. & Wolf, B. O. 2010 Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biol. Lett.* **6**, 253–256. (doi:10.1098/rsbl.2009.0702)
- 118 Meehl, G. A. & Tebaldi, C. 2004 More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* **305**, 994–997. (doi:10.1126/science.1098704)
- 119 Bennett, A. F., Huey, R. B., John-Alder, H. & Nagy, K. A. 1984 The parasol tail and thermoregulatory behavior of the Cape Ground Squirrel *Xerus inauris*. *Physiol. Zool.* **57**, 57–62.
- 120 Chappell, M. A. & Bartholomew, G. A. 1981 Activity and thermoregulation of the antelope ground squirrel *Ammospermophilus leucurus* in winter and summer. *Physiol. Zool.* **54**, 215–223.
- 121 Porter, W. P., Mitchell, J. W., Beckman, W. A. & DeWitt, C. B. 1973 Behavioral implications of mechanistic ecology. Thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia* **13**, 1–54. (doi:10.1007/BF00379617)
- 122 Savage, V. M. 2004 Improved approximations to scaling relationships for species, populations, and ecosystems across latitudinal and elevational gradients. *J. Theor. Biol.* **227**, 525–534. (doi:10.1016/j.jtbi.2003.11.030)
- 123 Dillon, M. E., Wang, G. & Huey, R. B. 2010 Global metabolic impacts of recent climate warming. *Nature* **467**, 704–706. (doi:10.1038/nature09407)

- 124 Chown, S., Hoffmann, A. A., Kristensen, T. N., Angilletta Jr, M. J., Stenseth, N. C. & Pertoldi, C. 2010 Adapting to climate change: a perspective from evolutionary physiology. *Clim. Res.* **43**, 3–15. (doi:10.3354/cr00879)
- 125 Kingsolver, J. G., Woods, H. A., Buckley, L. B., Potter, K. A., MacLean, H. J. & Higgins, J. K. 2011 Complex life cycles and the responses of insects to climate change. *Integr. Comp. Biol.* **51**, 719–732. (doi:10.1093/icb/icr015)
- 126 Bakken, G. S. 1992 Measurement and application of operative and standard operative temperatures in ecology. *Am. Zool.* **32**, 194–216. (doi:10.1093/icb/32.2.194)
- 127 Mitchell, N. J., Kearney, M. R., Nelson, N. J. & Porter, W. P. 2009 Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara? *Proc. R. Soc. B* **275**, 2185–2193. (doi:10.1098/rspb.2008.0438)
- 128 Hertz, P. E. 1992 Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology* **73**, 1405–1417. (doi:10.2307/1940686)
- 129 Dzialowski, E. M. 2005 Use of operative temperature and standard operative temperature models in thermal biology. *J. Therm. Biol.* **30**, 317–334. (doi:10.1016/j.jtherbio.2005.01.005)
- 130 O'Connor, M. P. 2000 Extracting operative temperatures from temperatures of physical models with thermal inertia. *J. Therm. Biol.* **25**, 329–343. (doi:10.1016/S0306-4565(99)00102-3)
- 131 Seebacher, F., Elsey, R. M. & Trosclair, P. L. I. 2003 Body temperature null distributions in reptiles with nonzero heat capacity: seasonal thermoregulation in the American Alligator (*Alligator mississippiensis*). *Physiol. Biochem. Zool.* **76**, 348–359. (doi:10.1086/375426)
- 132 Christian, K. A., Tracy, C. R. & Tracy, C. R. 2006 Evaluating thermoregulation in reptiles: an appropriate null model. *Am. Nat.* **168**, 421–430. (doi:10.1086/506528)
- 133 Tracy, C. R., Betts, G., Tracy, C. R. & Christian, K. A. 2007 Plaster models to measure operative temperature and evaporative water loss of amphibians. *J. Herpetol.* **41**, 597–604. (doi:10.1670/07-006.1)
- 134 Porter, W. P., Munger, J. C., Stewart, W. E., Budaraju, S. & Jaeger, J. 1994 Endotherm energetics: from a scalable individual-based model to ecological applications. *Aust. J. Zool.* **42**, 125–162. (doi:10.1071/ZO9940125)
- 135 Grant, B. W. & Dunham, A. E. 1988 Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* **69**, 167–176. (doi:10.2307/1943171)
- 136 Bakken, G. S., Erksine, D. J. & Santee, W. R. 1983 Construction and operation of heated taxidermic mounts used to measure standard operative temperature. *Ecology* **64**, 1658–1662. (doi:10.2307/1937520)
- 137 Chappell, M. A. 1980 Insulation, radiation, and convection in small arctic mammals. *J. Mammal.* **61**, 268–277. (doi:10.2307/1380048)
- 138 Bennett, A. F., Huey, R. B., John-Alder, H. B. & Nagy, K. 1984 The parasol tail and thermoregulatory behavior of the Cape Ground Squirrel (*Xerus inauris*). *Physiol. Zool.* **57**, 57–62.
- 139 Kearney, M. R., Ferguson, E., Fumei, S., Gallacher, A., Mitchell, P., Woodford, R. & Handasyde, K. 2011 A cost-effective method of assessing thermal habitat quality for endotherms. *Austral. Ecol.* **36**, 297–302. (doi:10.1111/j.1442-9993.2010.02150.x)
- 140 Havera, S. P. 1979 Temperature variation in a fox squirrel nest box. *J. Wildl. Manage.* **43**, 251–253. (doi:10.2307/3800666)
- 141 Cowles, R. B. & Bogert, C. M. 1944 A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* **83**, 261–296.
- 142 Stevenson, R. D. 1985 The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.* **126**, 362–386. (doi:10.1086/284423)
- 143 Heath, J. E. 1965 Temperature regulation and diurnal activity in horned lizards. *Univ. Calif. Publ. Zool.* **64**, 97–136.
- 144 Huey, R. B., Pianka, E. R. & Hoffmann, J. 1977 Seasonal variation in thermoregulatory behavior and body temperatures of diurnal Kalahari lizards. *Ecology* **58**, 1066–1075. (doi:10.2307/1936926)
- 145 Huey, R. B., Peterson, C. R., Arnold, S. J. & Porter, W. P. 1989 Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* **70**, 931–944. (doi:10.2307/1941360)
- 146 Huey, R. B., Hertz, P. E. & Sinervo, B. 2003 Behavioral drive versus behavioral inertia: a null model approach. *Am. Nat.* **161**, 357–366. (doi:10.1086/346135)
- 147 Bartholomew, G. A. 2005 Integrative biology: an organismic biologist's point of view. *Integr. Comp. Biol.* **45**, 330–332. (doi:10.1093/icb/45.2.330)
- 148 Hertz, P. E., Huey, R. B. & Stevenson, R. D. 1993 Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* **142**, 796–818. (doi:10.1086/285573)
- 149 Clusella-Trullas, S. & Chown, S. L. 2011 Comment on 'Erosion of lizard diversity by climate change and altered thermal niches'. *Science (Wash.)* **332**, 537. (doi:10.1126/science.1195193)
- 150 Kearney, M. & Porter, W. P. 2004 Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* **85**, 3119–3131. (doi:10.1890/03-0820)
- 151 Marais, E. & Chown, S. L. 2008 Beneficial acclimation and the Bogert effect. *Ecol. Lett.* **11**, 1027–1036. (doi:10.1111/j.1461-0248.2008.01213.x)
- 152 Kingsolver, J. G. & Huey, R. B. 1998 Evolutionary analyses of morphological and physiological plasticity in thermally variable environments. *Am. Zool.* **38**, 323–336. (doi:10.1193/icb/38.3.545)
- 153 Davison, T. F. 1969 Changes in temperature tolerance during life cycle of *Calliphora erythrocephala*. *J. Insect. Physiol.* **15**, 977–988. (doi:10.1016/0022-1910(69)90138-3)
- 154 Hoffmann, A. A., Sørensen, J. G. & Loeschcke, V. 2003 Adaptation of *Drosophila* to temperature extremes: bringing together quantitative and molecular approaches. *J. Therm. Biol.* **26**, 175–216. (doi:10.1016/S0306-4565(02)00057-8)
- 155 Pappas, C., Hyde, D., Bowler, K., Loeschcke, V. & Sørensen, J. G. 2007 Post-eclosion decline in 'knock-down' thermal resistance and reduced effect of heat hardening in *Drosophila melanogaster*. *Comp. Biochem. Physiol.—Part A: Mol. Integr. Physiol.* **146**, 355–359. (doi:10.1016/j.cbpa.2006.11.010)
- 156 Kearney, M. R., Briscoe, N. J., Karoly, D., Porter, W. P., Norgate, M. & Sunnucks, P. 2010 Early emergence in a butterfly causally linked to anthropogenic warming. *Biol. Lett.* **6**, 674–677. (doi:10.1098/rsbl.2010.0053)
- 157 Bowler, K. & Terblanche, J. S. 2008 Insect thermal tolerance: what is the role of ontogeny, ageing and senescence. *Biol. Rev. Camb. Phil. Soc.* **83**, 339–355. (doi:10.1111/j.1469-185X.2008.00046.x)
- 158 Coyne, J. A., Bundgaard, J. & Prout, T. 1983 Geographic variation of tolerance to environmental stress in *Drosophila pseudoobscura*. *Am. Nat.* **122**, 474–488. (doi:10.1086/284150)
- 159 Du, W.-G., Zhao, B., Chen, Y. & Shine, R. 2011 Behavioral thermoregulation by turtle embryos. *Proc. Natl*

- Acad. Sci. USA* **108**, 9413–9515. (doi:10.1073/pnas.1102965108)
- 160 David, J. & Clavel, M.-F. 1969 Influence de la température sur le nombre, le pourcentage d'éclosion et la taille des oeufs fondus par *Drosophila melanogaster*. *Ann. Soc. Ent. Fr.* **5**, 161–177.
- 161 Muth, A. 1980 Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: temperature and water relations. *Ecology* **61**, 1335–1343. (doi:10.2307/1939042)
- 162 Porter, W. P. & Tracy, C. R. 1983 Biophysical analyses of energetics, time-space utilization, and distributional limits. In *Lizard ecology: studies of a model organism* (eds R. B. Huey, E. R. Pianka & T. W. Schoener), pp. 55–83. Cambridge, MA: Harvard University Press.
- 163 Kingsolver, J. G. 1996 Experimental manipulation of wing pigment pattern and survival in western white butterflies. *Am. Nat.* **147**, 296–306. (doi:10.1086/285852)
- 164 Kingsolver, J. G. 1979 Thermal and hydric aspects of environmental heterogeneity in the pitcher plant mosquito. *Ecol. Monogr.* **49**, 357–376. (doi:10.2307/1942468)
- 165 Jones, J. S., Coyne, J. A. & Partridge, L. 1987 Estimation of the thermal niche of *Drosophila melanogaster* using a temperature-sensitive mutant. *Am. Nat.* **130**, 83–90. (doi:10.1086/284699)
- 166 Potter, K., Davidowitz, G. & Woods, H. A. 2009 Insect eggs protected from high temperatures by limited homeothermy of plant leaves. *J. Exp. Biol.* **212**, 3448–3454. (doi:10.1242/jeb.033365)
- 167 Feder, M. E., Blair, N. & Figueras, H. 1997 Oviposition site selection: unresponsiveness of *Drosophila* to cues of potential thermal stress. *Anim. Behav.* **53**, 585–588. (doi:10.1006/anbe.1996.0333)
- 168 Kolbe, J. J. & Janzen, F. J. 2002 Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology* **83**, 269–281. (doi:10.1890/0012-9658(2002)083[0269:IONSSO]2.0.CO;2)
- 169 Doody, J. S., Guarion, F., Georges, A., Corey, B., Murray, G. & Ewert, M. W. 2006 Nest site choice compensates for climate effects on sex ratios in a lizard with environmental sex determination. *Evol. Ecol.* **20**, 307–330. (doi:10.1007/s10682-006-0003-2)
- 170 Bradshaw, W. E. & Holzapfel, C. M. 2001 Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl Acad. Sci. USA* **98**, 14 509–14 511. (doi:10.1073/pnas.241391498)
- 171 Schwanz, L. E. & Janzen, F. J. 2008 Climate change and temperature-dependent sex determination: can individual plasticity in nesting phenology prevent extreme sex ratios? *Physiol. Biochem. Zool.* **81**, 826–834. (doi:10.1086/590220)
- 172 Cowles, R. B. 1930 The life history of *Varanus niloticus* (Linnaeus) as observed in Natal South Africa. *J. Entomol. Zool.* **22**, 1–32.
- 173 Shine, R. 1985 The evolution of viviparity in reptiles: an ecological analysis. In *Biology of the Reptilia* (eds C. Gans & F. Billet), pp. 605–694. New York, NY: Wiley-Interscience.
- 174 Bennett, A. F., Dao, K. M. & Lenski, R. E. 1990 Rapid evolution in response to high temperature selection. *Nature* **346**, 79–81. (doi:10.1038/346079a0)
- 175 Angilletta Jr, M. J., Bennett, A. F., Guderley, H., Navas, C. A., Seebacher, F. & Wilson, R. S. 2006 Coadaptation: a unifying principle in evolutionary thermal biology. *Physiol. Biochem. Zool.* **79**, 282–294. (doi:10.1086/499990)
- 176 Huey, R. B. & Bennett, A. F. 1987 Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* **41**, 1098–1115. (doi:10.2307/2409194)
- 177 Lynch, M. & Lande, R. 1993 Evolution and extinction in response to environmental change. In *Biotic interactions and global change* (eds P. M. Kareiva, J. G. Kingsolver & R. B. Huey), pp. 234–250. Sunderland, MA: Sinauer Associates.
- 178 Gomulkiewicz, R. & Holt, R. D. 1995 When does evolution by natural selection prevent extinction? *Evolution* **49**, 201–207. (doi:10.2307/2410305)
- 179 Hoffmann, A. A. & Sgro, C. M. 2011 Climate change and evolutionary adaptation. *Nature* **470**, 479–485. (doi:10.1038/nature09670)
- 180 Kingsolver, J. G. 2009 ASN Presidential Address: the well-temperated biologist. *Am. Nat.* **174**, 755–768. (doi:10.1086/648310)
- 181 Kearney, M., Porter, W. P., Williams, C. K., Ritchie, S. A. & Hoffmann, A. A. 2009 Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. *Funct. Ecol.* **23**, 528–538. (doi:10.1111/j.1365-2435.2008.01538.x)
- 182 Bogert, C. M. 1949 Thermoregulation in reptiles, a factor in evolution. *Evolution* **3**, 195–211. (doi:10.2307/2405558)
- 183 Bartholomew, G. A. 1964 The roles of physiology and behaviour in the maintenance of homeostasis in the desert environment. *Symp. Soc. Exp. Biol.* **18**, 7–29.
- 184 Ruibal, R. 1961 Thermal relations of five species of tropical lizards. *Evolution* **15**, 98–111. (doi:10.2307/2405846)
- 185 Tewksbury, J. J., Huey, R. B. & Deutsch, C. A. 2008 Putting the heat on tropical animals. *Science* **320**, 1296–1297. (doi:10.1126/science.1159328)
- 186 Diamond, S. E., Sorger, D. M., Hulcr, J., Pelini, S. L., Del Toro, I., Hirsch, C., Oberg, E. & Dunn, R. R. 2011 Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Glob. Change Biol.* **18**, 448–456. (doi:10.1111/j.1365-2486.2011.02542.x)
- 187 Corlett, R. T. 2011 Impacts of warming on tropical lowland rainforests. *Trends Ecol. Evol.* **26**, 606–613. (doi:10.1016/j.tree.2011.06.015)
- 188 Mahlstein, I., Knutti, R., Solomon, S. & Portmann, R. W. 2011 Early onset of significant local warming in low latitude countries. *Environ. Res. Lett.* **6**, 034009. (doi:10.1088/1748-9326/6/3/034009)
- 189 Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B. & Wood, S. 1998 Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**, 783–786. (doi:10.1038/35842)
- 190 Gorman, G. C. & Hillman, S. 1977 Physiological basis for climatic niche partitioning in two species of Puerto Rican *Anolis* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* **11**, 337–340. (doi:10.2307/1563246)
- 191 Clark, D. A., Piper, S. C., Keeling, C. D. & Clark, D. B. 2003 Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual variation during 1984–2000. *Proc. Natl Acad. Sci. USA* **100**, 5852–5857. (doi:10.1073/pnas.0935903100)
- 192 Feeley, K. J., Wright, S. J., Supardi, M. N. N., Kassim, A. R. & Davies, S. J. 2007 Decelerating growth in tropical forest trees. *Ecol. Lett.* **10**, 461–469. (doi:10.1111/j.1461-0248.2007.01033.x)
- 193 Vitt, L. J., Avila-Pires, T. C. S., Caldwell, J. P. & Oliveira, V. R. L. 1998 The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. *Conserv. Biol.* **12**, 654–664. (doi:10.1046/j.1523-1739.1998.96407.x)
- 194 Tracy, C. R. 1976 A model of the dynamic exchanges of water and energy between a terrestrial amphibian and its environment. *Ecology* **46**, 293–326. (doi:10.2307/1942256)

- 195 McJannet, D., Wallace, J. & Reddell, P. 2007 Precipitation interception in Australian tropical rainforests: II. Altitudinal gradients of cloud interception, stemflow, throughfall and interception. *Hydrol. Proc.* **21**, 1703–1718. (doi:10.1002/hyp.6346)
- 196 Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C. & Longino, J. T. 2008 Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**, 258–261. (doi:10.1126/science.1162547)
- 197 Raxworthy, C. J., Pearson, R. G., Rabibisoa, N., Rakotonirafy, A. M., Ramanamanjato, J.-B., Raselimanana, A. P., Wu, S., Nussbaum, R. A. & Stone, D. A. 2008 Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Glob. Change Biol.* **14**, 1703–1720. (doi:10.1111/j.1365-2486.2008.01596.x)
- 198 Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C. & Beissinger, S. R. 2008 Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**, 261–264. (doi:10.1126/science.1163428)
- 199 Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J. D., Cheye, V. K., Barlow, H. S., Hill, J. K. & Thomas, C. D. 2009 Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proc. Natl Acad. Sci. USA* **106**, 1479–1483. (doi:10.1073/pnas.0809320106)
- 200 Longino, J. T. & Colwell, R. K. 2011 Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere* **2**, art 29. (doi:10.1890/ES10-00200.1)
- 201 Sheldon, K. S., Yang, S. & Tewksbury, J. J. 2011 Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecol. Lett.* **14**, 1191–1200. (doi:10.1111/j.1461-0248.2011.01689.x)
- 202 McCain, C. M. & Colwell, R. K. 2011 Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecol. Lett.* **14**, 1236–1245. (doi:10.1111/j.1461-0248.2011.01695.x)
- 203 Crozier, L. & Dwyer, G. 2006 Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *Am. Nat.* **167**, 853–866. (doi:10.1086/504848)
- 204 Helmuth, B., Kingsolver, J. G. & Carrington, E. 2005 Biophysics, physiological ecology, and climate change: does mechanism matter? *Annu. Rev. Physiol.* **67**, 177–201. (doi:10.1146/annurev.physiol.67.040403.105027)
- 205 Holt, R. D. 1990 The microevolutionary consequences of climate change. *Trends Ecol. Evol.* **5**, 311–315. (doi:10.1016/0169-5347(90)90088-U)
- 206 Parsons, P. A. 1989 Conservation and global warming: a problem in biological adaptation to stress. *Ambio* **18**, 322–325.
- 207 Hoffmann, A. A., Hallas, R. J., Dean, J. A. & Schiffer, M. 2003 Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science* **301**, 100–102. (doi:10.1126/science.1084296)
- 208 Kellerman, V., van Heerwaarden, B., Sgrò, C. M. & Hoffmann, A. A. 2009 Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science* **325**, 1244–1246. (doi:10.1126/science.1175443)