

Research

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

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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 O₂, CO₂ 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

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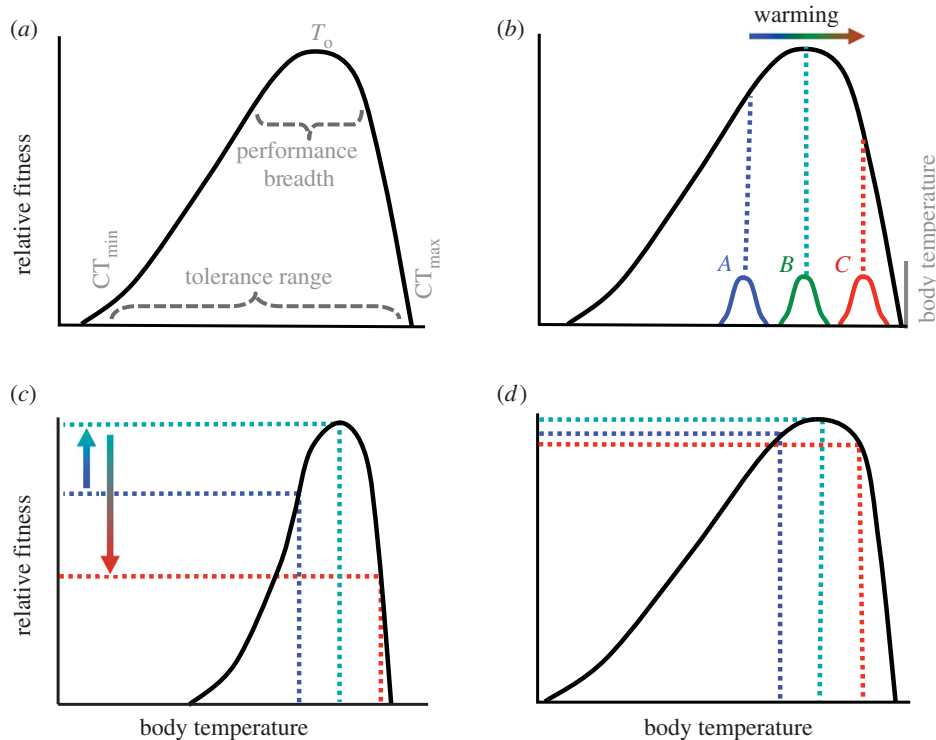


Figure 1. (a) Thermal fitness (performance) curve for a hypothetical ectotherm, with key descriptive parameters CT_{\min} , CT_{\max} , tolerance range, performance breadth and optimal temperature (T_o) identified (adapted from Huey [48]). (b) With climate warming, realized T_b distributions can shift 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].

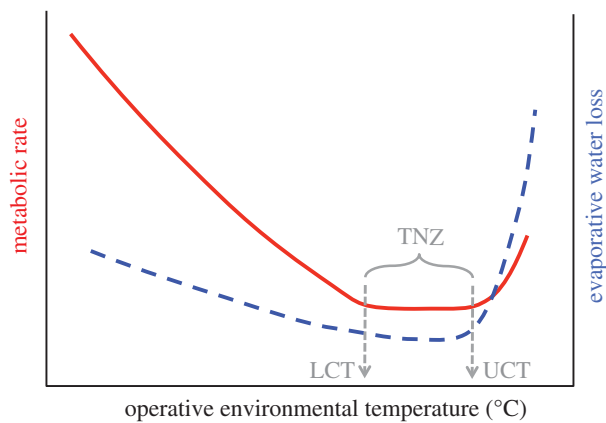


Figure 2. Effects of environmental temperature on rates of metabolic heat production (red) and of evaporative water loss (blue) of endotherms. At low environmental temperatures, energy expenditures and thus heat production are elevated to balance heat loss. At high ambient temperatures, rates of evaporative 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

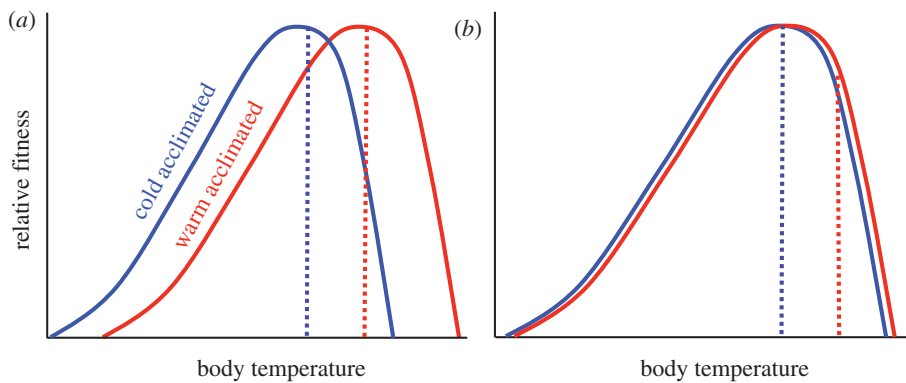


Figure 3. Acclimatization to low (blue dotted line) versus high (red dotted line) T_b (simulating an acute climate shift) sometimes induces a phenotypic shift in an ectotherm's thermal fitness curve. (a) Depicts an ectotherm with marked acclimatization capacities. Its elevated T_o (red) provides some 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.

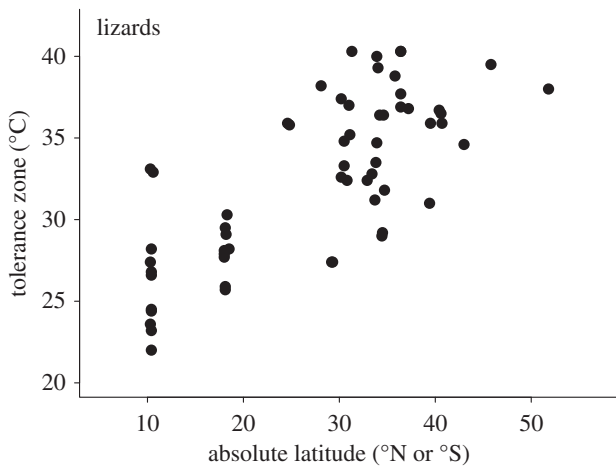


Figure 4. Tolerance zones ($CT_{max} - CT_{min}$; see figure 1a) of lizards increase with absolute latitude. The increase is due primarily to a shift in CT_{min} (rather than CT_{max}) with latitude (see text). Note: see Huey *et al.* [68] for a phylogenetic analyses.

[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.

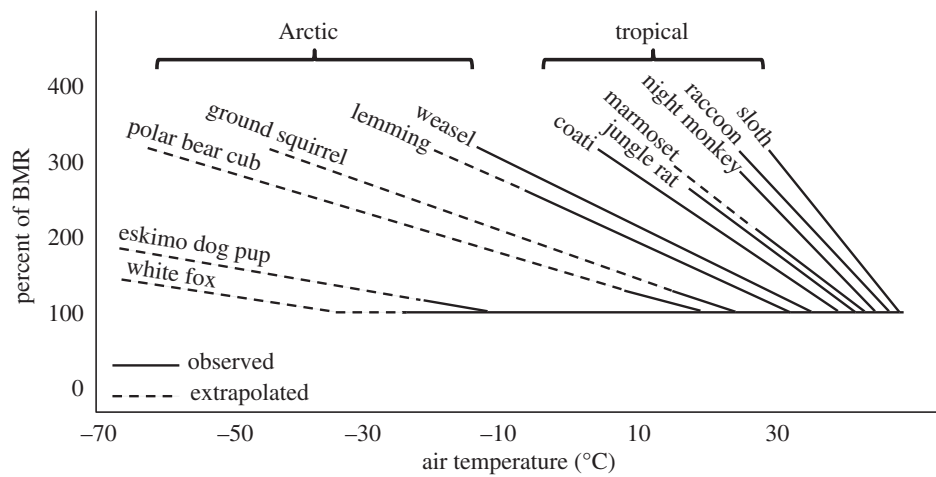


Figure 5. Metabolic rate as a percentage of basal metabolic rate (BMR) versus air temperature for Arctic and tropical mammals. Arctic mammals have relatively low LCTs, and thus relatively broad TNZs, assuming that UCTs are independent of latitude. Adapted from Porter & Kearney [26], which was based on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

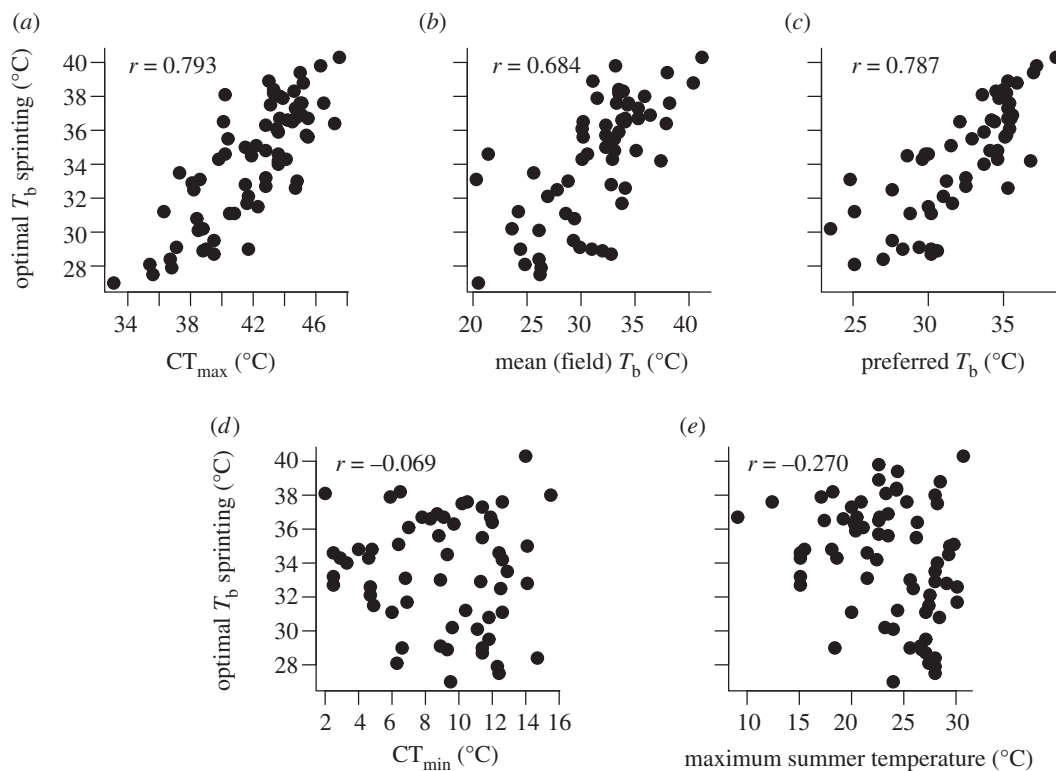


Figure 6. Potential proxies for optimal temperatures (T_o) with lizard data as exemplars: (a) CT_{max} , (b) mean T_b (field), (c) preferred T_b in laboratory thermal gradients, (d) CT_{min} and (e) mean maximum daily temperature for the three warmest months. CT_{max} , T_b and T_p predict T_o (a–c), 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

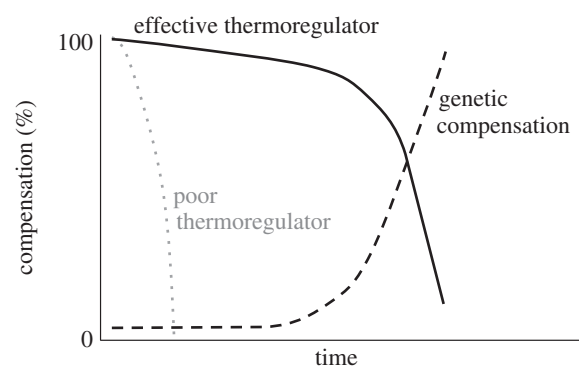


Figure 7. Consequences of differences in ability to compensate behaviourally (or via acclimatization) for climate warming. At the start, assume that mean T_c equals mean T_o , so that the thermal environment is ideal. If T_c increases from warming, a species with strong behavioural capacity to thermoregulate (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.

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