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Why tropical forest lizards are vulnerable to climate warming

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Biological impacts of climate warming are predicted to increase with latitude, paralleling increases in warming. However, the magnitude of impacts depends not only on the degree of warming but also on the number of species at risk, their physiological sensitivity to warming and their options for behavioural and physiological compensation. Lizards are useful for evaluating risks of warming because their thermal biology is well studied. We conducted macrophysiological analyses of diurnal lizards from diverse latitudes plus focal species analyses of Puerto Rican *Anolis* and *Sphaerodactylus*. Although tropical lowland lizards live in environments that are warm all year, macrophysiological analyses indicate that some tropical lineages (thermoconformers that live in forests) are active at low body temperature and are intolerant of warm temperatures. Focal species analyses show that some tropical forest lizards were already experiencing stressful body temperatures in summer when studied several decades ago. Simulations suggest that warming will not only further depress their physiological performance in summer, but will also enable warm-adapted, open-habitat competitors and predators to invade forests. Forest lizards are key components of tropical ecosystems, but appear vulnerable to the cascading physiological and ecological effects of climate warming, even though rates of tropical warming may be relatively low.

Keywords: climate warming; heat stress; body temperature; operative temperature

1. INTRODUCTION

Climate warming has profoundly affected terrestrial organisms (Walther *et al.* 2002; Parmesan 2006), and the magnitude of future effects is expected to increase with latitude (Root *et al.* 2003), paralleling the latitudinal increase in rate of warming (IPPC 2007). However, biotic impacts depend not only on the rate of warming but also on the number of species at risk, the behavioural and physiological abilities of organisms to buffer climate warming (Huey *et al.* 2003; Helmuth *et al.* 2005) and on physiological sensitivity to warming (Huey & Slatkin 1976; Deutsch *et al.* 2008; Tewksbury *et al.* 2008). The biodiversity of terrestrial ectotherms (e.g. insects, amphibians, reptiles) is of course vastly greater at lower latitudes. Moreover, many tropical ectotherms are surprisingly intolerant of high temperatures (Ruibal 1961; Parsons 1989) or are relatively sensitive to temperature change (Janzen 1967; van Berkum 1988; Deutsch *et al.* 2008). Nevertheless, biologists have given limited attention to whether tropical ectotherms are vulnerable to warming (Parsons 1989; Pounds *et al.* 1999; Root *et al.* 2003; Parmesan 2007; Colwell *et al.* 2008; Deutsch *et al.* 2008;

Raxworthy *et al.* 2008; Tewksbury *et al.* 2008; Williams *et al.* 2008; Chen *et al.* 2009; Kearney *et al.* 2009).

Reliable projections of the biological impacts of climate change require information on environmental biophysics as well as the body temperature, thermal physiology, behaviour and ecology of species (Huey & Slatkin 1976; Tracy & Christian 1983; Dunham 1993; Buckley 2008; Angilletta 2009; Kearney *et al.* 2009). Air temperatures recorded by weather stations are often used as a proxy for body temperature (T_b), but actual T_b s are far superior (Chown & Terblanche 2007). Unfortunately, T_b data are lacking for most ectotherms. However, such data (as well as habitats, thermoregulatory behaviours and activity patterns) are available for diverse species of lizards from many latitudes. Moreover, these data are often accompanied by laboratory data on thermal preferences (T_p), which are often co-adapted with optimal performance temperatures (T_o ; Huey & Bennett 1987; Martin & Huey 2008), by critical thermal temperatures (CT_{min} , CT_{max}) and sometimes by measures of the temperature sensitivity of physiological performance (Bennett 1980; Hertz *et al.* 1983; Angilletta *et al.* 2002). Our knowledge of lizard thermal performance comes largely from studies of sprint speed: accordingly, we compiled data on the thermal dependence of this ecologically relevant trait (Bennett 1980) for more than 70 species of lizards (see table 1 in the electronic supplementary material). The completeness and

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richness of behavioural and physiological data, as well as information on phylogenetic relationships, are unsurpassed for ectotherms and permit the first physiologically and phylogenetically based assessment of latitudinal patterns in the performance consequences of global warming.

We first conducted a comparative, macrophysiological analysis (Chown *et al.* 2004) of thermoregulatory behaviour and thermal sensitivity of lizards as a function of latitude. Then we focused on several Puerto Rican lizards. Using field T_b data collected several decades ago as a temporal baseline, as well as data on the thermal sensitivity of sprinting, we simulated how warming should affect both lizard T_b and relative performance during summer (Huey 1983). These complementary analyses use different approaches but lead to the same conclusion: some tropical forest lizards 'can't take the heat'. Moreover, theoretical models yield this same conclusion (Deutsch *et al.* 2008; Kearney *et al.* 2009). Given the huge diversity of ectotherms in the tropics, the implications of these consistent patterns are daunting.

2. MATERIAL AND METHODS

(a) Macrophysiological analyses

Data on mean values of CT_{min} , CT_{max} , T_b , T_b (of active lizards), habitat associations, basking behaviour and absolute latitude were compiled from the literature (see tables 1 and 2 in the electronic supplementary material). To minimize methodological noise (Chown *et al.* 2003; Ives *et al.* 2007), we analysed only species for which the thermal dependence of sprint speed had been quantified. Most studies (63 out of 70) were done by us, our students or our close colleagues; thus, protocols were uniform by comparative standards.

We include independent field data on habitat association (forest and open), thermoregulatory behaviour (basking and non-basking), T_b and T_a for lizards from 12 neotropical sites (available as table 2b in the electronic supplementary material). Most sites were approximately 1.5×1.5 km. These field data were collected by a single team of investigators (Vitt *et al.* 2008), and thus methods were consistent.

To evaluate an association of absolute latitude, taxonomic affinity and basking behaviour with the physiological traits, we computed (multiple) regressions involving the three independent variables and their interactions. Phylogenetic relationships were considered, and the tree (and sources) is available in table 3 in the electronic supplementary material.

We computed regressions in three ways (reviews in Garland *et al.* 2005; Lavin *et al.* 2008): conventional (non-phylogenetic) ordinary least squares (OLS); phylogenetic generalized least squares (PGLS); and regression in which residuals were modelled as having evolved via an Ornstein–Uhlenbeck process (RegOU), thus mimicking stabilizing selection. These three models form a continuum between assuming a star phylogeny with no hierarchical structure (OLS), a phylogeny as specified by the user (PGLS) and something that can take on values intermediate between the star and the specified hierarchical phylogeny (RegOU) (Garland *et al.* 2005). Candidate-independent variables included absolute latitude, a 0–1 dummy variable to code for non-basking versus basking and a series of dummy variables to code for 'family' membership (Lavin *et al.* 2008). Details of analysis and model comparisons are described in the electronic supplementary material.

(b) Focal species analyses of Puerto Rican lizards

Extensive field and laboratory data for several Puerto Rican lizards enable us to describe the thermal biology of these lizards several decades ago, and then to predict how warming will affect their T_b and relative sprint performance. Details of methods are given in the electronic supplementary material. Field data on T_b and T_a , laboratory thermal preference (T_p), CT_{max} and CT_{min} for *Anolis cristatellus* from Punta Salinas were collected in July 1973 (Huey 1974; Huey & Webster 1976). Thermal sensitivities of sprint speed were for lizards from this population collected in 1981 (Huey 1983). The preferred temperature range is arbitrarily delimited by the central 50 per cent of all T_p records (Hertz *et al.* 1993).

Field data for T_b s and operative temperatures (T_e) were obtained for *A. cristatellus* at San German in August 1983 (Hertz 1992). T_e s were obtained using a randomly placed array of 60 hollow electroformed copper models (calibrated against live lizards) that match the size and reflectivity of adults. Thermal preference shows no significant geographical variation (Huey & Webster 1976), and so we used T_p s from Punta Salinas.

Field data for T_b and T_a of *Anolis gundlachi* from El Verde were obtained in July 1972, and T_p were obtained in 1973 (Huey & Webster 1976). Long-term weather records are available for this site (<http://luq.lternet.edu/data/lterdb16/data/evtemp.htm>), enabling us to estimate the actual shift in mean July maximum temperature from 1975 to 2008. The predicted shift in T_a was 2.1°C (see figure 1 in the electronic supplementary material).

Field data for lowland populations of diurnal geckos (*Sphaerodactylus* spp.) were obtained in 1988–1991 (Álvarez 1992; table 2h in the electronic supplementary material). Basic techniques for obtaining T_b s and T_e s followed Hertz (1992), except that small polyvinyl chloride cylinders ($n=27$) were used to estimate T_e s.

3. RESULTS AND DISCUSSION

(a) Natural history, phylogeny and latitude

Basic natural history and phylogenetic issues lay a critical foundation for understanding latitudinal patterns of lizard thermal biology. Over four decades ago, Ruibal (1961) noted that temperate and tropical lizards (diurnal) differ in habitat use, thermoregulatory behaviour and T_b . Almost all temperate-zone lizards are restricted to open habitats where operative temperatures (T_e s) are high and sufficiently heterogeneous to enable thermoregulation (Porter *et al.* 1973; Bakken 1989): most species bask, thermoregulate relatively carefully and maintain high T_b that are often well above associated T_a (Porter *et al.* 1973; Huey 1982; van Berkum 1988). (The few exceptions are cryptozoic species that infrequently emerge from cover (see below).)

Some tropical and subtropical lizards also live in open habitats and generally share behavioural and physiological characteristics (e.g. basking behaviour, elevated T_b) with high-latitude species living in open habitats (Ruibal 1961; Porter & James 1979; van Berkum 1988; Vitt *et al.* 1998). However, many other tropical and subtropical lizards live below the canopy inside deeply shaded forests (Inger 1959; Ruibal 1961; Huey 1982), where T_e s are relatively low and homogeneous (Hertz 1992), making thermoregulation difficult or expensive (Huey 1974). In fact, these tropical forest lizards rarely bask and are active at

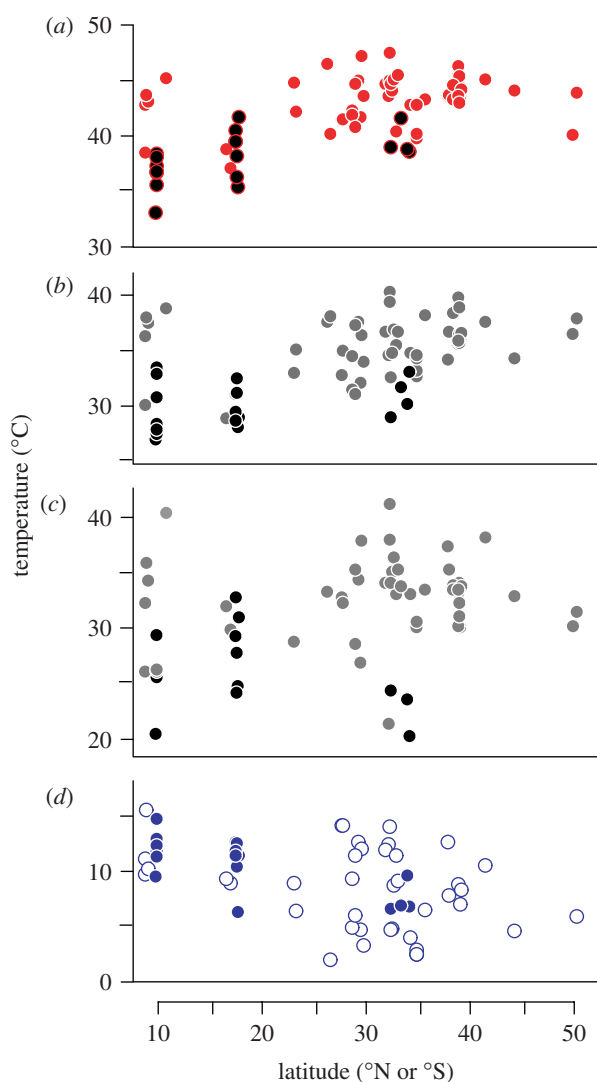


Figure 1. Thermal sensitivity of diurnal lizards versus latitude. (a) Heat tolerance (CT_{\max}), (b) optimal sprint temperature (T_b), (c) mean-field body temperature (T_b) and (d) cold tolerance (CT_{\min}) versus latitude. In phylogenetic analyses, CT_{\max} , T_b and T_b are independent of the latitude but are relatively low for certain taxa and for non-basking species, especially tropical ones (black circles; see text); by contrast, CT_{\min} decreases with latitude. The four points for non-baskers and mid-latitude are cryptozoic species (see text). Points for non-baskers are offset and shifted by 0.5° latitude to increase spread (see data in table 1 in the electronic supplementary material).

relatively low T_b s that are necessarily close to air temperatures (Inger 1959; Ruibal 1961; Huey 1982), because convection dominates heat exchange in such habitats (Bakken 1992).

In the neotropics, non-basking (forest) species often outnumber basking (open-habitat) species at lowland sites with mixed forest and open habitats (see table 2b in the electronic supplementary material). Thus, non-basking species constitute a major component of the diversity of neotropical lizards. In fact, these species constitute an average of 62 per cent of 63 species at 12 sites from Nicaragua to Brazil (see table 2b in the electronic supplementary material).

Close associations among habitat, basking behaviour and T_b are evident for neotropical species (see table 2b in the electronic supplementary material). Of the species

found in forests, only 1 out of 40 was basking. Of the species in open or edge habitats, 21 out of 24 were basking. Importantly, activity T_b s of tropical forest lizards averaged 6°C lower than that of tropical open-habitat lizards (t -test, $p \ll 0.001$, $28.9 \pm 0.31^\circ\text{C}$ ($n=38$) and $34.9 \pm 0.51^\circ\text{C}$ ($n=20$)).

These linkages appear to have phylogenetic and latitudinal components. Different neotropical lineages tend to comprise either predominately forest-dwelling, non-basking and low T_b species or open-edge dwelling, basking and high T_b species (see table 2a in the electronic supplementary material). (Note: these families show significant heterogeneity in percentages of basking and forest-dwelling species (non-phylogenetic χ^2 -tests, both $p < 0.01$.) Moreover, lineages in the tropics that include predominately forest-dwelling and low T_b species (e.g. diurnal Gekkonidae, Gymnophthalmidae, Polychrotidae) are largely restricted to tropical and subtropical regions, whereas lineages with a preponderance of open-habitat species and higher T_b species (e.g. Teiidae) often extend into the temperate zone.

Overall, most temperate-zone lizards are baskers, whereas tropical species can be either baskers or non-baskers. Moreover, these different 'thermal syndromes' tend to run in families. Exceptions do exist. A few temperate lineages are cryptozoic and have low T_b (e.g. Anguillidae; Kingsbury 1994; Xantusiidae; Mautz *et al.* 1992; some Scincidae; Bennett & John-Alder 1986; Shine 1999). Also, some tropical families and species (e.g. *A. cristatellus*) include both types. However, we are confident that these trends are general, at least for New World lizards.

(b) Field body temperatures

Early workers, who apparently expected that tropical lizards would have relatively high T_b simply because lowland tropical sites are always warm, were surprised to find that some tropical species were in fact active at T_b s well below those of most temperate-zone species (Brattstrom 1965). We evaluated field T_b s for species from diverse latitudes (figure 1c). In an ordinary least-squares analysis, which assumes a star phylogeny (Garland *et al.* 1992), T_b increased with latitude (two-tailed $p=0.0145$; see table 2c in the electronic supplementary material). However, field T_b showed a strong phylogenetic signal (Blomberg *et al.* 2003; $p=0.007$), and the best-fit regression model (RegOU) for T_b excluded latitude but included basking and family membership. Thus, the non-phylogenetic trend probably stems from the many non-basking, low T_b species in the tropics.

(c) Lizard thermal sensitivity

In the OLS regression, CT_{\min} decreased with absolute latitude ($p \ll 0.001$; figure 1d; see table 2d in the electronic supplementary material). Phylogenetic signal for CT_{\min} was significant ($p < 0.001$), and absolute latitude was the only variable in the best-fit model (RegOU). As in the non-phylogenetic analysis, CT_{\min} declined with latitude.

Optimal sprint temperature (T_b ; figure 1b) and heat tolerance (CT_{\max} ; figure 1d) shared similar patterns. In OLS, both variables increased with latitude (both $p \ll 0.001$; see table 2e,f in the electronic supplementary material). Both traits showed strong phylogenetic signal

($p \ll 0.001$), and the best-fit models (OLS) showed that T_o and CT_{max} are elevated for basking species versus non-baskers and differ among taxa. As with T_b , the non-phylogenetic trend with latitude may be a consequence of the tropical concentration of non-basking taxa.

Note that T_b , T_o and CT_{max} appear independent of latitude but are associated with basking behaviour and with taxon, whereas CT_{min} is independent of basking and taxon and depends only on latitude. These contrasting associations might reflect differential effectiveness of behaviour in buffering climate-associated selection on these thermal traits (van Berkum 1988). When active, a thermoregulating lizard in an open habitat at any latitude can usually achieve some control over its T_b and can simultaneously avoid stressfully high temperatures. Consequently, mean T_b (herein) and also maximal T_b (van Berkum 1988, p. 335) are generally independent of latitude (but see, Clark & Kroll 1974), but do tend to show strong phylogenetic conservatism (Huey 1982; Hertz *et al.* 1983) and a strong association with habitat and basking behaviour (herein, Ruibal 1961; Clark & Kroll 1974). Because T_b , T_o and CT_{max} are likely to be co-adapted traits (Huey & Bennett 1987; Huey & Kingsolver 1993; Angilletta *et al.* 2006; Martin & Huey 2008; Angilletta 2009), we are not surprised that these thermal traits were closely associated with phylogenetic affinities and basking behaviour.

By contrast, a lizard hibernating at high latitude in a winter refuge has relatively few options for behavioural thermoregulation. Consequently, temperatures of high-latitude lizards in winter (and CT_{min}) should decline with latitude (van Berkum 1988; Kearney *et al.* 2009). Thus, thermoregulatory behaviour may buffer selection (Bogert 1949; van Berkum 1988; Huey *et al.* 2003) on some thermal traits (e.g. T_b , CT_{max}), but not on all (CT_{min}).

(d) Some tropical lizards have narrow thermal safety margins

Whether climate warming is detrimental depends not only on the heat tolerance of species (i.e. on T_o and CT_{max}) but also on whether current T_e s (Roughgarden *et al.* 1981; Bakken 1992) are already high relative to an ectotherm's T_o (Tracy & Christian 1983; Huey 1991; Deutsch *et al.* 2008). If T_e s in shaded microenvironments are below an ectotherm's T_o and if shade is readily accessible, ectotherms confronting climate warming can find thermal refugia and thus remain active (Kearney *et al.* 2009). However, if T_e s in shade are currently equal to or greater than an ectotherm's T_o , climate warming will force ectotherms to retreat below ground or tolerate activity at a high T_b (Dunham 1993), which will probably induce stress and reduce performance (Huey 1983). If time restrictions and performance declines are substantive, the population might go extinct (Dunham 1993; Kearney *et al.* 2009).

We quantified potential access to an above-ground thermal refuge by computing a 'thermal safety margin', which is the difference between a lizard's T_o for sprinting and the maximal T_e in shade (Deutsch *et al.* 2008). Ideally, shade T_e should be calculated for lizards on a global scale (Kearney *et al.* 2009), but here we substituted mean maximal daytime air temperature ($T_{a,max}$) during the warmest three months of the year (New *et al.* 2002). $T_{a,max}$ will closely approximate the maximal average T_e for

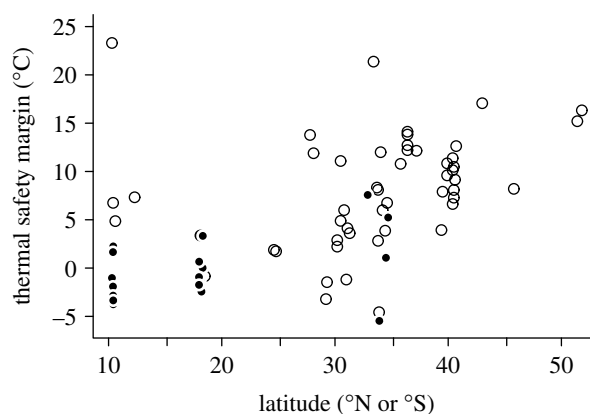


Figure 2. Thermal safety margin ($T_o - T_{a,max}$) for diurnal lizards increases with latitude. Open circles, basking species; filled circles, non-basking species. In a phylogenetic analysis, thermal safety margin increases with latitude. The tropical species with a large safety margin (*Sceloporus magister*) is montane.

small ectotherms in shade (Rogowitz 1996), because convection dominates heat exchange in shade (Bakken 1992). Of course, $T_{a,max}$ underestimates the maximal T_e in open microhabitats. Nevertheless, the issue here is whether lizards facing climate warming can access thermal refuges (Kearney *et al.* 2009), and thus $T_{a,max}$ is a relevant index.

Thermal safety margins showed only a weak phylogenetic signal ($p = 0.09$). OLS regression was the best-fit model (see table 2g in the electronic supplementary material), and safety margin increased with latitude and basking (figure 2). Thermal safety margins are thus small—and sometimes even slightly negative—for most tropical forest lizards. Because these forest species live in already warm environments, but have low T_b , T_o and CT_{max} , even a small increase in T_e may force them to reduce activity time (Kearney *et al.* 2009) or to suffer reduced performance in summer. Thus, tropical forest lizards may not be able to 'take the heat'.

By contrast, many higher latitude or high-altitude species will not need to retreat if T_e in shade increases with climate warming; rather, these species may even benefit (Kearney & Porter 2004; Chamaillé-Jammes *et al.* 2007; Buckley 2008; Kearney *et al.* 2009) because warming will improve the thermal quality of their habitat (Tracy & Christian 1983; Huey 1991; Hertz *et al.* 1993). Of course, some diurnal species (Dunham 1993) living in mid-latitude deserts (and cryptozoic species) also have small safety margins (figure 2), and these may also suffer from warming.

(e) Lizards in lowland Puerto Rico are already at risk

The latitudinal pattern of thermal safety margins (figure 2) suggests that lizards in tropical forests might be relatively vulnerable to climate warming in summer. However, such a macrophysiological approach ignores heterogeneity of microclimates and thermoregulatory behaviour. To add a biophysically and physiologically grounded approach, we analyse data for several lizards from Puerto Rico.

Anolis cristatellus is an abundant and widespread species, and its thermal biology is well known (e.g. Rand 1964; Huey & Webster 1976; Gorman & Hillman 1977; Hertz 1992). In shaded lowland habitats, this species lives

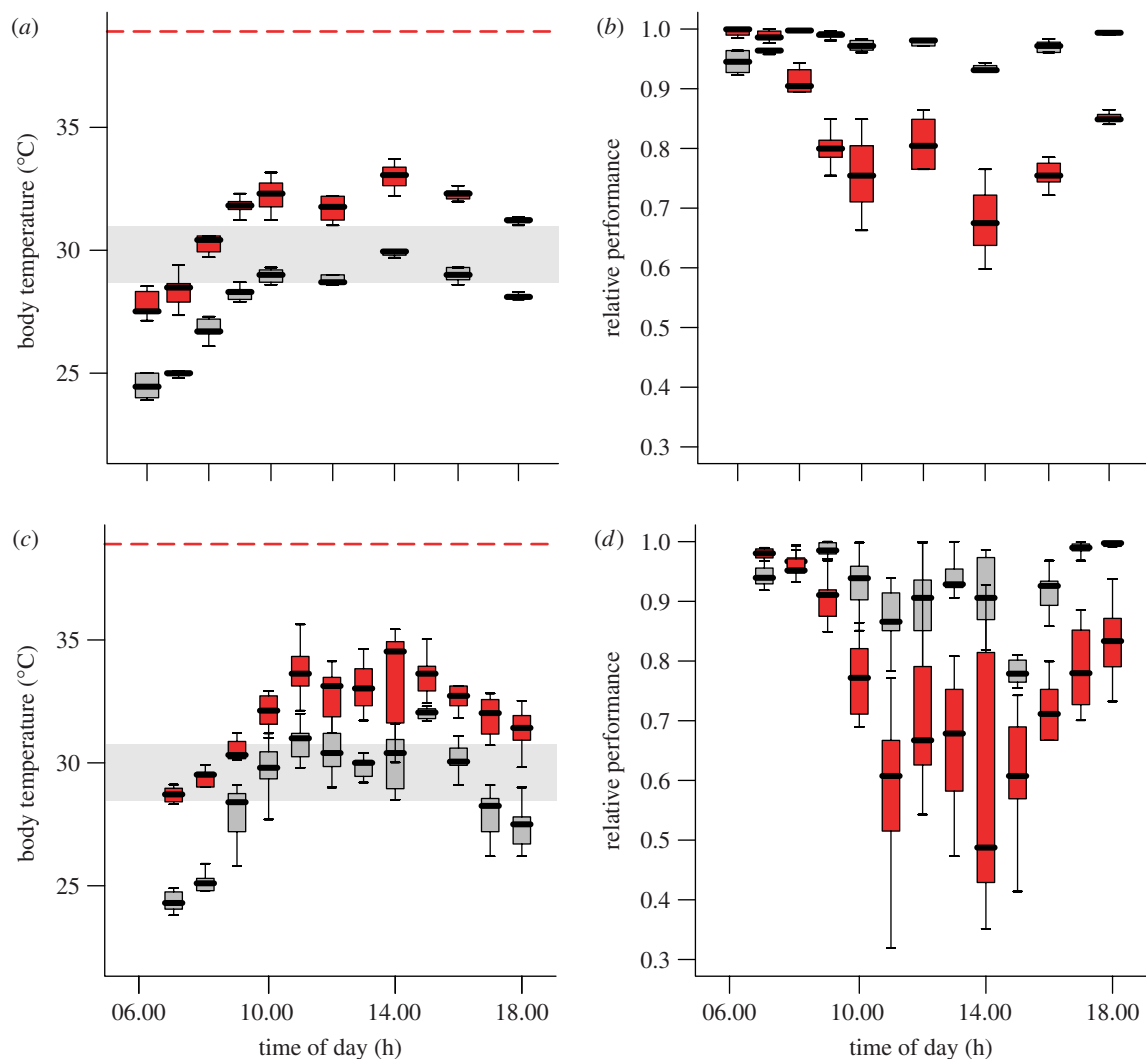


Figure 3. Impact of climate warming on T_b and performance of a tropical lizard. (a) Body temperature and (b) predicted relative sprint performance of *A. cristatellus* in a shaded forest at Punta Salinas, Puerto Rico before (grey boxes, 1973) and after (red boxes) predicted climate warming (air temperature increase of 3°C). (c) Body temperature and (d) predicted relative sprint performance of *A. cristatellus* in a forest at San German, Puerto Rico, before (1983–1984) and after predicted warming ($T_a = +3^\circ\text{C}$). In (a, c), the shaded grey rectangle delimits the preferred temperature range of this species, and the red dashed line indicates the CT_{max} (Huey & Webster 1976). Box plots depict the median, interquartile range and range.

on tree trunks, does not bask and is a thermoconformer, such that T_b closely matches T_a , and thus T_c (Huey 1974; Hertz 1992; see details of methods in the electronic supplementary material). It will bask in open lowland habitats, but only very early and late in the day (Huey 1974; Hertz 1992). Similar to other anoles (van Berkum 1988), it is relatively intolerant of high T_b (see table 1 in the electronic supplementary material).

Body and air temperatures and behaviour of *A. cristatellus* were monitored in summer approximately 35 years ago (1972 and 1973) at Punta Salinas on the northern coast (Huey 1974; Huey & Webster 1976), and we use the 1973 data as a temporal baseline. In a dense forest, these lizards were classic thermoconformers (figure 3): they were active from sunrise to sunset; had no opportunity to bask; and had T_b s that averaged only $0.6 \pm 0.05^\circ\text{C}$ above T_a (Huey 1974; Huey & Webster 1976). This habitat was thermally suitable for this species: even without thermoregulating, lizards had T_b s that usually fell within the T_p range (figure 3a) and that enabled them to sprint at greater than 90 per cent of their maximal speed from sunrise to sunset (figure 3b).

To estimate the impact of climate warming on *A. cristatellus* over the next 100 years, we conservatively assume that T_a will increase by 3°C above levels measured in the early 1970s (Malhi & Wright 2004; IPCC 2007). Because convection dominates heat exchange in forests, T_b will also increase by approximately 3°C . As a result, lizards will have elevated T_b (red boxes in figure 3a) that exceed T_p for most of the day, and their predicted sprint performance should be lower for most of the day (figure 3b).

Additional data (figure 3c) were collected for this species approximately 25 years ago (1983) at San German, a lowland forested site (90 m) on the warmer, southwestern side of Puerto Rico (Hertz 1992). Here, *A. cristatellus* were again active from sunrise to sunset and were thermoconformers. Their T_b s averaged only $0.6 \pm 0.09^\circ\text{C}$ above the mean T_c of their habitat. During most of the day, T_b and T_c were within the lizard's preferred temperature range, and only 20.8 per cent of T_b (and 7.8% of T_c) exceeded that range. If T_c increases by 3°C , 68.6 per cent of all predicted T_b records (and 70.6% of all T_c) should exceed the lizard's preferred range

(figure 3c). In fact, 92.1 per cent of all T_e should exceed the preferred range during midday (10.00–14.00 hours). Moreover, relative sprint performance at midday should decline precipitously (figure 3d).

Thermal data are also available for several species of the diurnal ground gecko, *Sphaerodactylus*, studied in 1988–1991 (Álvarez 1992). These geckos typically inhabit leaf litter. In cool seasons or at high altitude, these geckos sometimes bask; but in lowland forests, they rarely do so (Álvarez 1992). Similar to *Anolis*, these lizards are relatively intolerant of high temperatures: most have a CT_{max} below 40°C and a T_p only approximately 30°C (see table 2h in the electronic supplementary material). In 1991, lowland populations of four species were already living in environments that were stressfully warm in summer; in fact, mean T_e exceeded mean T_p and mean T_o by 3.2 ± 1.06 and 5.1 ± 0.70 °C, respectively. As a consequence, mean T_b during the day in summer (across species) exceeded mean T_p by 2.1 ± 0.43 °C on average and exceeded T_o for sprinting by 3.9 ± 1.16 °C on average (see table 2h in the electronic supplementary material). If T_e increases by 3°C because of climate warming, these lizards will probably experience severe heat stress because mean T_e over the day in summer will be only 3.5 ± 0.90 °C below the CT_{max} of these lizards.

Although climate warming may well stress Puerto Rican lizards in summer, it should benefit them in winter, as the slightly lower temperatures then depress reproduction (Gorman & Licht 1974; Lister 1981). Therefore, a full demographic model will be necessary to evaluate the overall effects of warming. However, because thermal fitness curves are asymmetric (Gilchrist 1995; Huey & Berrigan 2001), being ‘too hot’ is likely to be much worse physiologically than being ‘too cold’.

(f) Cascading effects of warming on ecological interactions

Climate warming will not only induce thermal stress in tropical forest lizards, but also probably force them to suffer increased competition and predation from warm-adapted, open-habitat lizards. Some open-habitat high- T_b lizards, such as *Ameiva festiva* (Costa Rica), make periodic forays into shaded forest habitats to search for food. However, they must soon return to the open to bask (van Berkum *et al.* 1986). As climate warming elevates T_e inside forests, *A. festiva* will cool more slowly, forage longer and thus put increased competitive and predatory pressures on forest lizards (Vitt *et al.* 1998).

Climate warming may even enable open-habitat species to displace tropical forest species. In the early 1970s at El Verde, Puerto Rico (approx. 350 m), *A. gundlachi* was a forest-dwelling, non-basking species, whereas *A. cristatellus* was restricted to open and edge habitats. Relative to *A. cristatellus*, *A. gundlachi* had a significantly lower field T_b (figure 4), T_p and CT_{max} (Huey & Webster 1976; Hertz 1992; Rogowitz 1996).

In July 1972, the thermal environment inside the forest at El Verde was highly suitable for *A. gundlachi* (Huey & Webster 1976); indeed, 74.7 per cent of all T_b s during the entire day (figure 4) were within 1°C of the T_p range for this species, and only 4.5 per cent of T_b s were 1°C or more above its T_p range. By contrast, forest T_b s would have been too cool for *A. cristatellus* (Gorman & Hillman 1977);

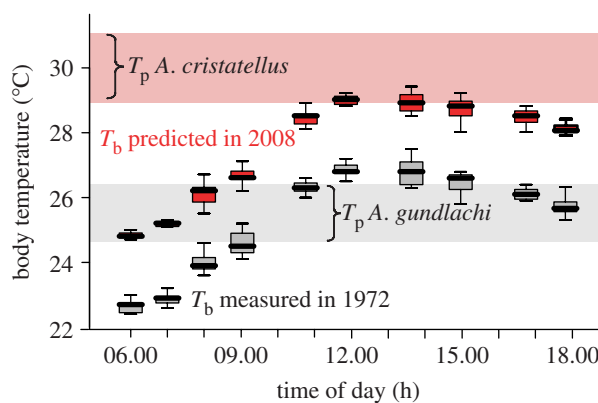


Figure 4. Predicted impact of recent climate warming on a tropical forest lizard. Observed climate warming between 1972 and 2008 (see figure 1 in the electronic supplementary material) is likely to make forest habitats (El Verde, Puerto Rico) less suitable in summer for resident forest species but more suitable for an open-habitat species. T_b s of the forest species (*A. gundlachi*) in July 1972 are shown in grey boxes, and most T_b s were close to the T_p range of this species (lower shaded grey rectangle). By 2008, observed warming of 2.1°C at El Verde should have elevated predicted T_b of lizards in the forest (red boxes). These predicted T_b are much higher than those preferred by *A. gundlachi*, but should now be close to the preferred temperatures (upper shaded red rectangle) of *A. cristatellus*, which was restricted to open habitats in 1972. If warming continues, *A. cristatellus* could displace *A. gundlachi*.

95.5 per cent of all predicted T_b s in summer would have been at least 1°C below its T_p range (figure 4).

The observed 2.1°C climate warming in summer since 1975 (see figure 1 in the electronic supplementary material) should have made the forest less suitable thermally for *A. gundlachi* in that season. Only 39.6 per cent of its predicted T_b s should now be within 1°C of its T_p range, and 60.3 per cent should be at least 1°C warmer than its T_p range, suggesting likely heat stress. By contrast, 60.4 per cent of predicted T_b of *A. cristatellus* should now be within 1°C of its T_p range (figure 4). Therefore, if warming continues, *A. cristatellus* might soon move into the forest, at least during summer, and potentially even displace *A. gundlachi*.

4. CONCLUDING REMARKS

Both macrophysiological (figures 1 and 2) and focal species (figures 3 and 4) approaches suggest that lowland lizards living in neotropical forests are at risk from climate warming; in fact, some species are probably already experiencing body temperatures at or above their physiological optima, at least in summer (figures 3 and 4; see table 2h in the electronic supplementary material). The cascading effects of increased competition and predation from open-habitat species will only compound problems for forest species and may have major effects on tropical forest food webs. Moreover, performance of some species may have already been harmed by recent climate warming (figure 4).

Other studies have raised concern for the vulnerability of tropical ectotherms (e.g. Parsons 1989; Pounds *et al.* 1999; Root *et al.* 2003; Parmesan 2007; Colwell *et al.* 2008; Deutsch *et al.* 2008; Raxworthy *et al.* 2008; Williams *et al.* 2008; Kearney *et al.* 2009). Moreover,

population declines of lowland forest lizards in Costa Rica have already been noted (Whitfield *et al.* 2007). Because lowland tropical forests are centres of biodiversity, these predictions and trends are disturbing.

A reviewer of a draft of this paper felt that we have taken a 'pessimistic stance'. We disagree. To be sure, physiological acclimation could potentially buffer the impact of climate warming (Chown & Terblanche 2007). However, the few available data suggest that tropical forest ectotherms—including Puerto Rican *Anolis* (Rogowitz 1996)—show limited acclimation responses (Brattstrom 1968; Feder 1982; Tsuji 1988; Ghalambor *et al.* 2006). Similarly, genetic adaptation could potentially buffer the impact (Hoffmann & Blows 1993; Travis & Futuyma 1993; Angilletta 2009), and rapid response to temperature in selection experiments is common in invertebrates (Santos *et al.* 2005). Nevertheless, artificial selection on heat tolerance of a fish was unsuccessful (Baer & Travis 2000). Unfortunately, the heritability of thermal traits in lizards is essentially unstudied (Sinervo 1990; Angilletta 2009). In any case, conservatism seems to be the rule in lizard thermal evolution (Hertz *et al.* 1983; Huey & Bennett 1987). Thus, adaptive rescue is feasible but unlikely.

For some species, thermoregulatory behaviour will effectively buffer the impact of climate warming (Huey *et al.* 2003; Angilletta 2009; Kearney *et al.* 2009). For example, many desert lizards readily evade heat stress by retreating underground during warm periods (Porter *et al.* 1973; Stevenson 1985). By contrast, tropical forest lizards, such as *Anolis* and *Sphaerodactylus*, have relatively few thermoregulatory options because forest T_c s are relatively homogeneous in space and time (Hertz 1992); the 'thermal mosaic' for such forest species is relatively monochromatic. Populations with access to a mountain could potentially migrate uphill (Colwell *et al.* 2008; Raxworthy *et al.* 2008; Chen *et al.* 2009), but the largest remaining tropical rainforest (Amazon basin) has mountains only on one edge.

The biotic pressure of open-habitat species on forest ectotherms will be exacerbated if climate change also opens tropical forest canopies (Clark *et al.* 2003; Feeley *et al.* 2007; Whitfield *et al.* 2007); more solar radiation will penetrate the forest, thus increasing T_e . Canopy opening will also reduce humidity and increase wind speed, harming ectotherms sensitive to desiccation (Parsons 1989; Pounds *et al.* 1999). More importantly, deforestation and fragmentation will directly accelerate extinction rates (Brook *et al.* 2003; Ferraz *et al.* 2003) as well as increase hot edge environments (Vitt *et al.* 1998).

Of course, climate warming would not be physiologically detrimental to all tropical forest lizards. Some species living in cool montane forests should benefit (Huey & Webster 1976; Hertz 1992; Hertz *et al.* 1993). Also, even lowland species may benefit during cool seasons, when T_c s and T_b s are slightly lower (Lister 1981; Hertz 1992) and reproduction is reduced (Gorman & Licht 1974; Lister 1981). Similarly, some high-latitude species may benefit because warmer temperatures will increase potential activity times and growth rates (Kearney & Porter 2004; Chamaillé-Jammes *et al.* 2007; Buckley 2008; Deutsch *et al.* 2008; Kearney *et al.* 2009).

Our prediction that neotropical forest lizards are vulnerable to climate warming can be evaluated in future studies. One predictive approach develops biophysical,

physiological and demographic models that transduce predicted climate change onto changes in vital demographic rates (Dunham 1993; Helmuth *et al.* 2005; Crozier & Dwyer 2006; Buckley 2008). Kearney *et al.* (2009) have recently made a major step in this direction. Our conclusions are remarkably consistent with theirs: the primary challenge for temperate-zone ectotherms is gaining heat, but that for tropical ectotherms is avoiding it.

A complementary approach involves field studies: if lowland forest populations are indeed currently heat stressed in summer (figures 3 and 4), those populations should now show reduced rates of growth and reproduction in summer, relative to cooler seasons (or preferably to earlier decades). Ultimately, time-series monitoring of population ecology (Chamaillé-Jammes *et al.* 2007; Whitfield *et al.* 2007), food resources (Buckley 2008), distributions (Colwell *et al.* 2008; Raxworthy *et al.* 2008), T_b , habitat usage and microclimates may be necessary to evaluate whether lowland tropical forest lizards are indeed on—and perhaps already even over—the thermal edge. Field data from earlier decades (e.g. figures 3 and 4; Chen *et al.* 2009) provide a critical baseline for monitoring climate-induced changes in temperatures and performance of tropical lizards.

We dedicate this paper to Rodolfo Ruibal, whose 1961 paper pioneered empirical studies of the thermobiology of tropical ectotherms and whose insights into tropical and temperate ectotherms laid the conceptual foundation for this paper. We thank M. Angilletta and M. Kearney for their comments. This study was supported by National Science Foundation grants to P.E.H., R.B.H., J.J.T., L.J.V. and T.G., and by a Program on Climate Change Fellowship to C.A.D. El Verde temperature data were provided courtesy of the Luquillo Experimental Forest (LTER).

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