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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  $CT_{min}$ ,  $CT_{max}$ ,  $T_o$ ,  $T_b$  (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  $1.5 \times 1.5$  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  $2.1^\circ\text{C}$  (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

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 2*b* 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 2*b* in the electronic supplementary material).

Close associations among habitat, basking behaviour and  $T_b$  are evident for neotropical species (see table 2*b* 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 2*a* in the electronic supplementary material). (Note: these families show significant heterogeneity in percentages of basking and forest-dwelling species (non-phylogenetic  $\chi^2$ -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. Anguidae: 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 1*c*). 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 2*c* 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 1*d*; see table 2*d* 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 ( $T_o$ ; figure 1*b*) and heat tolerance ( $CT_{\max}$ ; figure 1*d*) shared similar patterns. In OLS, both variables increased with latitude (both  $p \ll 0.001$ ; see table 2*e,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  $T_c$ 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  $T_c$ 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  $T_c$ s in shade are currently equal to or greater

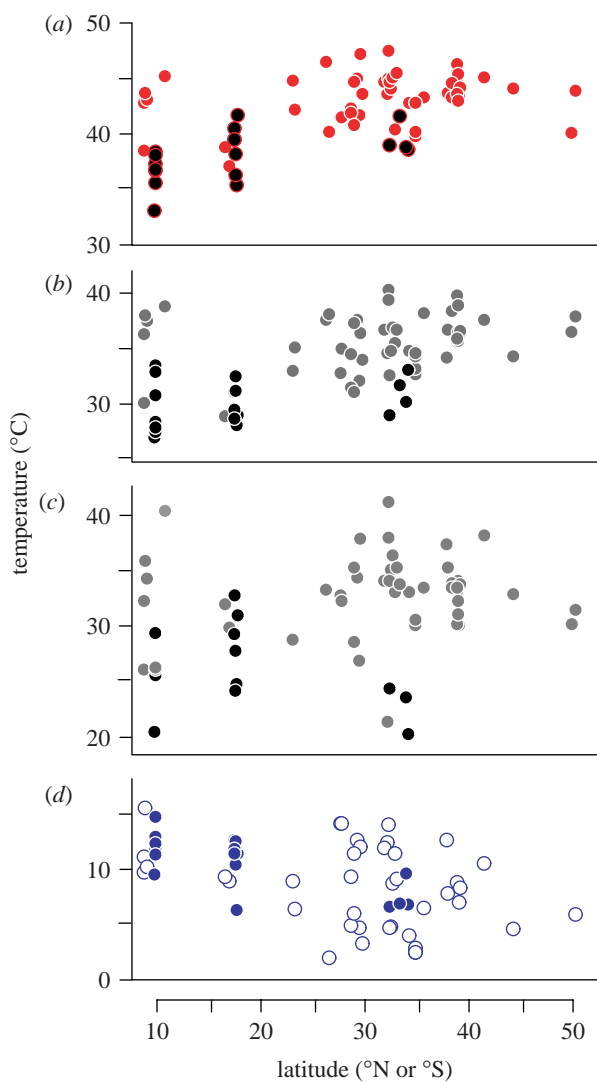


Figure 1. Thermal sensitivity of diurnal lizards versus latitude. (a) Heat tolerance ( $CT_{\max}$ ), (b) optimal sprint temperature ( $T_o$ ), (c) mean-field body temperature ( $T_b$ ) and (d) cold tolerance ( $CT_{\min}$ ) versus latitude. In phylogenetic analyses,  $CT_{\max}$ ,  $T_o$  and  $T_b$  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  $0.5^\circ$  latitude to increase spread (see data in table 1 in the electronic supplementary material).

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  $T_c$  in shade (Deutsch *et al.* 2008). Ideally, shade  $T_c$  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  $T_c$  for

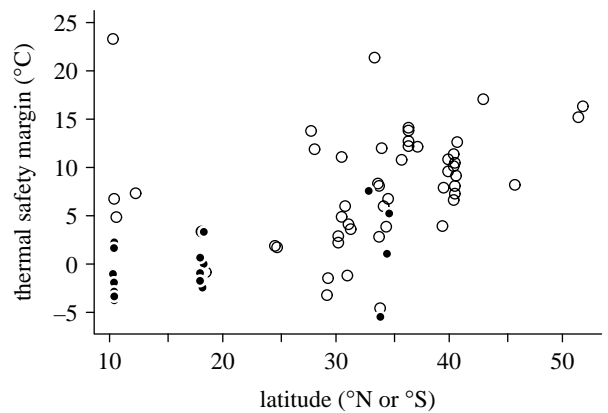


Figure 2. Thermal safety margin ( $T_o - T_{a,\max}$ ) for diurnal lizards increases with latitude. Open circles, basking species; filled circles, non-basking species. In a phylogenetic analysis, thermal safety margin increases with latitude. The tropical species with a large safety margin (*Sceloporus 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  $T_c$  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  $T_c$  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  $T_c$  in shade increases with climate warming; rather, these species may even benefit (Kearney & Porter 2004; Chamailé-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

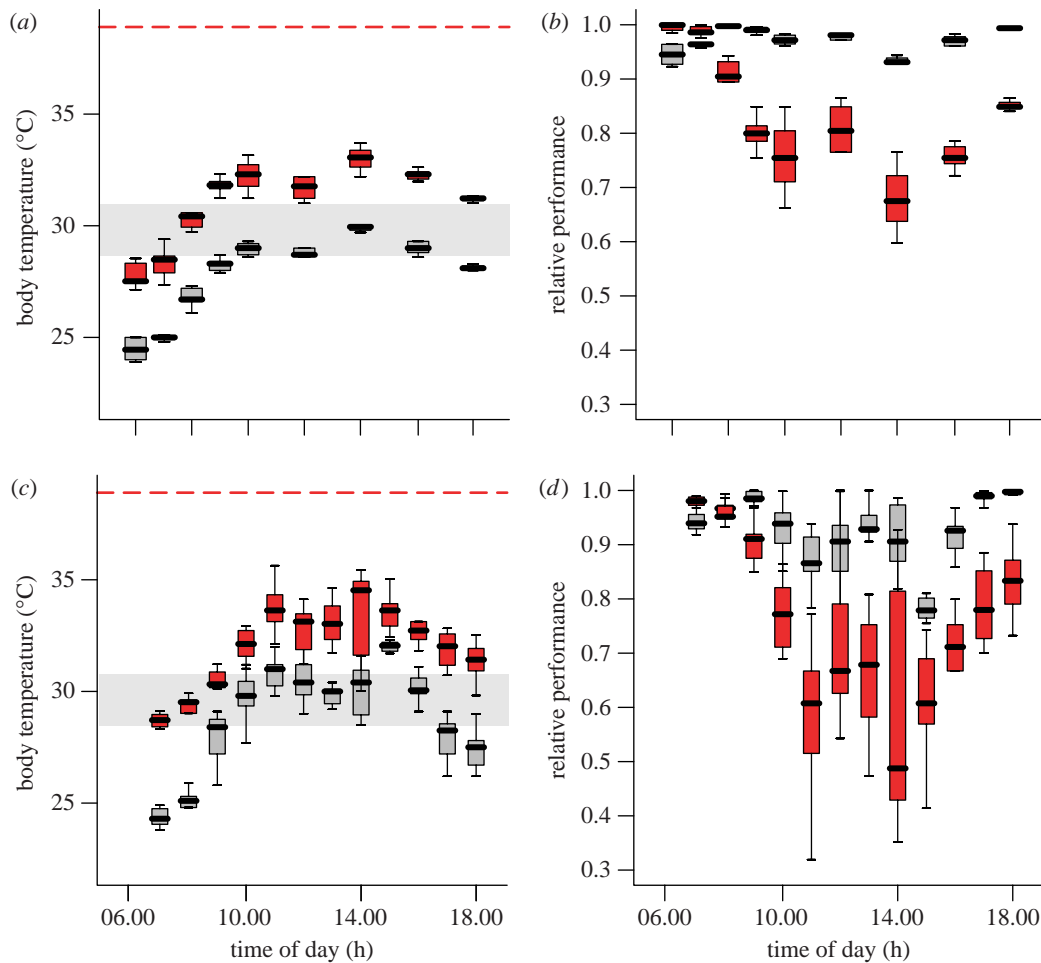


Figure 3. Impact of climate warming on  $T_b$  and performance of a tropical lizard. (a) Body temperature and (b) predicted relative sprint performance of *A. cristatellus* in a shaded forest at Punta Salinas, Puerto Rico before (grey boxes, 1973) and after (red boxes) predicted climate warming (air temperature increase of  $3^\circ\text{C}$ ). (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  $CT_{\text{max}}$  (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  $3^\circ\text{C}$  above levels measured in the early 1970s (Malhi & Wright 2004; IPCC 2007).

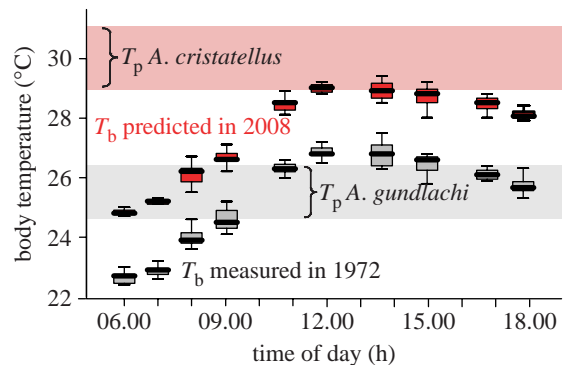


Figure 4. Predicted impact of recent climate warming on a tropical forest lizard. Observed climate warming between 1972 and 2008 (see figure 1 in the electronic supplementary material) is likely to make forest habitats (El Verde, Puerto Rico) less suitable in summer for resident forest species but more 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  $2.1^\circ\text{C}$  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*.

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  $T_e$  of their habitat. During most of the day,  $T_b$  and  $T_e$  were within the lizard's preferred temperature range, and only 20.8 per cent of  $T_b$  (and 7.8% of  $T_e$ ) exceeded that range. If  $T_e$  increases by 3°C, 68.6 per cent of all predicted  $T_b$  records (and 70.6% of all  $T_e$ ) 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  $3.2 \pm 1.06$  and  $5.1 \pm 0.70^\circ\text{C}$ , respectively. As a consequence, mean  $T_b$  during the day in summer (across species) exceeded mean  $T_p$  by  $2.1 \pm 0.43^\circ\text{C}$  on average and exceeded  $T_o$  for sprinting by  $3.9 \pm 1.16^\circ\text{C}$  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  $3.5 \pm 0.90^\circ\text{C}$  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  $T_e$ s would have been too cool for *A. cristatellus* (Gorman & Hillman 1977); 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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## Supplementary Tables 2

Table 2a. Summary thermal statistics (mean  $x \pm SE$ ) for lineages of lizards studied in the macrophysiological analysis. Region refers to the geographic association of species in our sample, not necessarily for the family as a whole. Predominantly tropical lineages are in boldface.

<i>Taxon</i>	<i>Region</i>	$N_{total}$	$N_{bask}$	$T_b$	$CT_{max}$	$T_o$	$CT_{min}$	<i>Safety zone</i>
Agamidae	temperate	3	3	35.5±1.22	45.6±0.79	36.9±0.36	12.2±0.22	10.5±5.48
Anguidae	temperate	1	1	21.4	43.6	34.6	12.4	8.3
Cordylidae	temperate	1	1	28.8	44.8	33.0	8.9	1.9
<b>Gekkonidae</b>	<b>tropical</b>	<b>6</b>	<b>0</b>	<b>29.0±1.34</b>	<b>39.3±0.76</b>	<b>30.3±0.61</b>	<b>11.7±0.33</b>	<b>0.8±0.87</b>
Iguania	widespread	13	13	34.8±0.73	43.5±0.50	36.0±0.66	9.5±1.05	4.9±1.50
Lacertidae	widespread	16	16	32.4±0.38	43.7±0.47	36.8±0.49	6.2±0.57	9.8±1.01
<b>Polychrotidae</b>	<b>tropical</b>	<b>11</b>	<b>4</b>	<b>26.7±0.90</b>	<b>37.2±0.67</b>	<b>29.4±0.61</b>	<b>10.4±0.90</b>	<b>-1.3±0.60</b>
Scincidae	widespread	13	11	30.4±1.53	42.1±0.64	34.1±0.59	6.0±0.91	8.1±1.25
Teiidae	widespread	3	3	38.2±1.30	44.7±0.48	38.1±0.35	13.0±2.04	10.4±3.35
Xantusiidae	widespread	3	0	29.1±3.84	39.6±1.05	31.2±1.15	8.3±1.52	1.3±3.79
Total		70						

**Table 2b.** Field thermal and behavioural data on lizards from specific Neotropical sites. Non-basking species, which occur inside forests, generally outnumber basking species at these sites (8 of 12). Non-basking species always (11 of 11 sites) have lower mean body temperatures ( $T_b$ ), and always have  $T_b$  only slightly elevated above air temperatures  $T_a$  (thus small average absolute( $T_b - T_a$ ), 11 of 11 sites), as would be expected in shaded forest habitats, where convection dominates heat exchange. Data are mean  $\pm$  s.e. (N). For details of field methods used by Vitt and colleagues, see Copeia 2008:142-151.

Locality	behaviour	N species	mean $T_b$ ( $^{\circ}\text{C}$ )	mean $T_a$ ( $^{\circ}\text{C}$ )	abs( $T_b - T_a$ ) ( $^{\circ}\text{C}$ )	Reference
Amazonas, Brazil 3.3°S	non-basking	11	28.4 $\pm$ 0.39 (6)	27.5 $\pm$ 0.23 (6)	1.1 $\pm$ 0.17 (6)	Vitt, unpubl. data
	basking	5	35.2 $\pm$ 1.02 (3)	29.7 $\pm$ 0.32 (3)	5.6 $\pm$ 0.75 (3)	
	<i>% non-basking</i>	68.6				
Barro Colorado Is., Panama 9.1°N	non-basking	19	---	---	---	Rand & Myers 1990
	basking	6	---	---	---	
	<i>% non-basking</i>	76.0	---	---	---	
Belém, Brazil 1.5°S	non-basking	10	28.3 $\pm$ 0.23 (4)	27.9 $\pm$ 0.38 (4)	0.4 $\pm$ 0.17 (4)	Crump 1971; Rand & Humphrey 1968
	basking	11	36.1 $\pm$ 1.03 (6)	29.6 $\pm$ 0.67 (6)	6.5 $\pm$ 0.46	
	<i>% non-basking</i>	47.6				
Caatinga 7.5°S	non-basking	2	32.9 $\pm$ 0.59 (2)	31.3 $\pm$ 1.70 (2)	2.1 $\pm$ 0.64 (2)	Vitt, unpubl. data
	basking	8	36.3 $\pm$ 0.78 (8)	32.0 $\pm$ 0.21 (8)	4.4 $\pm$ 1.30 (2)	
	<i>% non-basking</i>	20.0				
Cuyabeno, Ecuador 0.0°	non-basking	14	27.5 $\pm$ 0.30 (9)	26.2 $\pm$ 0.19 (9)	1.5 $\pm$ 0.13 (9)	Vitt, unpubl. data
	basking	4	32.7 $\pm$ 1.47 (2)	27.9 $\pm$ 0.24 (2)	4.8 $\pm$ 1.30 (2)	
	<i>% non-basking</i>	77.8				

Locality	behaviour	N species	mean $T_b$ (°C)	mean $T_a$ (°C)	abs( $T_b-T_a$ ) (°C)	Reference
Nicaragua 11.1°N	non-basking	7	28.9 ± 0.41 (6)	27.3 ± 0.41 (6)	1.6 ± 0.18 (6)	Vitt, unpubl. data
	basking	1	35.6 (1)	28.9 (1)	6.7 (1)	
	<i>% non-basking</i>	87.5				
Para, Brazil 3.2°S	non-basking	13	29.3 ± 0.33 (8)	27.5 ± 0.30 (8)	1.9 ± 0.26 (8)	Vitt, unpubl. data
	basking	4	35.6 ± 1.35 (4)	28.4 ± 0.38 (4)	7.2 ± 1.00 (4)	
	<i>% non-basking</i>	76.5				
Porto Walter, Brazil 8.3°S	non-basking	16	27.7 ± 0.25 (12)	26.7 ± 0.22 (12)	1.4 ± 0.16 (12)	Vitt, unpubl. data
	basking	3	35.8 ± 0.65 (3)	28.5 ± 0.06 (3)	7.3 ± 0.62 (3)	
	<i>% non-basking</i>	84.2				
Rio Ituxi, Brazil 8.3°S	non-basking	14	28.5 ± 0.62 (7)	26.7 ± 0.29 (7)	1.7 ± 0.38 (7)	Vitt, unpubl. data
	basking	5	34.7 ± 0.81 (5)	29.1 ± 0.43 (5)	5.8 ± 0.35 (5)	
	<i>% non-basking</i>	73.7				
Rondônia, Brazil 10.3°S	non-basking	16	29.5 ± 0.26 (10)	27.7 ± 0.21 (10)	1.9 ± 0.27 (10)	Vitt, unpubl. data
	basking	6	34.6 ± 0.98 (6)	29.8 ± 0.32 (6)	4.8 ± 0.75 (6)	
	<i>% non-basking</i>	72.7				
Roraima, Brazil 2.8°N	non-basking	1	33.9 (1)	29.2 (1)	4.7 (1)	Vitt, unpubl. data
	basking	5	35.9 ± 0.61 (5)	29.4 ± 1.90 (5)	6.6 ± 0.48 (5)	
	<i>% non-basking</i>	16.7				
Roraima, Brazil 3.0°N	non-basking	3	28.3 (1)	26.2 (1)	2.1 (1)	Vitt, unpubl. data
	basking	4	35.1 ± 0.73 (3)	28.2 ± 0.29 (3)	6.9 ± 0.74 (3)	

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**Table 2c. Mean field  $T_b$ , N = 61 species.**

Independent Variables	Model	d from REML	ln ML Likelihood	AIC	AICc
AbsLat	OLS		-176.684	359.367	359.788
	PGLS		-168.312	342.625	343.046
	RegOU	0.7105837	-162.869	333.738	334.452
Bask	OLS		-165.324	336.647	337.068
	PGLS		-165.091	336.181	336.602
	RegOU	0.6095391	-157.722	323.444	324.158
FamCode1	OLS		-153.702	329.404	334.792
	PGLS		-167.232	356.464	361.852
	RegOU	0.3706275	-148.646	321.293	327.793
Bask, AbsLat	OLS		-165.32	338.640	339.354
	PGLS		-164.535	337.071	337.785
	RegOU	0.6245386	-157.533	325.067	326.157
FamCode1, AbsLat	OLS		-153.565	331.129	337.629
	PGLS		-166.765	357.531	364.031
	RegOU	0.88654	-148.638	323.275	331.020
FamCode1, Bask	OLS		-143.930	311.860	318.360
	PGLS		-162.897	349.795	356.295
	RegOU	0.2569374	-141.299	308.597	316.342
FamCode1, Bask, AbsLat	OLS		-143.898	313.796	321.54
	PGLS		-162.199	350.398	358.143
	RegOU	0.2724039	-141.240	310.479	319.610



**Table 2d. CTmin, N = 59 species**

Independent Variables	Model	d from REML	ln ML Likelihood	AIC	AICc
AbsLat	OLS		-150.362	306.725	307.161
	PGLS		-158.583	323.165	323.602
	RegOU	0.2986203	-144.272	296.544	297.284
Bask	OLS		-155.614	317.229	317.665
	PGLS		-162.603	331.205	331.642
	RegOU	0.3283983	-148.282	304.565	305.305
FamCode1	OLS		-142.658	307.316	312.933
	PGLS		-162.280	346.560	352.177
	RegOU	0.2092041	-139.387	302.775	309.557
Bask, AbsLat	OLS		-150.266	308.532	309.273
	PGLS		-158.566	325.133	325.874
	RegOU	0.3101080	-144.257	298.515	299.647
FamCode1, AbsLat	OLS		-138.257	300.515	307.297
	PGLS		-158.181	340.362	347.144
	RegOU	0.2163928	-135.622	297.243	305.332
FamCode1, Bask	OLS		-140.372	304.744	311.526
	PGLS		-162.200	348.400	355.183
	RegOU	0.1496319	-137.634	301.267	309.356
FamCode1, Bask, AbsLat	OLS		-136.629	299.258	307.346
	PGLS		-158.135	342.270	350.359
	RegOU	0.1748034	-134.384	296.767	306.313

**Table 2e. Optimum  $T_b$ ,  $T_o$ ,  $N = 70$ .**

Independent Variables	Model	d from REML	ln ML Likelihood	AIC	AICc
AbsLat	OLS		-174.043	354.086	354.450
	PGLS		-168.322	342.644	343.007
	RegOU	0.6881707	-161.098	330.197	330.812
Bask	OLS		-163.029	332.058	332.422
	PGLS		-167.916	341.832	342.196
	RegOU	0.4849774	-156.145	320.290	320.906
FamCode1	OLS		-142.579	307.158	311.710
	PGLS		-168.066	358.133	362.685
	RegOU	0.09642502	-141.706	307.412	312.885
Bask, AbsLat	OLS		-160.579	329.158	329.773
	PGLS		-167.131	342.263	342.878
	RegOU	0.4859982	-156.119	322.238	323.176
FamCode1, AbsLat	OLS		-142.579	309.158	314.631
	PGLS		-167.268	358.535	364.009
	RegOU	0.1074314	-141.701	309.402	315.902
FamCode1, Bask	OLS		-140.587	305.174	310.647
	PGLS		-167.321	358.642	364.115
	RegOU	0.09033477	-139.898	305.797	312.297
FamCode1, Bask, AbsLat	OLS		-140.531	307.062	313.562
	PGLS		-166.439	358.879	365.379
	RegOU	0.1045310	-139.829	307.657	315.294

**Table 2f.  $CT_{max}$ , N = 70 species**

Independent Variables	Model	d from REML	ln ML Likelihood	AIC	AICc
AbsLat	OLS		-165.274	336.547	336.911
	PGLS		-166.201	338.402	338.765
	RegOU	0.5506289	-156.089	320.178	320.793
Bask	OLS		-153.749	313.498	313.862
	PGLS		-163.098	332.196	332.560
	RegOU	0.3625394	-147.849	303.698	304.313
FamCode1	OLS		-141.618	305.237	309.789
	PGLS		-165.166	352.332	356.884
	RegOU	0.1318155	-140.092	304.185	309.659
Bask, AbsLat	OLS		-149.951	307.903	308.518
	PGLS		-162.290	332.580	333.196
	RegOU	0.2825182	-145.521	301.042	301.980
FamCode1, AbsLat	OLS		-140.258	304.515	309.989
	PGLS		-164.330	352.661	358.134
	RegOU	0.1237131	-138.613	303.225	309.725
FamCode1, Bask	OLS		-133.872	291.743	297.217
	PGLS		-162.520	349.041	354.515
	RegOU	0.05370689	-132.899	291.798	298.298
FamCode1, Bask, AbsLat	OLS		-133.140	292.281	298.781
	PGLS		-161.738	349.477	355.977
	RegOU	0.06321541	-132.075	292.149	299.786

**Table 2g. Safety margin, N = 70 species**

Independent Variables	Model	d from REML	ln ML Likelihood	AIC	AICc
AbsLat	OLS		-217.532	441.065	441.428
	PGLS		-256.192	518.384	518.747
	RegOU	e-010	-217.450	442.900	443.515
Bask	OLS		-216.567	439.133	439.497
	PGLS		-256.055	518.111	518.475
	RegOU	e-008	-216.356	440.712	441.327
FamCode1	OLS		-207.576	437.152	441.703
	PGLS		-256.145	534.291	538.842
	RegOU	e-011	-207.553	439.105	444.579
<b>Bask, AbsLat</b>	<b>OLS</b>		<b>-212.888</b>	<b>433.776</b>	<b>434.392</b>
	PGLS		-255.991	519.982	520.598
	RegOU	e-009	-212.744	435.488	436.426
FamCode1, AbsLat	OLS		-207.004	438.007	443.481
	PGLS		-256.081	536.163	541.636
	RegOU	e-012	-207.008	440.015	446.515
FamCode1, Bask	OLS		-206.527	437.054	442.528
	PGLS		-255.954	535.908	541.382
	RegOU	e-011	-206.503	439.007	445.507
FamCode1, Bask, AbsLat	OLS		-206.148	438.295	444.795
	PGLS		-255.898	537.796	544.296
	RegOU	e-011	-206.148	440.295	447.932

**Table 2h.** Thermal data for species of *Sphaerodactylus* in Puerto Rico (Álvarez 1992).  $T_b$  = mean body temperature (range),  $T_e$  = mean operative temperature,  $T_p$  = preferred body temperature,  $T_o$  = optimal temperature for sprinting,  $CT_{max}$  = critical thermal maximum. Also reported are deviations between various temperatures (e.g.,  $T_e - T_p$ ). Mean  $T_b$  and  $T_e$  are usually several degrees above  $T_p$  or  $T_o$ , suggesting that these geckos were experiencing above optimal and probably stressful temperatures during the day in summer.

<b>Trait</b>	<i>S. roosevelti</i> (Guanica)	<i>S. townsendi</i> (Fajardo)	<i>S. nicholsi</i> (Guanica)	<i>S. microlepis</i> (Isabela)	
$T_b$	32.8 (28.2-37.5)	31.0 (27.6-35.3)	32.8 (28.2-36.9)	30.3 (28.9-31.8)	
$T_e$	33.1	36.3	33.1	35.1	
$T_p$	30.2 ± 1.2	30.2 ± 1.5	30.2 ± 1.2	28.1 ± 1.6	
$T_o$	29.2 ± 1.3	29.6 ± 1.4	29.2 ± 1.4	29.3 ± 1.6	
$CT_{max}$	39.5 ± 0.8	42.1 ± 0.5	39.5 ± 0.5	39.5 ± 0.5	
<b>Deviation</b>					<b>Mean deviation</b>
$T_b - T_p$	2.6	0.8	2.6	2.2	<b>2.1</b>
$T_b - T_o$	3.6	1.4	3.6	7	<b>3.9</b>
$T_e - T_p$	2.9	6.1	2.9	1	<b>3.2</b>
$T_e - T_o$	3.9	6.7	3.9	5.8	<b>5.1</b>

## Phylogenetic information

General phylogenetic relations follow the supertree for squamate reptiles in Wiens et al. (2006), with additions. *Anolis* relationships follow Nicholson et al. (2005). *Sceloporus* follow Leaché (2008). Lacertids follow Fu(2000) and (Oliverio et al. 2000). Skink relationships are uncertain (T. Reeder, 2008 personal communication): we follow Rabosky (2007), but note that other relationships have been proposed for some Australian genera (Reeder 2003; Skinner 2007). *Eulamprus* relationships follow O'Connor and Moritz (2003). *Sphaerodactylus* relationships are from Haas (1996) modified by unpublished data (C. Haas, 2008 personal communication).

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Phylogenetic tree used for analyses. The file below (**ALL70.PDI**) was produced by the DOS PDTREE.EXE program (Garland et al., 1993, 1999), available on request from Theodore Garland, Jr. (<http://www.biology.ucr.edu/people/faculty/Garland/PDAP.html>). The program PDDIST.EXE was then used to produce the phylogenetic matrix (ALL70.DSC) used in the Matlab programs PHYSIG\_LL.m and REGRESSIONv2.m (Blomberg et al., 2003; Lavin et al., 2008) (<http://www.biology.ucr.edu/people/faculty/Garland/PHYSIG.html>).

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A2	\$\$	0.0000000000E+00
A3	A2	5.0000000000E+00
A4	A3	9.0000000000E+01
E1	A4	1.4300000000E+02
A6	A4	5.0000000000E+00
A7	A6	1.3300000000E+02
A8	A7	4.0000000000E+00
LB	A8	1.0000000000E+00
Lk	A8	1.0000000000E+00
Ts	A7	5.0000000000E+00
AC	A6	1.5000000000E+01
AD	AC	8.3000000000E+01
a1	AD	4.0000000000E+01
AF	AD	5.0000000000E+00
AG	AF	1.0000000000E+01
tr	AG	2.5000000000E+01
AI	AG	5.0000000000E+00
Ai	AI	2.0000000000E+01
AK	AI	5.0000000000E+00
AL	AK	1.0000000000E+01
Ah	AL	5.0000000000E+00
cu	AL	5.0000000000E+00
AO	AK	5.0000000000E+00
mu	AO	1.0000000000E+01
AQ	AO	5.0000000000E+00
li	AQ	5.0000000000E+00
Al	AQ	5.0000000000E+00
AT	AF	2.0000000000E+01
Ag	AT	1.5000000000E+01
AV	AT	1.0000000000E+01
Ac	AV	5.0000000000E+00
ck	AV	5.0000000000E+00
AY	AC	8.8000000000E+01
AZ	AY	5.0000000000E+00
Gw	AZ	3.0000000000E+01
Dd	AZ	3.0000000000E+01
B2	AY	5.0000000000E+00
Um	B2	3.0000000000E+01
B4	B2	2.5000000000E+00
Us	B4	2.7500000000E+01
B6	B4	2.5000000000E+00
B7	B6	5.0000000000E+00
B8	B7	5.0000000000E+00
B9	B8	5.0000000000E+00
BA	B9	5.0000000000E+00

BB	BA	4.0000000000E+00
Su	BB	1.0000000000E+00
Sc	BB	1.0000000000E+00
BE	BA	4.0000000000E+00
So	BE	1.0000000000E+00
oc	BE	1.0000000000E+00
ch	B9	1.0000000000E+01
Sg	B8	1.5000000000E+01
BJ	B7	1.9000000000E+01
bo	BJ	1.0000000000E+00
SM	BJ	1.0000000000E+00
Sv	B6	2.5000000000E+01
BN	A3	5.5000000000E+01
BO	BN	6.0000000000E+01
BP	BO	1.0300000000E+02
Af	BP	1.5000000000E+01
BR	BP	5.0000000000E+00
Cm	BR	1.0000000000E+01
At	BR	1.0000000000E+01
BU	BO	3.0000000000E+01
BV	BU	4.0000000000E+01
BW	BV	3.8000000000E+01
BX	BW	5.0000000000E+00
Pa	BX	5.0000000000E+00
Ph	BX	5.0000000000E+00
C0	BW	5.0000000000E+00
Gy	C0	5.0000000000E+00
Gs	C0	5.0000000000E+00
C3	BV	4.3000000000E+01
Tp	C3	5.0000000000E+00
Tx	C3	5.0000000000E+00
C6	BU	4.0000000000E+01
Ae	C6	4.8000000000E+01
C8	C6	5.0000000000E+00
C9	C8	1.8000000000E+01
CA	C9	5.0000000000E+00
CB	CA	1.0000000000E+01
CC	CB	5.0000000000E+00
hh	CC	5.0000000000E+00
bc	CC	5.0000000000E+00
oa	CB	1.0000000000E+01
ou	CA	2.0000000000E+01
if	C9	2.5000000000E+01
CI	C8	2.8000000000E+01
Lm	CI	1.5000000000E+01
CK	CI	5.0000000000E+00
CL	CK	5.0000000000E+00
La	CL	5.0000000000E+00
Rt	CL	5.0000000000E+00
Zv	CK	1.0000000000E+01
CP	BN	1.6000000000E+01
CQ	CP	1.3700000000E+02
CR	CQ	1.0000000000E+01
CS	CR	1.0000000000E+01
Pb	CS	5.0000000000E+00
Pe	CS	5.0000000000E+00
CV	CR	5.0000000000E+00



Ew	CV	1.0000000000E+01
CX	CV	5.0000000000E+00
N1	CX	5.0000000000E+00
N2	CX	5.0000000000E+00
D0	CQ	5.0000000000E+00
D1	D0	1.5000000000E+01
Hd	D1	5.0000000000E+00
Hp	D1	5.0000000000E+00
D4	D0	5.0000000000E+00
D5	D4	5.0000000000E+00
Et	D5	1.0000000000E+01
D7	D5	5.0000000000E+00
Ek	D7	5.0000000000E+00
Eq	D7	5.0000000000E+00
DA	D4	5.0000000000E+00
Cr	DA	1.0000000000E+01
DC	DA	5.0000000000E+00
ta	DC	5.0000000000E+00
Cu	DC	5.0000000000E+00
DF	CP	1.3700000000E+02
Pi	DF	2.5000000000E+01
DH	DF	1.5000000000E+01
Lf	DH	1.0000000000E+01
DJ	DH	5.0000000000E+00
Xr	DJ	5.0000000000E+00
Xv	DJ	5.0000000000E+00
DM	A2	2.1800000000E+02
DN	DM	5.0000000000E+00
DO	DN	5.0000000000E+00
DP	DO	5.0000000000E+00
St	DP	5.0000000000E+00
Sn	DP	5.0000000000E+00
Sk	DO	1.0000000000E+01
ga	DN	1.5000000000E+01
DU	DM	1.5000000000E+01
ml	DU	5.0000000000E+00
Sr	DU	5.0000000000E+00

E1	0E+01	0E+01
LB	0E+01	0E+01
Lk	0E+01	0E+01
Ts	0E+01	0E+01
a1	0E+01	0E+01
tr	0E+01	0E+01
Ai	0E+01	0E+01
Ah	0E+01	0E+01
cu	0E+01	0E+01
mu	0E+01	0E+01
li	0E+01	0E+01
Al	0E+01	0E+01
Ag	0E+01	0E+01
Ac	0E+01	0E+01
ck	0E+01	0E+01
Gw	0E+01	0E+01
Dd	0E+01	0E+01
Um	0E+01	0E+01
Us	0E+01	0E+01

Su	0E+01	0E+01
Sc	0E+01	0E+01
So	0E+01	0E+01
oc	0E+01	0E+01
ch	0E+01	0E+01
Sg	0E+01	0E+01
bo	0E+01	0E+01
SM	0E+01	0E+01
Sv	0E+01	0E+01
Af	0E+01	0E+01
Cm	0E+01	0E+01
At	0E+01	0E+01
Pa	0E+01	0E+01
Ph	0E+01	0E+01
Gy	0E+01	0E+01
Gs	0E+01	0E+01
Tp	0E+01	0E+01
Tx	0E+01	0E+01
Ae	0E+01	0E+01
hh	0E+01	0E+01
bc	0E+01	0E+01
oa	0E+01	0E+01
ou	0E+01	0E+01
if	0E+01	0E+01
Lm	0E+01	0E+01
La	0E+01	0E+01
Rt	0E+01	0E+01
Zv	0E+01	0E+01
Pb	0E+01	0E+01
Pe	0E+01	0E+01
Ew	0E+01	0E+01
N1	0E+01	0E+01
N2	0E+01	0E+01
Hd	0E+01	0E+01
Hp	0E+01	0E+01
Et	0E+01	0E+01
Ek	0E+01	0E+01
Eq	0E+01	0E+01
Cr	0E+01	0E+01
ta	0E+01	0E+01
Cu	0E+01	0E+01
Pi	0E+01	0E+01
Lf	0E+01	0E+01
Xr	0E+01	0E+01
Xv	0E+01	0E+01
St	0E+01	0E+01
Sn	0E+01	0E+01
Sk	0E+01	0E+01
ga	0E+01	0E+01
ml	0E+01	0E+01
Sr	0E+01	0E+01

## DETAILS OF METHODS

### *Macrophysiological analyses*

To quantify the thermal dependence of sprinting, we fit curves (Deutsch et al. 2008) to mean speeds at each  $T_b$  interval to curves and estimated the optimal temperature ( $T_o$ ) for sprinting. Most studies used similar protocols. For example, all estimates of  $CT_{max}$  and  $CT_{min}$  used loss of the righting response as the endpoint, and most used heating or cooling rates of 0.5°C to 1°C/min. Inevitably, methodological variation remains (Lutterschmidt & Hutchison 1997; Chown et al. 2008), especially with regard to length and temperatures of acclimation. Such residual variation should only add noise rather introduce systematic error (van Berkum 1988; Chown et al. 2003; Ives et al. 2007).

We did not partition data within species by sex because sexes of lizards rarely differ in field  $T_b$  and related measures (Huey & Pianka 2007). Furthermore, only one study reported sex-specific results for locomotion (Lailvaux et al. 2003). [For this species we used an un-weighted average of sexes.] Multiple populations (Garland & Adolph 1991) were sampled for a few species (e.g., *Sceloporus undulatus*). For these we included only the two most geographically divergent populations.

As mentioned in the text, we used three models to look at relationships involving thermal traits, latitude, basking, and lineage: least squares (OLS), phylogenetic generalized least squares (PGLS); and regression in which residuals

were modelled as having evolved via an Ornstein-Uhlenbeck process (RegOU). The RegOU models contains an additional parameter,  $d$ , which estimates the transformation of the phylogenetic branch lengths (Blomberg et al. 2003; Lavin et al. 2008), and hence its fit can be compared with the OLS or GLS models by a  $\ln$  maximum likelihood ratio test, where twice the difference in the  $\ln$  maximum likelihood is assumed to be distributed asymptotically as a  $\chi^2$  with 1 d.f., for which the critical value at  $\alpha = 0.05$  is 3.841. Similar tests were used to compare the fit of models within the OLS, PGLS or RegOU classes when they contained nested subsets of independent variables. As a heuristic indicator of model support, we report the Akaike Information Criterion (AIC), where  $AIC = (-2 * \ln \text{maximum likelihood}) + (2 * \# \text{ of parameters})$ . Because sample sizes were relatively small, we also computed the AICc (Burnham & Anderson 2002), which in all cases gave results consistent with AIC.

When determining the best-fit model from a set of models, nested or not, we follow Burnham and Anderson (2002) and select the one with the lowest AIC and do not report specific  $P$  values of component variables. [Note: readers wishing  $P$  values can calculate them from the likelihoods ( $\ln$  likelihood ratio tests) of the models. In any case, all variables included in the best-fitting models were statistically significant ( $P < 0.05$ ) via partial- $F$  tests.] As a rule of thumb, models whose AIC was within 2 units of the best model were considered to have substantial support (Burnham & Anderson 2002). Note that maximum likelihoods

were used for computing AIC and likelihood ratio tests, whereas REML was used for estimating coefficients in the model. REML estimates of the OU transformation parameter,  $d$ , are also reported. All of the regression models (results in electronic supplemental materials, tables 2c-g) were computed using the Matlab Regressionv2.m program of Lavin et al. (2008), available on request from T.G.

### ***Focal-species analyses of Puerto Rican lizards***

Details on field and laboratory methods for *A. cristatellus* at Punta Salinas are found in Huey (1974) and Huey and Webster (1976). Field data for 1973 are from one day in July. However, mean  $T_b$  in 1973 differed by less than  $0.1^\circ\text{C}$  from that of a full-day sample in July 1972 (Huey & Webster 1976).

Field  $T_{bs}$  of *Sphaerodactylus* were measured between 0930 and 1430 h, and  $T_{es}$  were measured between 0900 and 1600 h. The thermal dependence of sprint speed was measured in a 2-m racetrack.  $CT_{\max}$ , and  $CT_{\min}$ ,  $T_b$ , and  $T_p$  were measured using standard procedures (Huey & Webster 1976).

### ***Predicting $T_b$ and relative performance after climate warming***

Predicting the change in  $T_b$  of a basking lizard (following warming of  $T_a$ ) requires a biophysical model (Kearney et al. 2009), as radiation often dominates

overall heat exchange. For the *Anolis* lizards studied here, predicting the change in  $T_b$  does not require biophysics because these lizards are thermoconformers (Huey 1974). This is evident both from field observations of the infrequency of basking behaviour in these lizards (Huey 1974; Huey & Webster 1976; Hertz 1992), as well as from the 1:1 regressions of  $T_b$  on  $T_a$ .

<b>Population</b>	<b>Intercept <math>\pm</math> S.E.</b>	<b>Slope <math>\pm</math> S.E.</b>	<b>R<sup>2</sup></b>
<i>A. cristatellus</i> Pta. Salinas	-1.50 $\pm$ 0.817	1.08 $\pm$ 0.03	0.936
<i>A. cristatellus</i> San German	1.85 $\pm$ 1.670	1.00 $\pm$ 0.062	0.681
<i>A. gundlachi</i> El Verde	0.22 $\pm$ 0.589	1.00 $\pm$ 0.024	0.944

Therefore, we could use field data from 1973 and the above regression to predict  $T_b$ s following a hypothetical 3°C increase in  $T_a$ s. Relative sprint performance versus  $T_b$  was estimated by fitting a normal X exponential curve (Deutsch et al. 2008). Using this curve, we predicted relative sprint speed at different times of day (Huey 1983) before and after warming.

For *A. cristatellus* at San German, We computed a regression of hourly mean  $T_b$  on hourly mean  $T_e$  ( $T_b = -0.01 + 1.02 * T_e$ ,  $R^2 = 0.924$ ), and then predicted  $T_b$  and relative performance before and after warming. Thermal preference shows no significant geographic variation (Huey & Webster 1976), and so we used  $T_p$ s from Pta. Salinas.

To predict  $T_b$  of *A. gundlachi* in 2008, we used actual weather records from El Verde to estimate the average change in maximum July temperature (see main text) from 1975 to 2008; this was 2.1°C (see main text). We then increased each  $T_a$  from 1972 by 2.1°C and used the above regression equation to predict the new  $T_b$ .

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**Fig. 1. Observed climate warming at El Verde, Puerto Rico**

Mean maximum temperature in July (summer) has increased significantly ( $-104.3 + 0.066 \cdot \text{year}$ ,  $P < 0.001$ ) between 1975 and 2007. Mean minimum temperature in July (not show) has also increased significantly ( $-39.95 + 0.031 \cdot \text{year}$ ,  $P = 0.001$ ). [Note: the URL indicates that data are substituted for several years. If these records are excluded, the pattern is very similar (maximum:  $-110.1 + 0.069 \cdot \text{year}$ ,  $P = 0.003$ ; minimum:  $-27.9 + 0.025 \cdot \text{year}$ ).] Data from <http://luq.lternet.edu/data/lterdb17/metadata/lterdb17.htm>.

