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 tolerant 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
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 $T_i$ for lizards from 12 neotropical sites (available as table 2 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) were used to estimate $T_b$ from 12 neotropical sites.

We computed regressions in three ways (reviews in Garland et al. 2005; Lavín 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 (Lavín 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 $T_i$, 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 $T_b$ records (Hertz et al. 1993).

Field data for $T_{bs}$ and operative temperatures ($T_e$) were obtained for A. cristatellus at San German in August 1983 (Hertz 1992). $T_{bs}$ 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 $T_{bs}$ from Punta Salinas.

Field data for $T_b$ and $T_i$ of Anolis gundlachi from El Verde were obtained in July 1972, and $T_b$ were obtained in 1973 (Huey & Webster 1976). Long-term weather records are available for this site (http://luq.lternet.edu/data/iterdb16/data/evtemp.htm), enabling us to estimate the actual shift in mean July maximum temperature from 1975 to 2008. The predicted shift in $T_b$ 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 2 in the electronic supplementary material). Basic techniques for obtaining $T_{bs}$ and $T_{es}$ followed Hertz (1992), except that small polyvinyl chloride cylinders ($n = 27$) were used to estimate $T_{bs}$.

### 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 ($T_{es}$) 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 $T_i$ (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 $T_{es}$ 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 \( T_{bs} \)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 \( T_{bs} \)s 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 \( T_{bs} \)s of tropical forest lizards averaged 6°C lower than that of tropical-open-habitat lizards (\( t \)-test, \( p \ll 0.001\); 28.9 ± 0.31°C (\( n = 38 \)) and 34.9 ± 0.51°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 \( T_{bs} \) species or open-edge dwelling, basking and high \( T_{bs} \) 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 \( \chi^2 \)-tests, both \( p \ll 0.01 \)).) Moreover, lineages in the tropics that include predominately forest-dwelling and low \( T_{bs} \) 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 \( T_{bs} \) species (e.g. Teiidae) often extend into the temperate zone.

Overall, most temperate-zone lizards are baskers, whereas tropical species can be either baskers on non-baskers. Moreover, these different ‘thermal syndromes’ tend to run in families. Exceptions do exist. A few temperate lineages are cryptozoic and have low \( T_{bs} \) (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 \( T_{bs} \)s simply because lowland tropical sites are always warm, were surprised to find that some tropical species were in fact active at \( T_{bs} \)s well below those of most temperate-zone species (Brattstrom 1965). We evaluated field \( T_{bs} \)s for species from diverse latitudes (figure 1c). In an ordinary least-squares analysis, which assumes a star phylogeny (Garland et al. 1992), \( T_{bs} \) increased with latitude (two-tailed \( p = 0.0145 \); see table 2c in the electronic supplementary material). However, field \( T_{bs} \) showed a strong phylogenetic signal (Blomberg et al. 2003; \( p = 0.007 \)), and the best-fit regression model (RegOU) for \( T_{bs} \) excluded latitude but included basking and family membership. Thus, the non-phylogenetic trend probably stems from the many non-basking, low \( T_{bs} \) 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 (\( T_o \); 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 (\( p < 0.001 \)), 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 \( T_{bs} \), the non-phylogenetic trend with latitude may be a consequence of the tropical concentration of non-basking taxa.

Note that \( T_{bs} \), \( T_o \) 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 \( T_{bs} \) and can simultaneously avoid stressfully high temperatures. Consequently, mean \( T_{bs} \) (herein) and also maximal \( T_{bs} \) (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 \( T_{bs} \), \( T_o \) 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. \( T_{bs} \), \( CT_{max} \)) 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 \( T_{bs} \) and \( CT_{max} \)) but also on whether current \( T_{bs} \)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 \( T_{bs} \)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 \( T_{bs} \)s in shade are currently equal to or greater
Figure 1. Thermal sensitivity of diurnal lizards versus latitude. (a) Heat tolerance ($CT_{\text{max}}$), (b) optimal sprint temperature ($T_o$), (c) mean-field body temperature ($T_b$) and (d) cold tolerance ($CT_{\text{min}}$) versus latitude. In phylogenetic analyses, $CT_{\text{max}}$ $T_o$ 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, $CT_{\text{min}}$ decreases with latitude. The four 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 $T_e$ 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 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 $T_o$, $T_b$ and $CT_{\text{max}}$ 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...
on tree trunks, does not bask and is a thermoconformer, such that \( T_b \) closely matches \( T_a \), and thus \( T_e \) (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 \( T_{bs} \) 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 \( T_{bs} \) 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 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.

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### 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. \( T_{bs} \) of the forest species (\( A. \) gundlachi) in July 1972 are shown in grey boxes, and most \( T_{bs} \) 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 $T_e$ 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 thermoformers. Their $T_{bs}$ averaged only $0.6 \pm 0.09°C$ 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 $T_b$ 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 $T_e$ 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 $T_b$ 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); 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 $T_b$s 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 Tfas 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. 2009; 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 Tc. 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 Tfas and T8s 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; Helmscht 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), Tfas, 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.

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