

# Why tropical forest lizards are vulnerable to climate warming

Raymond B. Huey<sup>1,\*</sup>, Curtis A. Deutsch<sup>2</sup>, Joshua J. Tewksbury<sup>1</sup>, Laurie J. Vitt<sup>3</sup>, Paul E. Hertz<sup>4</sup>, Héctor J. Álvarez Pérez<sup>5</sup> and Theodore Garland Jr<sup>6</sup>

<sup>1</sup>Department of Biology, University of Washington, PO Box 351800, Seattle, WA 98195, USA

<sup>2</sup>Department of Atmospheric and Oceanic Science, University of California, Los Angeles, CA 90095, USA

<sup>3</sup>Sam Noble Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, OK 73072, USA

<sup>4</sup>Department of Biology, Barnard College, New York, NY 10027, USA

<sup>5</sup>Faculty of Education, University of Puerto Rico, Rio Piedras, PR 00931, USA

<sup>6</sup>Department of Biology, University of California, Riverside, CA 92521, USA

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*. 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.* in press).

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.* in press). 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

\* Author for correspondence (hueyrb@u.washington.edu).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.1957> or via <http://rspb.royalsocietypublishing.org>.

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.* in press). Given the huge diversity of ectotherms in the tropics, the implications of these consistent patterns are daunting.

## 2. MATERIAL AND METHODS

### (a) Macrophysiological analyses

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

We include independent field data on habitat association (forest and open), thermoregulatory behaviour (basking and non-basking),  $T_b$  and  $T_a$  for lizards from 12 Neotropical sites (available as table 2b in the electronic supplementary material). Most sites were approximately  $1.5 \times 1.5$  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

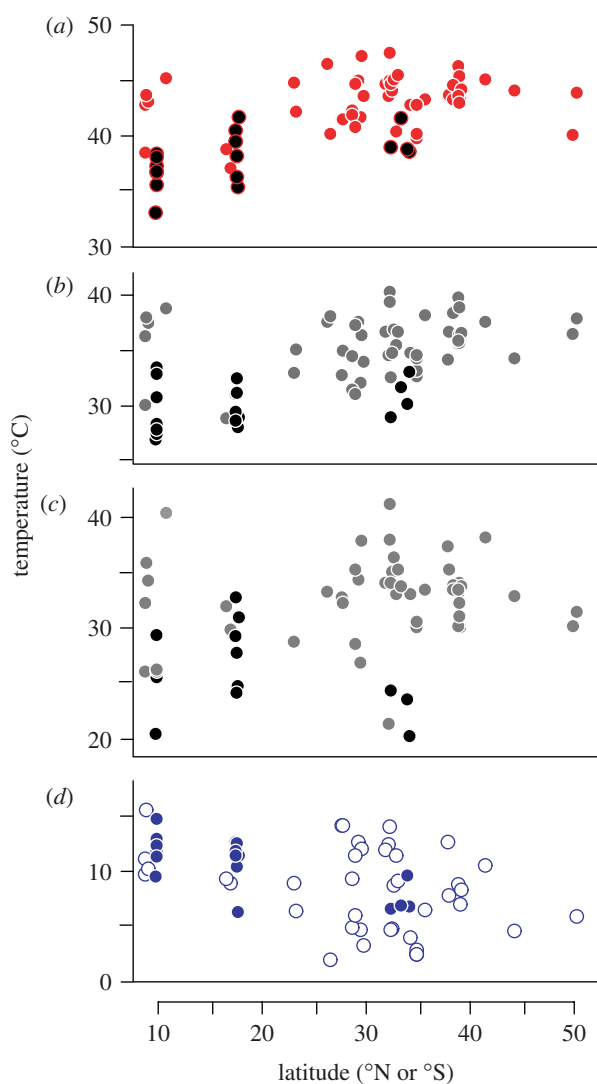


Figure 1. Thermal sensitivity of diurnal lizards versus latitude. (a) Heat tolerance ( $CT_{max}$ ), (b) optimal sprint temperature ( $T_b$ ), (c) mean-field body temperature ( $T_b$ ) and (d) cold tolerance ( $CT_{min}$ ) versus latitude. In phylogenetic analyses,  $CT_{max}$ ,  $T_b$  and  $T_b$  are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

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

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

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

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

These linkages appear to have phylogenetic and latitudinal components. Different Neotropical lineages tend to comprise either predominately forest-dwelling, non-basking and low  $T_b$  species or open-edge dwelling, basking and high  $T_b$  species (see table 2a in the electronic supplementary material). (Note: these families show significant heterogeneity in percentages of basking and forest-dwelling species (non-phylogenetic  $\chi^2$ -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 (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  $T_b$  (e.g. Anguinae; Kingsbury 1994; Xantusiidae; Mautz et al. 1992; some Scincidae; Bennett & John-Alder 1986; Shine 1999). Also, some tropical families and species (e.g. *A. cristatellus*) include both types. However, we are confident that these trends are general, at least for New World lizards.

### (b) Field body temperatures

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

### (c) Lizard thermal sensitivity

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

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

385  $T_o$  and  $CT_{max}$  are elevated for basking species versus non-  
 386 baskers and differ among taxa. As with  $T_b$ , the  
 387 non-phylogenetic trend with latitude may be a conse-  
 388 quence of the tropical concentration of non-basking taxa.

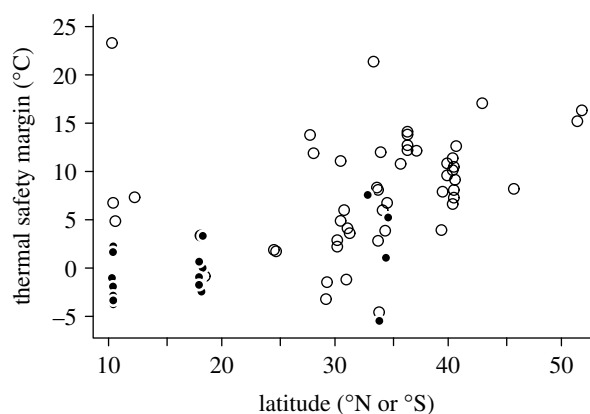
389 Note that  $T_b$ ,  $T_o$  and  $CT_{max}$  appear independent of  
 390 latitude but are associated with basking behaviour and  
 391 with taxon, whereas  $CT_{min}$  is independent of basking and  
 392 taxon and depends only on latitude. These contrasting  
 393 associations might reflect differential effectiveness of  
 394 behaviour in buffering climate-associated selection on  
 395 these thermal traits (van Berkum 1988). When active,  
 396 a thermoregulating lizard in an open habitat at any latitude  
 397 can usually achieve some control over its  $T_b$  and can  
 398 simultaneously avoid stressfully high temperatures.  
 399 Consequently, mean  $T_b$  (herein) and also maximal  $T_b$   
 400 (van Berkum 1988, p. 335) are generally independent of  
 401 latitude (but see, Clark & Kroll 1974), but do tend to  
 402 show strong phylogenetic conservatism (Huey 1982;  
 403 Hertz *et al.* 1983) and a strong association with habitat  
 404 and basking behaviour (herein, Ruibal 1961; Clark &  
 405 Kroll 1974). Because  $T_b$ ,  $T_o$  and  $CT_{max}$  are likely to be  
 406 co-adapted traits (Huey & Bennett 1987; Huey &  
 407 Kingsolver 1993; Angilletta *et al.* 2006; Martin & Huey  
 408 2008; Angilletta 2009), we are not surprised that these  
 409 thermal traits were closely associated with phylogenetic  
 410 affinities and basking behaviour.

411 By contrast, a lizard hibernating at high latitude in a  
 412 winter refuge has relatively few options for behavioural  
 413 thermoregulation. Consequently, temperatures of high-  
 414 latitude lizards in winter (and  $CT_{min}$ ) should decline with  
 415 latitude (van Berkum 1988; Kearney *et al.* in press). Thus,  
 416 thermoregulatory behaviour may buffer selection (Bogert  
 417 1949; van Berkum 1988; Huey *et al.* 2003) on some  
 418 thermal traits (e.g.  $T_b$ ,  $CT_{max}$ ), but not on all ( $CT_{min}$ ).

#### 420 (d) Some tropical lizards have narrow thermal 421 safety margins

422 Whether climate warming is detrimental depends not only  
 423 on the heat tolerance of species (i.e. on  $T_o$  and  $CT_{max}$ ) but  
 424 also on whether current  $T_e$ s (Roughgarden *et al.* 1981;  
 425 Bakken 1992) are already high relative to an ectotherm's  
 426  $T_o$  (Tracy & Christian 1983; Huey 1991; Deutsch *et al.*  
 427 2008). If  $T_e$ s in shaded microenvironments are below an  
 428 ectotherm's  $T_o$  and if shade is readily accessible,  
 429 ectotherms confronting climate warming can find thermal  
 430 refugia and thus remain active (Kearney *et al.* in press).  
 431 However, if  $T_e$ s in shade are currently equal to or greater  
 432 than an ectotherm's  $T_o$ , climate warming will force  
 433 ectotherms to retreat below ground or tolerate activity at  
 434 a high  $T_b$  (Dunham 1993), which will probably induce  
 435 stress and reduce performance (Huey 1983). If time  
 436 restrictions and performance declines are substantive, the  
 437 population might go extinct (Dunham 1993; Kearney  
 438 *et al.* in press).

439 We quantified potential access to an above-ground  
 440 thermal refuge by computing a 'thermal safety margin',  
 441 which is the difference between a lizard's  $T_o$  for sprinting  
 442 and the maximal  $T_e$  in shade (Deutsch *et al.* 2008). Ideally,  
 443 shade  $T_e$  should be calculated for lizards on a global scale  
 444 (Kearney *et al.* in press), but here we substituted mean  
 445 maximal daytime air temperature ( $T_{a,max}$ ) during the  
 446 warmest three months of the year (New *et al.* 2002).  
 447  $T_{a,max}$  will closely approximate the maximal average  $T_e$  for  
 448 small ectotherms in shade (Rogowitz 1996), because



449  
450  
451  
452  
453  
454  
455  
456  
457  
458  
459  
460  
461  
462  
463  
464  
465  
466  
467  
468  
469  
470  
471  
472  
473  
474  
475  
476  
477  
478  
479  
480  
481  
482  
483  
484  
485  
486  
487  
488  
489  
490  
491  
492  
493  
494  
495  
496  
497  
498  
499  
500  
501  
502  
503  
504  
505  
506  
507  
508  
509  
510  
511  
512

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.

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.* in press), and thus  $T_{a,max}$  is a relevant index.

Thermal safety margins showed only a weak phylogenetic signal ( $p=0.09$ ). OLS regression was the best-fit model (see table 2g in the electronic supplementary material), and safety margin increased with latitude and basking (figure 2). Thermal safety margins are thus small—and sometimes even slightly negative—for most tropical forest lizards. Because these forest species live in already warm environments, but have low  $T_b$ ,  $T_o$  and  $CT_{max}$ , even a small increase in  $T_e$  may force them to reduce activity time (Kearney *et al.* in press) 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.* in press) 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.

#### 500 (e) Lizards in lowland Puerto Rico are already 501 at risk

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

510 *Anolis cristatellus* is an abundant and widespread  
 511 species, and its thermal biology is well known (e.g. Rand  
 512 1964; Huey & Webster 1976; Gorman & Hillman 1977;  
 Hertz 1992). In shaded lowland habitats, this species lives

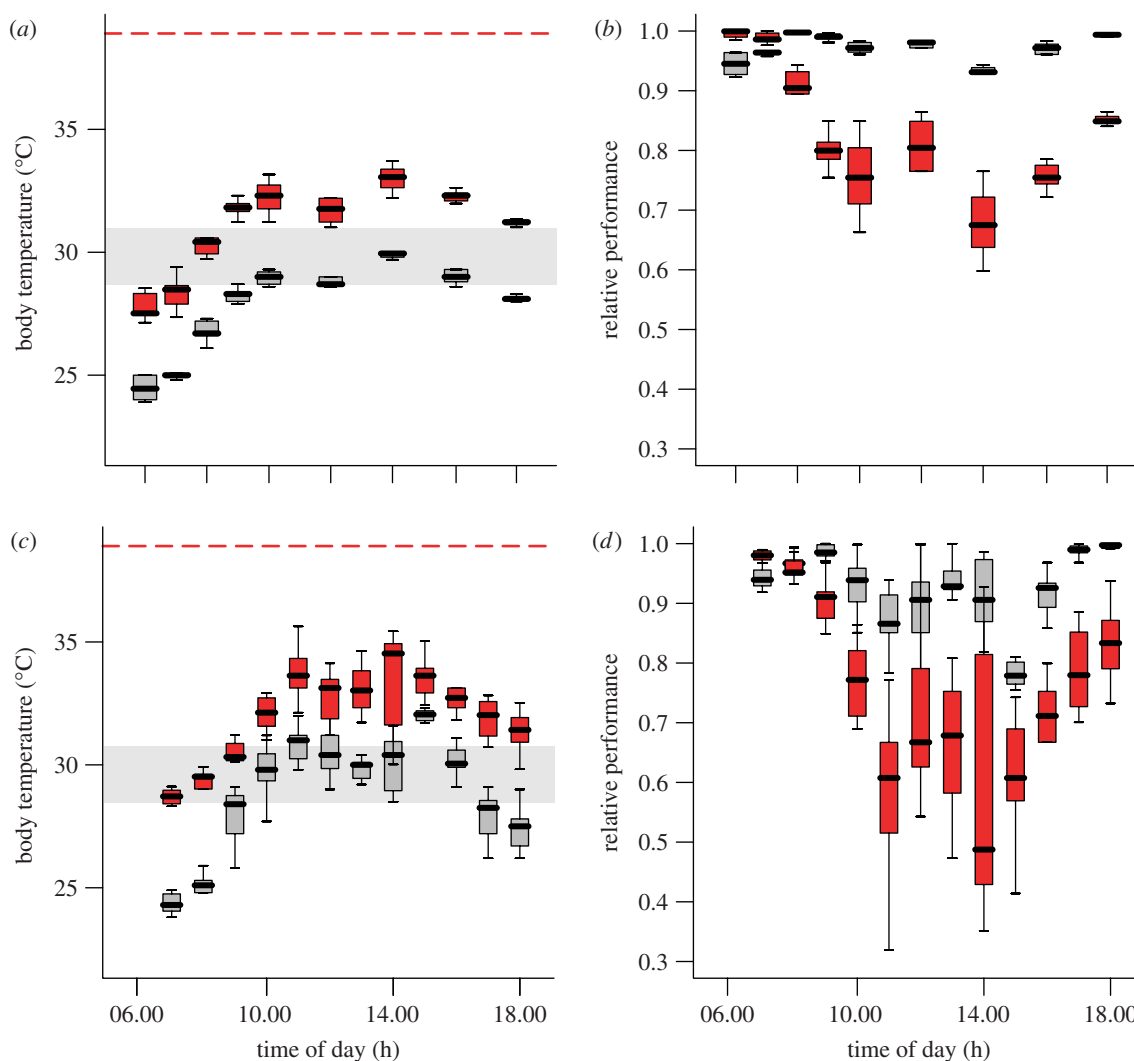


Figure 3. Impact of climate warming on  $T_b$  and performance of a tropical lizard. (a) Body temperature and (b) predicted relative sprint performance of *A. cristatellus* in a shaded forest at Punta Salinas, Puerto Rico before (grey boxes, 1973) and after (black boxes) predicted climate warming (air 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  $CT_{\max}$  (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). Because convection dominates heat exchange in forests,  $T_b$  will also increase by approximately  $3^\circ\text{C}$ . As a result, lizards will have elevated  $T_b$  (red boxes in figure 3a) that exceed  $T_p$  for most of the day, and their predicted sprint performance should be lower for most of the day (figure 3b).

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

(figure 3c). In fact, 92.1 per cent of all  $T_c$  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  $T_c$  exceeded mean  $T_p$  and mean  $T_o$  by  $3.2 \pm 1.06$  and  $5.1 \pm 0.70$ °C, respectively. As a consequence, mean  $T_b$  during the day in summer (across species) exceeded mean  $T_p$  by  $2.1 \pm 0.43$ °C on average and exceeded  $T_o$  for sprinting by  $3.9 \pm 1.16$ °C on average (see table 2h in the electronic supplementary material). If  $T_c$  increases by 3°C because of climate warming, these lizards will probably experience severe heat stress because mean  $T_c$  over the day in summer will be only  $3.5 \pm 0.90$ °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  $T_c$  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  $T_c$ s would have been too cool for *A. cristatellus* (Gorman & Hillman 1977);

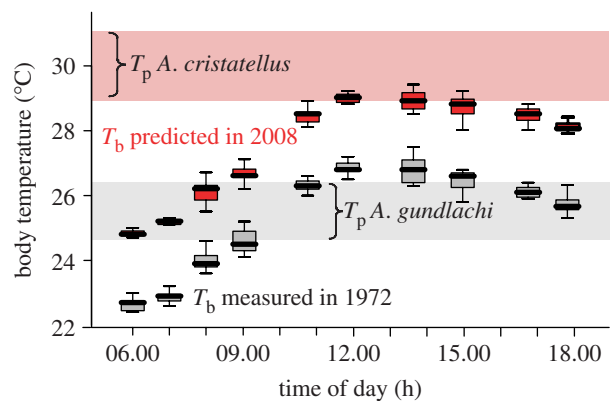


Figure 4. Predicted impact of recent climate warming on a tropical forest lizard. Observed climate warming between 1972 and 2008 (see figure 1 in the electronic supplementary material) is likely to make forest habitats (El Verde, Puerto Rico) less suitable in summer for resident forest species but more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

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

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

#### 4. CONCLUDING REMARKS

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

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

773 A reviewer of a draft of this paper felt that we have taken  
774 a 'pessimistic stance'. We disagree. To be sure, physio-  
775 logical acclimation could potentially buffer the impact of  
776 climate warming (Chown & Terblanche 2007). However,  
777 the few available data suggest that tropical forest  
778 ectotherms—including Puerto Rican *Anolis* (Rogowitz  
779 1996)—show limited acclimation responses (Brattstrom  
780 1968; Feder 1982; Tsuji 1988; Ghalambor *et al.* 2006).  
781 Similarly, genetic adaptation could potentially buffer the  
782 impact (Hoffmann & Blows 1993; Travis & Futuyma  
783 1993; Angilletta 2009), and rapid response to temperature  
784 in selection experiments is common in invertebrates  
785 (Santos *et al.* 2005). Nevertheless, artificial selection on  
786 heat tolerance of a fish was unsuccessful (Baer & Travis  
787 2000). Unfortunately, the heritability of thermal traits in  
788 lizards is essentially unstudied (Sinervo 1990; Angilletta  
789 2009). In any case, conservatism seems to be the rule in  
790 lizard thermal evolution (Hertz *et al.* 1983; Huey & Bennett  
791 1987). Thus, adaptive rescue is feasible but unlikely.

792 For some species, thermoregulatory behaviour will  
793 effectively buffer the impact of climate warming (Huey  
794 *et al.* 2003; Angilletta 2009; Kearney *et al.* in press). For  
795 example, many desert lizards readily evade heat stress by  
796 retreating underground during warm periods (Porter *et al.*  
797 1973; Stevenson 1985). By contrast, tropical forest  
798 lizards, such as *Anolis* and *Sphaerodactylus*, have relatively  
799 few thermoregulatory options because forest  $T_c$ s are  
800 relatively homogeneous in space and time (Hertz 1992);  
801 the 'thermal mosaic' for such forest species is relatively  
802 monochromatic. Populations with access to a mountain  
803 could potentially migrate uphill (Colwell *et al.* 2008;  
804 Raxworthy *et al.* 2008; Chen *et al.* 2009), but the largest  
805 remaining tropical rainforest (Amazon basin) has moun-  
806 tains only on one edge.

807 The biotic pressure of open-habitat species on forest  
808 ectotherms will be exacerbated if climate change also  
809 opens tropical forest canopies (Clark *et al.* 2003; Feeley  
810 *et al.* 2007; Whitfield *et al.* 2007); more solar radiation will  
811 penetrate the forest, thus increasing  $T_e$ . Canopy opening  
812 will also reduce humidity and increase wind speed,  
813 harming ectotherms sensitive to desiccation (Parsons  
814 1989; Pounds *et al.* 1999). More importantly, deforesta-  
815 tion and fragmentation will directly accelerate extinction  
816 rates (Brook *et al.* 2003; Ferraz *et al.* 2003) as well as  
817 increase hot edge environments (Vitt *et al.* 1998).

818 Of course, climate warming would not be physiologically  
819 detrimental to all tropical forest lizards. Some species living  
820 in cool montane forests should benefit (Huey & Webster  
821 1976; Hertz 1992; Hertz *et al.* 1993). Also, even lowland  
822 species may benefit during cool seasons, when  $T_c$ s and  $T_b$ s  
823 are slightly lower (Lister 1981; Hertz 1992) and reproduc-  
824 tion is reduced (Gorman & Licht 1974; Lister 1981).  
825 Similarly, some high-latitude species may benefit because  
826 warmer temperatures will increase potential activity  
827 times and growth rates (Kearney & Porter 2004;  
828 Chamaillé-Jammes *et al.* 2007; Buckley 2008; Deutsch  
829 *et al.* 2008; Kearney *et al.* in press).

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

physiological and demographic models that transduce  
predicted climate change onto changes in vital demo-  
graphic rates (Dunham 1993; Helmuth *et al.* 2005;  
Crozier & Dwyer 2006; Buckley 2008). Kearney *et al.*  
(in press) 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 reproduc-  
tion 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 per-  
formance of tropical lizards.

We dedicate this paper to Rodolfo Ruibal, whose 1961 study  
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).

## REFERENCES

- Álvarez, H. J. 1992 *Thermal characteristics of Sphaerodactylus species in Puerto Rico and their implications for the distribution of species in Puerto Rico*. San Juan, PR: University of Puerto Rico.
- Angilletta, M. J. 2009 *Thermal adaptation: a theoretical and empirical synthesis*. Oxford, UK: Oxford University Press.
- Angilletta Jr, M. J., Niewiarowski, P. H. & Navas, C. A. 2002 The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* **27**, 249–268. (doi:10.1016/S0306-4565(01)00094-8)
- Angilletta Jr, M. J., Bennett, A. F., Guderley, H., Navas, C. A., Seebacher, F. & Wilson, R. S. 2006 Coadaptation: a unifying principle in evolutionary thermal biology. *Physiol. Biochem. Zool.* **79**, 282–294. (doi:10.1086/499990)
- Baer, C. F. & Travis, J. 2000 Direct and correlated responses to artificial selection on acute thermal stress tolerance in a livebearing fish. *Evolution* **54**, 238–244. (doi:10.1111/j.0014-3820.2000.tb00024.x)
- Bakken, G. S. 1989 Arboreal perch properties and the operative temperature experienced by small animals. *Ecology* **70**, 922–930. (doi:10.2307/1941359)
- Bakken, G. S. 1992 Measurement and application of operative and standard operative temperatures in ecology. *Am. Zool.* **32**, 194–216. (doi:10.1093/icb/32.2.194)
- Bennett, A. F. 1980 The thermal dependence of lizard behaviour. *Anim. Behav.* **26**, 455–462.
- Bennett, A. F. & John-Alder, H. B. 1986 Thermal relations of some Australian skinks (Sauria: Scincidae). *Copeia* **1986**, 57–64. (doi:10.2307/1444888)

- 897 Bogert, C. M. 1949 Thermoregulation in reptiles, a factor in  
898 evolution. *Evolution* **3**, 195–211. (doi:10.2307/2405558)
- 899 Brattstrom, B. H. 1965 Body temperatures of reptiles. *Am.*  
900 *Midl. Nat.* **73**, 376–422. (doi:10.2307/2423461)
- 901 Brattstrom, B. H. 1968 Thermal acclimation in anuran  
902 amphibians as a function of latitude and altitude. *Comp.*  
903 *Biochem. Physiol.* **24**, 93–111. (doi:10.1016/0010-406X  
904 (68)90961-4)
- 905 Brook, B. W., Sodhi, N. S. & Ng, P. K. L. 2003 Catastrophic  
906 extinctions follow deforestation. *Nature* **424**, 420–423.  
907 (doi:10.1038/nature01795)
- 908 Buckley, L. B. 2008 Linking traits to energetics and  
909 population dynamics to predict lizard ranges in changing  
910 environments. *Am. Nat.* **171**, E1–E8. (doi:10.1086/  
911 523949)
- 912 Chamailé-Jammes, S., Massot, M., Aragón, P. & Clobert, J.  
913 2007 Global warming and positive fitness response in  
914 mountain populations of common lizards *Lacerta vivipara*.  
915 *Glob. Change Biol.* **12**, 392–402. (doi:10.1111/j.1365-  
916 2486.2005.01088.x)
- 917 Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J. D., Chey,  
918 V. K., Barlow, H. S., Hill, J. K. & Thomas, C. D. 2009  
919 Elevation increases in moth assemblages over 42 years on a  
920 tropical mountain. *Proc. Natl Acad. Sci. USA* **106**,  
921 1479–1483. (doi:10.1073/pnas.0809320106)
- 922 Chown, S. L. & Terblanche, J. S. 2007 Physiological diversity  
923 in insects: ecological and evolutionary contexts. *Adv. Insect*  
924 *Physiol.* **33**, 50–152.
- 925 Chown, S. L., Addo-Bediako, A. & Gaston, K. J. 2003  
926 Physiological diversity: listening to the large-scale signal.  
927 *Funct. Ecol.* **17**, 562–572. (doi:10.1046/j.1365-2435.  
928 2003.07622.x)
- 929 Chown, S. L., Gaston, K. J. & Robinson, D. 2004  
930 Macrophysiology: large-scale patterns in physiological  
931 traits and their ecological implications. *Funct. Ecol.* **18**,  
932 159–167. (doi:10.1111/j.0269-8463.2004.00825.x)
- 933 Clark Jr, D. R. & Kroll, J. C. 1974 Thermal ecology of anoline  
934 lizards: temperate versus tropical strategies. *Southwest.*  
935 *Nat.* **19**, 9–19. (doi:10.2307/3669786)
- 936 Clark, D. A., Piper, S. C., Keeling, C. D. & Clark, D. B. 2003  
937 Tropical rain forest tree growth and atmospheric  
938 carbon dynamics linked to interannual variation during  
939 1984–2000. *Proc. Natl Acad. Sci. USA* **100**, 5852–5857.  
940 (doi:10.1073/pnas.0935903100)
- 941 Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C. &  
942 Longino, J. T. 2008 Global warming, elevational range  
943 shifts, and lowland biotic attrition in the wet tropics.  
944 *Science* **322**, 258–261. (doi:10.1126/science.1162547)
- 945 Crozier, L. & Dwyer, G. 2006 Combining population-  
946 dynamic and ecophysiological models to predict climate-  
947 induced insect range shifts. *Am. Nat.* **167**, 853–866.  
948 (doi:10.1086/504848)
- 949 Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S.,  
950 Ghalambor, C. K., Haak, D. C. & Martin, P. R. 2008  
951 Impacts of climate warming on terrestrial ectotherms  
952 across latitude. *Proc. Natl Acad. Sci. USA* **105**,  
953 6668–6672. (doi:10.1073/pnas.0709472105)
- 954 Dunham, A. E. 1993 Population responses to environmental  
955 change: physiologically structured models, operative  
956 environments, and population dynamics. In *Biotic*  
957 *interactions and global change* (eds P. M. Kareiva, J. G.  
958 Kingsolver & R. B. Huey), pp. 95–119. Sunderland, MA:  
959 Sinauer Associates.
- 960 Feder, M. E. 1982 Environmental variability and thermal  
961 acclimation of metabolism in tropical anurans. *J. Therm.*  
962 *Biol.* **7**, 23–28. (doi:10.1016/0306-4565(82)90015-8)
- 963 Feeley, K. J., Wright, S. J., Supardi, M. N. N., Kassim,  
964 A. R. & Davies, S. J. 2007 Decelerating growth in tropical  
965 forest trees. *Ecol. Lett.* **10**, 461–469. (doi:10.1111/j.1461-  
966 0248.2007.01033.x)
- 967 Ferraz, G., Russell, G. J., Stouffer, P. C., Bierregaard Jr, R. O.  
968 & Pimm, S. L. 2003 Rapid species loss from Amazonian  
969 forest fragments. *Proc. Natl Acad. Sci. USA* **100**,  
970 14069–14073. (doi:10.1073/pnas.2336195100)
- 971 Garland Jr, T., Harvey, P. H. & Ives, A. R. 1992 Procedures  
972 for the analysis of comparative data using phylogenetically  
973 independent contrasts. *Syst. Biol.* **41**, 18–32. (doi:10.  
974 2307/2992503)
- 975 Garland Jr, T., Bennett, A. F. & Rezende, E. L. 2005  
976 Phylogenetic approaches in comparative physiology.  
977 *J. Exp. Biol.* **208**, 3015–3035. (doi:10.1242/jeb.01745)
- 978 Ghalambor, C. K., Huey, R. B., Martin, P. R., Tewksbury,  
979 J. J. & Wang, G. 2006 Are mountain passes higher in the  
980 tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.*  
981 **46**, 5–17. (doi:10.1093/icb/icj003)
- 982 Gilchrist, G. W. 1995 Specialists and generalists in changing  
983 environments. I. Fitness landscapes of thermal sensitivity.  
984 *Am. Nat.* **146**, 252–270. (doi:10.1086/285797)
- 985 Gorman, G. C. & Hillman, S. 1977 Physiological basis for  
986 climatic niche partitioning in two species of Puerto Rican  
987 *Anolis* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* **11**,  
988 337–340. (doi:10.2307/1563246)
- 989 Gorman, G. C. & Licht, P. 1974 Seasonality in ovarian cycles  
990 among tropical *Anolis* lizards. *Ecology* **55**, 360–369.  
991 (doi:10.2307/1935223)
- 992 Helmuth, B., Kingsolver, J. G. & Carrington, E. 2005  
993 Biophysics, physiological ecology, and climate change:  
994 does mechanism matter? *Annu. Rev. Physiol.* **67**, 177–201.  
995 (doi:10.1146/annurev.physiol.67.040403.105027)
- 996 Hertz, P. E. 1992 Temperature regulation in Puerto Rican  
997 *Anolis* lizards: a field test using null hypotheses. *Ecology* **73**,  
998 1405–1417. (doi:10.2307/1940686)
- 999 Hertz, P. E., Huey, R. B. & Nevo, E. 1983 Homage to Santa  
1000 Anita: thermal sensitivity of sprint speed in agamid lizards.  
1001 *Evolution* **37**, 1075–1084. (doi:10.2307/2408420)
- 1002 Hertz, P. E., Huey, R. B. & Stevenson, R. D. 1993 Evaluating  
1003 temperature regulation by field-active ectotherms: the  
1004 fallacy of the inappropriate question. *Am. Nat.* **142**,  
1005 796–818. (doi:10.1086/285573)
- 1006 Hoffmann, A. A. & Blows, M. W. 1993 Evolutionary genetics  
1007 and climate change: will animals adapt to global warming?  
1008 In *Biotic interactions and global change* (eds P. M. Kareiva,  
1009 J. G. Kingsolver & R. B. Huey), pp. 165–178. Sunderland,  
1010 MA: Sinauer Associates.
- 1011 Huey, R. B. 1974 Behavioral thermoregulation in lizards:  
1012 importance of associated costs. *Science* **184**, 1001–1003.  
1013 (doi:10.1126/science.184.4140.1001)
- 1014 Huey, R. B. 1982 Temperature, physiology, and the ecology  
1015 of reptiles. In *Biology of the Reptilia*, vol. 12 (eds C. Gans &  
1016 F. H. Pough), Physiology (C), pp. 25–91. London, UK:  
1017 Academic Press.
- 1018 Huey, R. B. 1983 Natural variation in body temperature and  
1019 physiological performance in a lizard. In *Advances in*  
1020 *herpetology and evolutionary biology: essays in honor of Ernest*  
1021 *E. Williams* (eds A. G. J. Rhodin & K. Miyata), pp. 484–  
1022 490. Cambridge, MA: Museum of Comparative Zoology.
- 1023 Huey, R. B. 1991 Physiological consequences of habitat  
1024 selection. *Am. Nat.* **137**, S91–S115. (doi:10.1086/285141)
- 1025 Huey, R. B. & Bennett, A. F. 1987 Phylogenetic studies of  
1026 coadaptation: preferred temperatures versus optimal  
1027 performance temperatures of lizards. *Evolution* **41**,  
1028 1098–1115. (doi:10.2307/2409194)
- 1029 Huey, R. B. & Berrigan, D. 2001 Temperature, demography,  
1030 and ectotherm fitness. *Am. Nat.* **158**, 204–210. (doi:10.  
1031 1086/321314)
- 1032 Huey, R. B. & Kingsolver, J. G. 1993 Evolution of resistance  
1033 to high temperature in ectotherms. *Am. Nat.* **142**,  
1034 S21–S46. (doi:10.1086/285521)

- Huey, R. B. & Slatkin, M. 1976 Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* **51**, 363–384. (doi:10.1086/409470)
- Huey, R. B. & Webster, T. P. 1976 Thermal biology of *Anolis* lizards in a complex fauna: the *crisatellus* group on Puerto Rico. *Ecology* **57**, 985–994. (doi:10.2307/1941063)
- Huey, R. B., Hertz, P. E. & Sinervo, B. 2003 Behavioral drive versus behavioral inertia: a null model approach. *Am. Nat.* **161**, 357–366. (doi:10.1086/346135)
- IPPC 2007 *Climate change 2007: the physical science basis*. Cambridge, UK: Cambridge University Press.
- Inger, R. F. 1959 Temperature responses and ecological relations of two Bornean lizards. *Ecology* **40**, 127–136. (doi:10.2307/1929930)
- Ives, A. R., Midford, P. E. & Garland Jr, T. 2007 Within-species variation and measurement error in phylogenetic comparative methods. *Syst. Biol.* **56**, 252–270. (doi:10.1080/10635150701313830)
- Janzen, D. H. 1967 Why mountain passes are higher in the tropics. *Am. Nat.* **101**, 233–249. (doi:10.1086/282487)
- Kearney, M. & Porter, W. P. 2004 Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* **85**, 3119–3131. (doi:10.1890/03-0820)
- Kearney, M., Shine, R. & Porter, W. P. In press. The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proc. Natl Acad. Sci. USA*.
- Kingsbury, B. A. 1994 Thermal constraints and eurythermy in the lizard *Elgaria multicarinata*. *Herpetologica* **50**, 266–273.
- Lavin, S. R., Karasov, W. H., Ives, A. R., Middleton, K. M. & Garland Jr, T. 2008 Morphometrics of the avian small intestine, compared with that nonflying mammals: a phylogenetic approach. *Physiol. Biochem. Zool.* **81**, 536–550. (doi:10.1086/590395)
- Lister, B. C. 1981 Seasonal niche relationships of rain forest anoles. *Ecology* **62**, 1548–1560. (doi:10.2307/1941511)
- Malhi, Y. & Wright, J. 2004 Spatial patterns and recent trends in the climate of tropical rainforest regions. *Phil. Trans. R. Soc. B* **359**, 311–329. (doi:10.1098/rstb.2003.1433)
- Martin, T. L. & Huey, R. B. 2008 Why suboptimal is optimal: Jensen's inequality and ectotherm thermal preferences. *Am. Nat.* **171**, E102–E118. (doi:10.1086/527502)
- Mautz, W. J., Daniels, C. B. & Bennett, A. F. 1992 Thermal dependence of locomotion and aggression in a xantusiid lizard. *Herpetologica* **48**, 271–279.
- New, M., Lister, D., Hulme, M. & Makin, I. 2002 A high-resolution data set of surface climate over global land areas. *Clim. Res.* **21**, 1–25. (doi:10.3354/cr021001)
- Parnesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
- Parnesan, C. 2007 Influence of species, latitudes and methodologies on estimate of phenological response to global warming. *Glob. Change Biol.* **13**, 1860–1872. (doi:10.1111/j.1365-2486.2007.01404.x)
- Parsons, P. A. 1989 Conservation and global warming: a problem in biological adaptation to stress. *Ambio* **18**, 322–325.
- Porter, W. P. & James, F. C. 1979 Behavioral implications of mechanistic ecology II: the African rainbow lizard, *Agama agama*. *Copeia* **1979**, 594–619. (doi:10.2307/1443867)
- Porter, W. P., Mitchell, J. W., Beckman, W. A. & DeWitt, C. B. 1973 Behavioral implications of mechanistic ecology. Thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia* **13**, 1–54. (doi:10.1007/BF00379617)
- Pounds, J. A., Fogden, M. P. L. & Campbell, J. H. 1999 Biological response to climate change on a tropical mountain. *Nature* **398**, 611–615. (doi:10.1038/19297)
- Rand, A. S. 1964 Ecological distribution in anoline lizards of Puerto Rico. *Ecology* **45**, 745–752. (doi:10.2307/1934922)
- Raxworthy, C. J., Pearson, R. G., Rabibisoa, N., Rakotondrazafy, A. M., Ramanamanjato, J.-B., Raselimanana, A. P., Wu, S., Nussbaum, R. A. & Stone, D. A. 2008 Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Glob. Change Biol.* **14**, 1703–1720. (doi:10.1111/j.1365-2486.2008.01596.x)
- Rogowitz, G. L. 1996 Evaluation of thermal acclimation and altitudinal variation of metabolism in the Neotropical lizard, *Anolis gundlachi*. *Copeia* **1996**, 535–542. (doi:10.2307/1447517)
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. L. 2003 Fingerprints of global warming on wild animals and plants. *Nature* **421**, 37–42. (doi:10.1038/nature01333)
- Roughgarden, J., Porter, W. P. & Heckel, D. 1981 Resource partitioning of space and its relationship to body temperatures in *Anolis* lizard populations. *Oecologia* **50**, 256–264. (doi:10.1007/BF00348048)
- Ruibal, R. 1961 Thermal relations of five species of tropical lizards. *Evolution* **15**, 98–111. (doi:10.2307/2405846)
- Santos, M., Céspedes, W., Balanya, J., Trotta, V., Calboli, F. C. F., Fontdevila, A. & Serra, L. 2005 Temperature-related genetic changes in laboratory populations of *Drosophila subobscura*: evidence against simple climatic-based explanations for latitudinal clines. *Am. Nat.* **165**, 258–273. (doi:10.1086/427093)
- Shine, R. 1999 Egg-laying reptiles in cold climates: determinants and consequences of nest temperatures in montane lizards. *J. Evol. Biol.* **12**, 918–926. (doi:10.1046/j.1420-9101.1999.00093.x)
- Sinervo, B. 1990 Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). *Oecologia* **83**, 228–237. (doi:10.1007/BF00317757)
- Stevenson, R. D. 1985 The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.* **126**, 362–386. (doi:10.1086/284423)
- Tewksbury, J. J., Huey, R. B. & Deutsch, C. A. 2008 Putting the heat on tropical animals. *Science* **320**, 1296–1297. (doi:10.1126/science.1159328)
- Tracy, C. R. & Christian, K. A. 1983 Ecological relations among space, time and thermal niche axes. *Ecology* **67**, 609–615. (doi:10.2307/1937684)
- Travis, J. & Futuyama, D. J. 1993 Global change: lessons from and for evolutionary biology. In *Biotic interactions and global change* (eds P. M. Kareiva, J. G. Kingsolver & R. B. Huey), pp. 251–263. Sunderland, MA: Sinauer Associates.
- Tsuji, J. S. 1988 Thermal acclimation of metabolism in *Sceloporus* lizards from different latitudes. *Physiol. Zool.* **61**, 241–253.
- van Berkum, F. H. 1988 Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am. Nat.* **132**, 327–343. (doi:10.1086/284856)
- van Berkum, F. H., Huey, R. B. & Adams, B. 1986 Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). *Physiol. Zool.* **59**, 464–472.
- Vitt, L. J., Avila-Pires, T. C. S., Caldwell, J. P. & Oliveira, V. R. L. 1998 The impact of individual tree harvesting on

1153	thermal environments of lizards in Amazonian rain forest.	Whitfield, S. M., Bell, K. E., Philippi, T., Sasa, M., Bolaños,	1217
1154	<i>Conserv. Biol.</i> <b>12</b> , 654–664. (doi:10.1046/j.1523-1739.	F., Chaves, G., Savage II, J. M. & Donnelly, M. A. 2007	1218
1155	1998.96407.x)	Amphibian and reptile declines over 35 years at La Selva,	1219
1156	Vitt, L. J., Shepard, D. B., Vieira, G. H. C., Caldwell, J. P.,	Costa Rica. <i>Proc. Natl Acad. Sci. USA</i> <b>104</b> , 8352–8356.	1220
1157	Colli, G. R. & Mesquita, D. O. 2008 Ecology of <i>Anolis</i>	(doi:10.1073/pnas.0611256104)	1221
1158	<i>nitens brasiliensis</i> in cerrado woodlands of Cantão. <i>Copeia</i>	Williams, S. E., Isaac, J. L. & Shoo, L. P. 2008	1222
1159	<b>2008</b> , 142–151. (doi:10.1643/CP-06-251)	The impact of climate change on the biodiversity	1223
1160	Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C.,	and ecosystem functions of the wet tropics. In <i>Living</i>	1224
1161	Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. &	<i>in a dynamic tropical forest landscape</i> (eds N. E. Stork &	1225
1162	Bairlein, F. 2002 Ecological responses to recent climate	S. M. Turton), pp. 282–294. Malden, MA: Blackwell	1226
1163	change. <i>Nature</i> <b>416</b> , 389–395. (doi:10.1038/416389a)	Publishing.	1227
1164			1228
1165			1229
1166			1230
1167			1231
1168			1232
1169			1233
1170			1234
1171			1235
1172			1236
1173			1237
1174			1238
1175			1239
1176			1240
1177			1241
1178			1242
1179			1243
1180			1244
1181			1245
1182			1246
1183			1247
1184			1248
1185			1249
1186			1250
1187			1251
1188			1252
1189			1253
1190			1254
1191			1255
1192			1256
1193			1257
1194			1258
1195			1259
1196			1260
1197			1261
1198			1262
1199			1263
1200			1264
1201			1265
1202			1266
1203			1267
1204			1268
1205			1269
1206			1270
1207			1271
1208			1272
1209			1273
1210			1274
1211			1275
1212			1276
1213			1277
1214			1278
1215			1279
1216			1280

1281 **Author Queries**1282 *JOB NUMBER:* 200819571283 *JOURNAL:* RSPB

1284

1285

1286 Q1 In figure legend 2, 'dashed line' is indicated but does  
1287 not appear in the figure. please check1288 Q2 Please provide an alternative title not more than 200  
1289 characters for the electronic supplementary materials  
1290 '1, 2, 3, 4 and 5' that does not include the words  
1291 'supplemental' or 'supplementary' as this label  
1292 appears as standard.1293 Q3 Please provide an alternative description not more  
1294 than 200 characters for the electronic supplementary  
1295 material 3 that does not include the words 'supple-  
1296 mental' or 'supplementary' as this label appears as  
1297 standard.1298 Q4 Please update publication details in Kearney *et al.* (in  
1299 press).1300 Q Your paper has exceeded the free page extent and will  
1301 attract page charges.

1302

1303

1304

1305

1306

1307

1308

1309

1310

1311

1312

1313

1314

1315

1316

1317

1318

1319

1320

1321

1322

1323

1324

1325

1326

1327

1328

1329

1330

1331

1332

1333

1334

1335

1336

1337

1338

1339

1340

1341

1342

1343

1344

1345

1346

1347

1348

1349

1350

1351

1352

1353

1354

1355

1356

1357

1358

1359

1360

1361

1362

1363

1364

1365

1366

1367

1368

1369

1370

1371

1372

1373

1374

1375

1376

1377

1378

1379

1380

1381

1382

1383

1384

1385

1386

1387

1388

1389

1390

1391

1392

1393

1394

1395

1396

1397

1398

1399

1400

1401

1402

1403

1404

1405

1406

1407

1408