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Climatic Predictors of Temperature Performance Curve Parameters in Ectotherms Imply Complex Responses to Climate Change

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ABSTRACT: Determining organismal responses to climate change is one of biology's greatest challenges. Recent forecasts for future climates emphasize altered temperature variation and precipitation, but most studies of animals have largely focused on forecasting the outcome of changes in mean temperature. Theory suggests that extreme thermal variation and precipitation will influence species performance and hence affect their response to changes in climate. Using an information-theoretic approach, we show that in squamate ectotherms (mostly lizards and snakes), two fitness-influencing components of performance, the critical thermal maximum and the thermal optimum, are more closely related to temperature variation and to precipitation, respectively, than they are to mean thermal conditions. By contrast, critical thermal minimum is related to mean annual temperature. Our results suggest that temperature variation and precipitation regimes have had a strong influence on the evolution of ectotherm performance, so that forecasts for animal responses to climate change will have to incorporate these factors and not only changes in average temperature.

Keywords: reptiles, species distributions, reaction norm, operative temperature, arid zones, thermoregulation.

Introduction

How organisms respond to ongoing anthropogenic climate change and what conservation actions should be taken to assist species to respond are among the most significant and controversial topics in biology today (Hoegh-Guldberg et al. 2008; Williams et al. 2009). While it is widely appreciated that increases in temperature have significantly affected species ranges and their phenologies (e.g., Stachowicz et al. 2002; Forcada et al. 2006; Parmesan 2006), several unexpected outcomes of change have also been

identified, including substantial current and forecast impacts on tropical organisms (Pounds et al. 2006; Deutsch et al. 2008; Raxworthy et al. 2008; Chen et al. 2009; Huey et al. 2009; Sinervo et al. 2010).

Much of this research, at least for ectotherms, has been concerned with the responses of species to changing average thermal conditions (mostly, mean maximum temperature or mean ambient temperature conditions) or to the altered timing of particular events (e.g., Bradshaw and Holzapfel 2006; Deutsch et al. 2008; but see Kearney et al. 2009, McKechnie and Wolf 2010). However, major components of current and forecast climate change include an increase in the frequency of extreme events, alteration of the diurnal temperature range, changes in precipitation and cloud cover, and interactions between temperature and precipitation change (Vose et al. 2005; Solomon et al. 2007; Adler et al. 2008; Zhou et al. 2009b). Changes in precipitation and cloud cover are more complex and spatially variable than those in temperature conditions. Nonetheless, expected rainfall trends include an increase in the frequency of large events and a decline in predictability (Jentsch et al. 2007; Knapp et al. 2008), an increase in tropical and high-latitude rainfall, a decline at midlatitudes, and substantial variation between hemispheres (Meehl et al. 2007; Trenberth et al. 2007; Adler et al. 2008; Zhou et al. 2009b). Changes in cloud-base height and fog in several coastal and montane areas are also predicted (Nair et al. 2003; Williams et al. 2008; Fischer et al. 2009; Rovito et al. 2009). How these changes are likely to influence organismal responses has not been clearly resolved, although interactions between precipitation and temperature change and changes in their variability are likely to be significant (e.g., Bonebrake and Mastrandrea 2010).

Ectotherms are the predominant group of terrestrial animal species that either largely comply with their surrounding thermal environment or rely mostly on behav-

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ioral thermoregulation for optimum performance, fitness maximization, and ultimately, survival (Angilletta 2009). Several lines of evidence suggest that the performance of most animals should therefore be affected by temperature variation, precipitation, and cloud cover. First, extreme events may impose strong selection that can lead to substantial population change (for theory, see Endler 1986; Hoffman and Parsons 1997; for empirical support, see Grant and Grant 1993; Brown and Brown 1998; Parmesan et al. 2000; Gutschick and BassiriRad 2003; Jentsch et al. 2007; Parker et al. 2008; Wegner et al. 2008; Welbergen et al. 2008; Pelini et al. 2009).

Second, from a theoretical perspective, thermal tolerance breadth should increase in more variable environments to optimize fitness (Janzen 1967; Stevens 1989; see also Snyder and Weathers 1975; Addo-Bediako et al. 2000; Ghalambor et al. 2006). However, predictions from optimality models of thermal performance curves (Lynch and Gabriel 1987; Gilchrist 1995) have received mixed empirical support (Angilletta 2009) and have been little explored with regard to precipitation variability. Bonebrake and Mastrandrea (2010) have recently applied the optimality model of Lynch and Gabriel (1987) to predict relative changes in fitness given variation in both temperature and precipitation across the globe. Their results indicate that changes in precipitation variability significantly influence performance curves and relative fitness across latitudes, with several outcomes differing substantially from those of models based on temperature alone.

Third, the range and frequency of operative temperatures (T_e) that integrate not just ambient temperature but multiple energy paths (radiation, convection, transpiration, conduction; Gates 1980) within the habitat influence the thermoregulatory opportunities of ectotherms and thus likely affect the fitness of these organisms. The effects of precipitation on performance curves can result from either a direct effect on the availability of optimal T_e for thermoregulation (Avery 1971; Kingsbury 1994; Marquis et al. 2008; Clusella-Trullas et al. 2009) or a direct effect on hydration status, or both. For example, selected body temperatures can be lower in arid areas with high dehydration risks (Lorenzon et al. 1999; Hertz 1992). Finally, precipitation could also have an indirect effect on temperature performance curves by affecting resource availability and thus altering the potential amount of energy intake of reptiles (Dunham 1978; Tinkle et al. 1993; Lorenzon et al. 2001). In productive areas, faster rates of digestion from higher preferred body temperatures may provide increased food consumption, growth rate, and predator avoidance (e.g., Harlow et al. 1976; Blouin-Demers and Weatherhead 2001), whereas food deprivation in poor resource areas may result in lower selected body

temperatures to minimize metabolic costs (Brown and Griffin 2005; Wang et al. 2006).

Given the potential significance of temperature and precipitation changes for ectotherm fitness, covariation between these environmental variables and the major parameters of ectotherm performance curves, such as critical temperature limits and optimal temperature, should be pronounced. If occasional high-temperature events have had a significant role in shaping the thermal performance curve of ectotherms, we predict that the upper limits to performance should covary less with mean temperature conditions than with a measure of variation in temperature, such as diurnal or interannual variation in extremes of temperature. Theory demonstrates that relatively small increases in temperature variance are strong predictors of an increase in the likelihood of extreme events (Katz and Brown 1992; Meehl et al. 2000; Jentsch et al. 2007). Similarly, if high precipitation and cloud cover strongly affect thermoregulatory capability and energy flow relationships, we predict that optimal or preferred body temperatures (T_p) should be more related to these climate variables than to mean temperature conditions. Moreover, thermoregulatory constraints due to increased rainfall should result in a negative relationship between T_p and rainfall, whereas dehydration and low energy resources in arid areas should result in a positive relationship.

To examine the extent to which temperature variation, precipitation regimes, and their interaction are likely to influence thermal performance curves, we focus on squamate reptiles (mostly lizards and snakes), using a macrophysiological approach (Gaston et al. 2009). In particular, we assess at a global scale how the preferred body temperature (T_p ; the temperature selected by an animal in a laboratory thermal gradient that provides a broad range of thermal opportunities, free of physical and biotic constraints, and that generally reflects the optimal temperature for physiological processes; Dawson 1975; Stevenson et al. 1985; Bauwens et al. 1995), the lower critical temperature for movement (CT_{min} : critical thermal minimum), and the upper critical temperature for movement (CT_{max} : critical thermal maximum) relate to a set of four climate variable groups and their interactions. The four groups include (1) mean temperature conditions, (2) temperature variation, (3) mean precipitation conditions, and (4) precipitation seasonality. We use an information-theoretic approach (Burnham and Anderson 2002) to identify the most likely model for the relationship between performance parameters and environmental variables given the a priori predictions while also considering potential phylogenetic effects. In addition, we test models that include ecological and life-history variables that are known to affect critical temperature limits and preferred body temperature or that influence the thermal environment experienced by these

species and therefore may influence the performance curves.

Methods

Data Selection

We used data on critical thermal maximum (CT_{max}), critical thermal minimum (CT_{min}), and preferred body temperature (T_p) of squamates compiled from the literature (652 data points from 396 species in 16 squamate families; available in Dryad, <http://dx.doi.org/10.5061/dryad.8665>). Data were not included in the database if the methods used to determine these parameters were not described or if methods differed substantially from standard protocols (Cowles and Bogert 1944; Licht et al. 1966; Lutterschmidt and Hutchison 1997). In cases where more than one study was found for the same species, priority was given to (1) studies that measured CT_{max} , CT_{min} , and T_p (or CT_{max} and CT_{min}) for the same population; (2) field-fresh individuals over those given short-term acclimations and short-term-acclimated individuals over those given long-term acclimations; (3) data taken during active phases (i.e., daytime for diurnal and nighttime for nocturnal species) and active seasons; (4) data taken in a fasted state over a fed state; (5) photothermal and thigmothermal gradients for heliothermic and thigmothermic species, respectively; (6) arithmetic mean over median T_p (due to the higher availability of the former); (7) the loss of righting response over the onset of spasms (OS) as the end point of CT_{max} and CT_{min} (due to the paucity of OS usage across species; Lutterschmidt and Hutchison 1997); and (8) acclimation at 20° or 25°C when only studies with acclimated individuals were available; if data at these temperatures were not available, the arithmetic mean of acclimation groups was used. If data for several populations were reported for the same species and the criteria above did not favor one study over another, an arithmetic mean was calculated for the species. While some variation associated with method is expected among studies, especially where different investigators are involved, we assume, as have many other macrophysiological investigations, that any error will add random variation to the data rather than bias them significantly in one direction or another (Chown et al. 2003; Huey et al. 2009).

Latitudinal and longitudinal coordinates of the populations sampled for CT_{max} , CT_{min} , and T_p were determined from the geographic locations given in each respective study. When locations were not given (26% of the data) or multiple populations were used (<1% of the data), the center of the species range was determined using species distribution maps (Cogger 1994; Behler and King 1996; Spawls et al. 2004) and occurrence data from museum

specimen records (<http://data.gbif.org/>). The latitudinal and longitudinal coordinates of the populations sampled for CT_{max} , CT_{min} , and T_p were used to extract 18 climate variables from WorldClim (30" spatial resolution; records from 1950 to 2000; Hijmans et al. 2005), using ArcView 9.2. The broad geographical nature of this study complicates the use of extreme value theory statistics (Gaines and Denny 1993; Katz et al. 2005), which are often a preferred approach for investigating climate extremes and their impacts. Therefore, we relied on the close relationship between climate variance and extremes (Katz and Brown 1992) and used high-resolution interpolated climate surfaces based on monthly means (Hijmans et al. 2005). The following variables were used: (1) mean temperature conditions: annual mean temperature (Ann_Ta), mean of the maximum temperature of the warmest month of a year (Max_Ta), mean of the minimum temperature of the coldest month of a year (Min_Ta), mean temperature of warmest quarter, mean temperature of coldest quarter, mean temperature of wettest quarter, and mean temperature of driest quarter; (2) temperature variation: mean diurnal temperature range (i.e., mean of the monthly maximum temperature – minimum temperature), mean annual temperature range (i.e., mean of Max_Ta – Min_Ta), and temperature seasonality (i.e., standard deviation of Ann_Ta \times 100), (3) mean precipitation conditions: annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter; and (4) precipitation variation: precipitation seasonality (coefficient of variation; for additional information see <http://www.worldclim.org>).

The relationships between the parameters of the performance curves and environmental variables are likely to be influenced by life-history variation. First, nocturnal species generally have lower CT_{max} and T_p than diurnal species (e.g., Greer 1980; Avery 1982; Bennett and John-Alder 1986; Huey et al. 1989), with some exceptions (Huey and Bennett 1987; Kearney and Prevedec 2000). Second, the habitat type used by reptiles strongly affects their capacity to buffer climate changes through behavior (Huey et al. 2003). Therefore, we expect that species most constrained by the availability of optimal microsites will be those most likely to endeavor a shift in performance curves. For example, fossorial or burrowing species should have a lower preferred body temperature than terrestrial or arboreal species (Greer 1980). A phylogenetically explicit analysis that accounts for differences in activity and habitat type across species is needed to assess these effects. Third, reproduction mode (viviparity vs. oviparity) may explain variation in the thermal biology of squamates, as viviparity occurs most frequently in species occupying cold climates,

likely providing a selective advantage by maintaining embryos at optimal temperatures via maternal thermoregulation (Shine 2005). Fourth, body mass is associated directly with physiological processes such as digestion and locomotion capacity and indirectly via its influence on the rate of body temperature change (Gates 1980). It is therefore expected that body mass will contribute to variation in thermal performance traits.

The categorical variable “activity” was included in the models to assess the effect of diurnal versus nocturnal activity on performance curve parameters. Crepuscular species were classified as nocturnal species given that in the former, basking is limited. Categories of habitat type were “burrowing” (including fossorial and cryptozoic species), “rock dwelling,” “ground dwelling” (mostly terrestrial), “aquatic” (including semiaquatic species), and “arboreal” (including semiarboreal species). The primary habitat type was chosen when populations or species were known to utilize multiple habitat types. Species were also identified as oviparous or viviparous (including ovoviviparous species; Blackburn 2000). For species that have bimodal reproductive status, the mode from the population or region investigated for physiological traits was used in the analyses. Mean body mass (body mass [BM] in g; $n = 279$ out of a total of 397 species) and snout-vent length (SVL in mm) were taken from studies comprising performance parameters. If these data were not reported, measurements were sought in the literature. In the absence of size data for *Masticophis anthonyi*, BM of its close relative *Masticophis flagellum* was used. Allometric equations based on species for which we had both SVL and BM were used to calculate BM for legged-lizard species ($\log_{10} \text{BM} = -4.1877 + 2.7513 \times \log_{10} \text{SVL}$, $R^2 = 0.92$, $n = 108$ spp.) and for serpentiform species (e.g., snakes, amphisbaenians, and legless lizard species, $\log_{10} \text{BM} = -3.386 + 1.9293 \times \log_{10} \text{SVL}$, $R^2 = 0.89$, $n = 30$). The use of such equations has some limitations (see Meiri 2010), but inferred body masses represented less than 30% of the data set.

Analyses

Body mass and most precipitation variables were \log_{10} transformed given data skewness in preliminary data plots. Ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) regression methods (Martins and Hansen 1997; Garland and Ives 2000) were then used to examine relationships between the performance curve parameters (i.e., T_p , CT_{\max} , and CT_{\min}) and the environmental variables. The PGLS analyses adjust for the phylogenetic dependence of the traits investigated by incorporating the expected covariance among species into a model fitted by generalized least squares. PGLS is equivalent to the more

widely used phylogenetic independent contrasts method (Felsenstein 1985; Pagel 1993) when assuming a Brownian motion model of character evolution and using a resolved phylogeny (for a comparison of the two analytical approaches, see Garland and Ives 2000). However, PGLS offers increased flexibility in the specification of the evolutionary model and in the usage of statistical diagnostics typical of standard least squares regressions (Garland and Ives 2000). For example, several alternative evolutionary models can be incorporated by changing the error structure of the models, and both continuous and categorical explanatory variables can be used in the same model (e.g., Halsey et al. 2006). In this study, the covariance matrix was constructed following a Brownian motion model of evolution (Rohlf 2001) and assuming both equal (punctuated model of evolution) and proportional (gradualistic models of evolution) branch lengths in the phylogeny (available in Dryad, <http://dx.doi.org/10.5061/dryad.8665>). A maximum likelihood approach provided λ , which indicated the degree of phylogenetic correlation in the data ($\lambda = 0$ indicates no phylogenetic effect, and $\lambda = 1$ indicates a strong phylogenetic effect equivalent to that expected under the Brownian motion model; for details see Halsey et al. 2006). The best model in the set used to predict a response variable has the lowest Akaike Information Criterion (AIC), and models with ΔAIC (model AIC minus that of the best-fit model) < 2 are considered as acceptable alternative models; models with $4 \leq \Delta\text{AIC} \leq 7$ have considerable less support, and models with $\Delta\text{AIC} > 10$ have no support (Burnham and Anderson 2001). The Akaike weight, w_i , which is the likelihood of a particular model normalized across the total set of candidate models, was calculated for each model. Akaike weights provide the probability that a model is the best fit among those tested, with values close to 1 being the best models and models with similar weights having similar levels of support in the data (Burnham and Anderson 2001; Johnson and Omland 2004). All the analyses were implemented in R, version 2.11.1 (R Development Core Team 2010), using the APE package (Paradis et al. 2004) and the R function for PGLS from Duncan et al. (2007).

We used several sets of analyses to test for the relationship between performance curve parameters and climate variables. First, we used single-predictor models to test the influence of each climate predictor on each performance variable. We then used low AIC values, low collinearity, and high tolerance levels between variables (Quinn and Keough 2002) to guide variable selection for multiple predictor models. Each model started with the lowest single-predictor AIC value, and the next strongest predictor was sequentially added. In line with the a priori predictions, we tested for models that included solely variables relating to (1) mean temperature conditions, (2) temperature var-

iation, (3) mean precipitation, and (4) precipitation variation and a series of models that include best predictors across climate variable groups (e.g., mean temperature conditions + precipitation seasonality; mean temperature conditions + temperature variation). Generally, variables within each category (e.g., mean temperature conditions) and a few across climate categories were moderately to highly correlated, reducing substantially the number of models tested (correlation matrices are available in Dryad, <http://dx.doi.org/10.5061/dryad.8665>). Finally, the same approach was used including categorical variables (activity mode, reproduction mode, habitat type) and body mass in the model. Candidate models obtained from these sets of analyses were compared for each performance parameter using Akaike weights since data sets were consistent across models.

Given several statistical problems associated with the coefficient of determination (R^2) as a measure of goodness of fit in generalized least squares estimations (Blomquist 1980; Judge et al. 1985; and see Lavin et al. 2008 for a more recent discussion), we report R^2 values only from the best predictive nonphylogenetic (OLS) models.

Results

The sampling of squamate species for physiological studies has not been taxonomically uniform. Out of ~7,800 species of squamates globally, we found thermal physiology data for 396 species, of which the Iguanidae and Scincidae included 24% of the species each (193 species in total); the Gekkonidae, Colubridae, Lacertidae, and Agamidae comprised 7%–10% of the species each, and the remaining families (Chamaeleonidae, Varanidae, Viperidae, Teiidae, Cordylidae, Boidae, Xantusidae, Anguinae, Amphisbaenidae, and Helodermatidae) comprised less than 3% of the total number of species each. Similarly, some regions seem to be favored for reptile studies. Generally, Australia, the United States, and southwestern Europe (but not for CT_{\min}) are well covered compared to the rest of the world (a map with species locations is available in Dryad, <http://dx.doi.org/10.5061/dryad.8665>).

PGLS models incorporating proportional branch lengths were consistently better than models with no phylogeny (OLS models) or those with equal branch lengths (fig. 1; tables A1, A2 in the online edition of the *American Naturalist*). The consistently high maximum likelihood value λ (>0.85) in PGLS models indicated the high degree of phylogenetic correlation in the data. Precipitation of the driest month was the best single predictor of T_p in squamate reptiles (fig. 1A): areas with low precipitation have species with high T_p (fig. 2A). The inclusion of other climatic variables (mean temperature conditions or temperature variation) barely improved the fit of multivariate

models, and the best model including only mean temperature conditions had a low likelihood as judged by its Akaike weight (<0.0001; table 1; see table A2 for all models tested). The best multivariate predictive model of T_p incorporated precipitation of the driest month (significant negative slope) and body mass (significant negative slope) as continuous variables, a positive interaction between precipitation and body mass and habitat type as a covariate (table 1). Small-sized species tended to have slightly lower T_p than larger species in high-rainfall regions, while larger species had substantially higher T_p than small species in arid regions (table 2). Negative relationships between T_p and precipitation were consistent across habitat types and while most groups had similar intercepts, the effect of habitat type seemed to originate from the lower T_p of burrowing species (fig. 2A; table 2). Indeed, a model that groups species from all habitat types (except for burrowing) versus burrowing species improved the model significantly ($\Delta AIC = 4$) and confirmed that burrowing species had on average lower T_p (26.6°C) than nonburrowing species (32.3°C).

Diurnal temperature range was the best single climate predictor of CT_{\max} (fig. 1B): species with high CT_{\max} are located in areas with greater mean diurnal temperature variation (fig. 2B). Variables that described temperature variation were consistently better predictors of CT_{\max} than were mean temperature variables, and inclusion of mean temperature and/or precipitation variables did not improve the model (table 1; see table A2 for all models tested). The best predictive multivariate model of CT_{\max} incorporated reproduction mode and habitat type as covariates (table 1). Viviparous species have on average lower CT_{\max} than oviparous species (fig. 2B). Although burrowing species seemed to have lower CT_{\max} than other habitat-type species, a model that clustered burrowing from the rest of habitat-type categories did not improve the model ($\Delta AIC = 1.4$). Instead, the improvement of the initial climate model with inclusion of habitat type as a covariate ($\Delta AIC = 14$) suggested that the variation across all habitat types explained a meaningful amount of CT_{\max} variation.

By contrast with T_p and CT_{\max} , mean temperature conditions were the best single climate predictors of CT_{\min} (fig. 1C), indicating that species in areas with warmer average temperature have higher CT_{\min} (fig. 2C). Both mean annual temperature and mean temperature of the wettest quarter resulted in similar model outcomes (table A1). The best multivariate model included mean temperature of the wettest quarter (significant positive slope) and temperature seasonality (significant negative slope) as continuous variables and reproduction mode as a categorical variable (table 1; see table A2 for all models tested). Areas with high mean temperature conditions have species with higher CT_{\min} whereas areas with greater temperature sea-

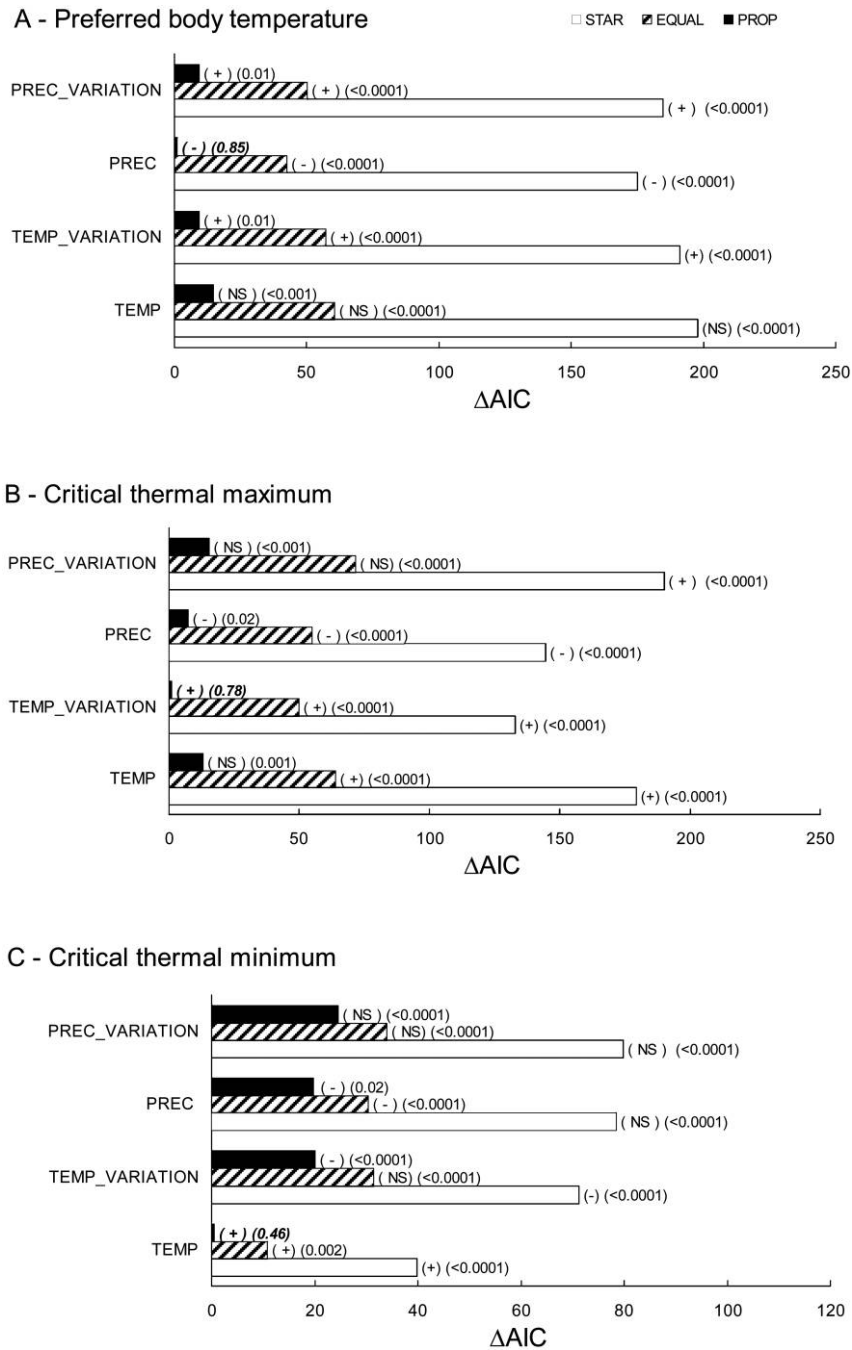
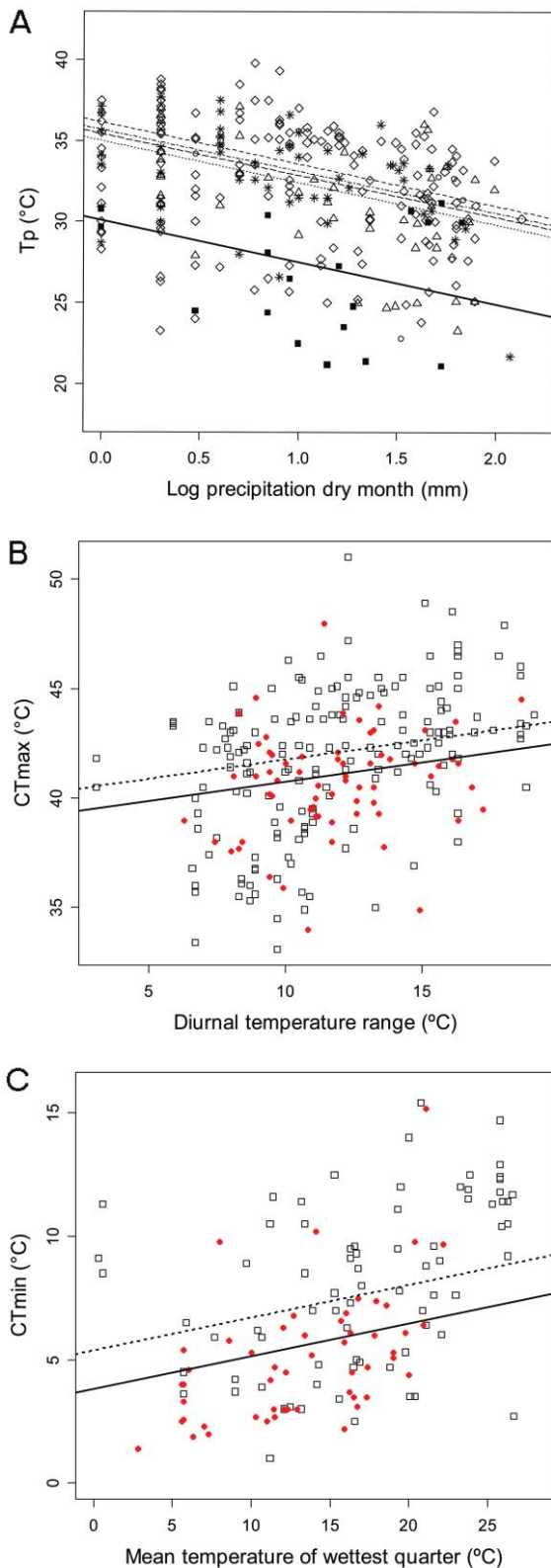


Figure 1: Rescaled Akaike Information Criterion ($\Delta AIC = \text{model AIC} - \text{minimum AIC}$; Burnham and Anderson 2001) for the best single climate predictor within each climate variable category (precipitation seasonality, mean precipitation conditions, temperature variation, and mean temperature conditions). For each thermal performance curve parameter, the preferred body temperature (T_p ; A), the critical thermal maximum (CT_{max} ; B), and the critical thermal minimum (CT_{min} ; C), three evolutionary models were tested (PROP = proportional branch length, EQUAL = equal branch length phylogeny, and STAR = no phylogeny or ordinary least square analysis). Proportional branch length models were consistently better models, indicated by lower ΔAIC . In A, T_p is best explained by mean precipitation (precipitation of driest month); in B, CT_{max} is best explained by temperature variation (diurnal temperature range); and in C, CT_{min} is best explained by mean temperature conditions (mean temperature of wettest quarter). For a breakdown and summary of all predictors tested within each climate group, see table A1 in the online edition of the *American Naturalist*. Slope sign and Akaike weights (w_i) are shown in parentheses, with the best model italicized.



sonality have species with lower CT_{\min} (table 2). Finally, viviparous species have on average lower CT_{\min} (5°C) than oviparous species (8.1°C ; fig. 2C).

For T_p , the coefficient of determination (R^2) of the best predictive OLS model ($T_p \sim$ precipitation of driest month \times body mass + habitat type) was 0.24. When adding taxonomic family as a predictor, the R^2 increased to 0.60. For CT_{\max} , the R^2 of the best OLS model ($CT_{\max} \sim$ diurnal temperature range + habitat type + reproduction mode) was 0.26 and 0.45 with Family included. Finally, for CT_{\min} , the R^2 for the best predictive OLS model ($CT_{\min} \sim$ mean temperature of wettest quarter + temperature seasonality + reproduction mode) was 0.35, and 0.51 with Family included.

Discussion

The macrophysiological approach adopted here provides fresh insights into the factors influencing the evolution of performance curves in squamate reptiles. In particular, it is clear that precipitation and temperature variation rather than mean temperature conditions are the best predictors of T_p and CT_{\max} , respectively, across the group of species investigated. These climate variables have therefore likely played a significant role in the evolution of thermal sensitivity of ectotherm performance.

In general, the thermal preference of an ectotherm closely matches the optimal temperature for performance and thus is the temperature that the organism seeks to achieve, through thermoregulation, to maximize fitness (Angilletta 2009). The influence of precipitation on T_p indicates that species in habitats with high rainfall have fewer opportunities for behavioral thermoregulation than those in drier habitats. A dearth of optimal microsites for thermoregulation may be found in both temperate and tropical areas. In high-rainfall temperate areas such as the Pacific Coast of the United States, frequent overcast conditions and high rainfall constrain some species to use suboptimal microhabitats (Kingsbury 1994), while the

Figure 2. Phylogenetically adjusted scatter plots and analyses indicate that species in locations with high precipitation have a lower preferred body temperature (T_p) than those in dry areas (A), species from areas with high diurnal temperature variation have higher critical thermal maximum (CT_{\max}) than those in less variable areas (B), and species inhabiting areas with high mean temperature of the wettest quarter have higher critical thermal minimum (CT_{\min}) than those from colder habitats (C). A, Burrowing species (filled squares; solid line) have lower T_p than other habitat-type dwellers (aquatic [circle], arboreal [triangle], ground- [diamond] and rock-dwellers [asterisk]; all represented by thin lines). Viviparous species (red circles; solid line) have lower CT_{\max} (B) and lower CT_{\min} (C) than oviparous species (open squares; stippled line).

Table 1: Best predictive models incorporating climate variables and life-history variables for each performance curve parameter

Model	λ	AIC	w_i
Preferred temperature (T_p):			
1. Precipitation driest month \times mass + habitat	.89	1,327.38	.79
2. Mean annual temperature + mass + habitat	.89	1,349.28	<.0001
3. Mass + habitat	.89	1,348.53	<.0001
Critical thermal maximum (CT_{max}):			
1. Diurnal temperature range + habitat + reproduction	.93	1,012.73	.70
2. Mean annual temperature + habitat + reproduction	.94	1,029.44	<.001
3. Habitat + reproduction	.94	1,028.48	<.001
Critical thermal minimum (CT_{min}):			
1. Mean temperature of the wettest quarter + temperature seasonality + reproduction	.94	601.74	.56
2. Precipitation coldest quarter + reproduction	.87	624.99	<.0001
3. Reproduction	.87	625.56	<.0001

Note: For each parameter, we present the best model overall (1), the best model including mean temperature conditions (or precipitation in the case of CT_{min} since temperature was the best climate predictor for this parameter; 2), and the best model including life-history variables only (3). All models include a proportional phylogeny branch-length assumption. The categorical variable habitat distinguishes across species habitat-type usage, and reproduction indicates reproductive mode. Body mass (mass) and precipitation variables are log transformed. λ = phylogenetic dependence; AIC = Akaike Information Criterion; and w_i = Akaike weights calculated from AIC values of all tested models given in table A2 in the online edition of the *American Naturalist*.

presence of dense-canopy forests in tropical areas constrain reptiles to use shaded microsites despite the potential availability of gaps and edges (Hertz 1974; Huey 1974). Given the high dependence of heat-transfer budgets of ectotherms on their surrounding physical environment (Gates 1980), the reduced availability of optimal operative temperatures in areas with high rainfall restricts activity periods and likely imposes lower body temperatures (e.g., Marquis et al. 2008; Clusella-Trullas et al. 2009). Similarly, the reduction in available operative temperatures favorable for activity in arid areas may force individuals to select high body temperatures in these regions (e.g., Grant 1990). Moreover, the similarity of effects of precipitation on T_p for burrowing species suggests that the mechanism underlying this relationship may involve more than the reduced availability of basking sites (i.e., direct solar radiation). Instead, fossorial species in high rainfall areas are likely to be as much constrained by suboptimal microsites as are species that spend more time above ground. Despite the relationship of body mass and T_p being variable across rainfall gradients (i.e., a body mass \times T_p interaction), possibly due to the mixed effects that water availability can have on growth rate, adult body size, fecundity, and predation rates (e.g., Tinkle et al. 1993; Sears and Angilletta 2003, 2004), precipitation consistently remained the best predictor of T_p , reinforcing its marked influence on thermoregulation opportunities.

For CT_{max} , variables that reflect temperature variation were consistently better predictors than mean temperature variables. Because an increase in temperature variance is also a strong indicator of temperature extremes (Katz and Brown 1992; Meehl et al. 2000), this might reflect selection for survival of occasional extremes rather than simply variation in temperature range, especially because diurnal temperature range is a consequence of variation in both minimum and maximum temperature, of which the former tends to be most pronounced (Bonan 2002; Chown et al. 2004). That strong selection for increasing CT_{max} might be a consequence of extreme events is in keeping with theory (see "Introduction") and indicates that some variation for change in this trait might exist despite its known limited range compared to lower critical limits (see discussion in Chown 2001; Hoffmann et al. 2003). Moreover the direction of these climate effects is consistent across habitat-type groups and between reproductive modes. Although viviparity is thought to have evolved in cold and/or unpredictable climates to enhance fitness (e.g., cold climate hypothesis, maternal manipulation hypothesis; Tinkle and Gibbons 1977; Shine 1995, 2004; but see Crespi and Semeniuk 2004), strong selection for increased CT_{max} (and lower CT_{min}) in more variable environments is likely in viviparous species.

Predictions of animal, and especially ectotherm, responses to ongoing and forecast climate change have

Table 2: Predictor coefficients for the best-fit models for each performance curve parameter

	Estimate	SE
Preferred temperature:		
Log precipitation driest month	-2.59	.60
Log mass	-1.62	.49
Log precipitation driest month × log mass	.81	.33
Habitat:		
Aquatic species	36.16	1.93
Arboreal species	35.01	.98
Burrowing species	30.11	1.31
Ground-dwelling species	35.71	.88
Rock-dwelling species	35.45	.93
Critical thermal maximum:		
Diurnal temperature range	.18	.04
Habitat:		
Aquatic species	42.01	1.65
Arboreal species	40.76	.95
Burrowing species	37.84	1.07
Ground-dwelling species	40.16	.88
Rock-dwelling species	40.84	1.01
Reproduction:		
Oviparous	40.01	1.43
Viviparous	38.99	.42
Critical thermal minimum:		
Mean temperature of the wettest quarter	.14	.03
Temperature seasonality	-.003	.001
Reproduction:		
Oviparous	6.67	1.65
Viviparous	5.10	.51

placed much emphasis on temperature change and especially on increases in mean temperature (e.g., Thomas et al. 2004; Parmesan 2006; Musolin 2007; Huey et al. 2009). However, a major implication of our results is that forecasts of the effects of future climate change on terrestrial reptiles must take changes in precipitation and temperature variation into account. For example, if the evolved variation in T_p is largely a consequence of variation in precipitation, and if mean temperature increases in tropical regions are accompanied by increasing precipitation and/or cloud cover (Solomon et al. 2007; Adler et al. 2008), changes in mean thermal conditions may have little influence on the thermal safety margin of ectotherms in these regions, unlike previous forecasts (Deutsch et al. 2008; Huey et al. 2009). By contrast, forecast reductions in mid-latitude precipitation and cloud area fraction (see "Introduction"; Fung et al. 2011) suggest that species in these areas will be more at risk than previously thought. Indeed, if a thermal safety margin plot of the kind previously used to indicate risks to tropical ectotherm species (Deutsch et al. 2008; i.e., T_p - ambient temperature) is constructed using mean temperature of the warmest or wettest quarter

(the times of greatest reptile activity; Pianka and Vitt 2006) or using mean annual temperature (as in Deutsch et al. 2008), it is clear that species in midlatitudes, rather than in the tropics, are those already most at risk (fig. 3).

Further complexity is introduced when predicting impacts of climate change on performance curves by the fact that changes in diurnal temperature range, the primary climatic correlate of squamate CT_{max} , show strong spatial structure. While a decreasing diurnal temperature range is largely accompanied by increased cloud cover and precipitation in terrestrial areas, the most pronounced reductions in diurnal temperature range are taking place over arid regions or those with sparse or short vegetation, largely as a consequence of increases in daily minimum temperature. Here, greater than average warming and reductions in precipitation and cloud cover are also expected (Vose et al. 2005; Zhou et al. 2009a). Therefore, in these regions, one climatic signature that should promote further selection for resistance to unpredictable climate extremes in species already at the margins of their tolerance (fig. 3) is weakening. Given the positive relationship between T_p and CT_{max} ($R^2 = 0.55$, $P < .0001$; plot available in Dryad, <http://dx.doi.org/10.5061/dryad.8665>), these environmental influences on CT_{max} are likely to interact with those affecting T_p . However, relatively high variation around the relationship between CT_{max} and T_p and differences in the likelihood of trait evolution in ectotherm generalists versus specialists (Kellerman et al. 2009) imply that considerable complexity of future evolved responses to climate change is likely. Although frequently neglected in modeling approaches, evolutionary dynamics are likely to be critical for species responses to changing climates (Kellerman et al. 2009).

As opposed to the two other parameters of the performance curve, both mean temperature conditions and temperature variation were the strongest predictors of lower temperature limits. These findings are closest to what intuitively might be expected: lower limits to ectotherm activity are likely to be set by ambient temperatures because initial movement for thermoregulation is dependent on ambient temperatures at the start of activity (Cowles and Bogert 1944) and by temperature variation because higher frequency or magnitude of temperature extremes may impose additional selection on the lower margin of performance (Levins 1968; Watson and Hoffmann 1996). Increasing ambient temperatures in future climate scenarios would thus seem generally to have little negative significance for the lower limits to ectotherm performance. However, in temperate areas where increases in mean ambient temperature are not being accompanied by changes in the timing of low temperature extremes in the spring (e.g., Mulholland et al. 2009), any selection for an increase in CT_{min} as a consequence of increasing ambient temperatures

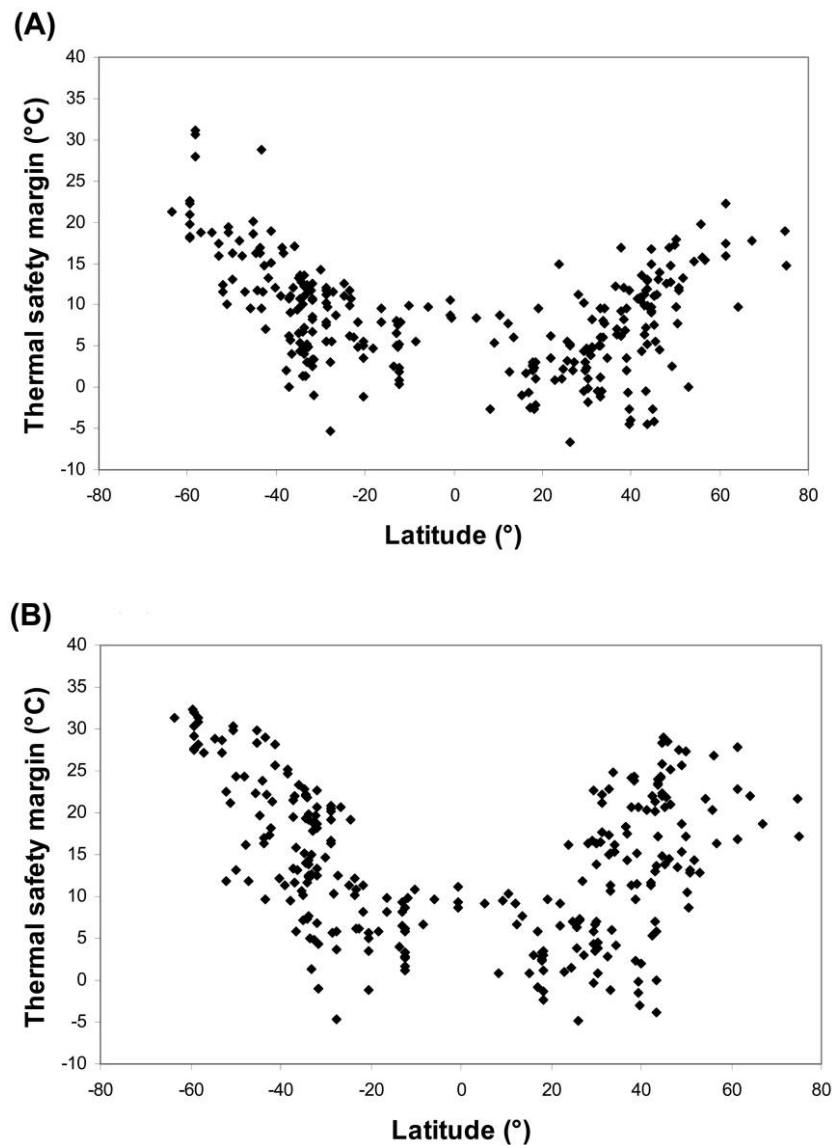


Figure 3: Plot of thermal safety margin (following Deutsch et al. 2008) against latitudinal position adjusted for altitude. *A*, Thermal safety margin is calculated as the difference between optimal temperature (here, preferred temperature T_p) and mean temperature of the warmest quarter. Species at midlatitudes have the lowest safety margin, indicating that the optimum body temperature for these species is closest to average ambient temperature conditions, increasing the likelihood of reduced performance with warming. *B*, This pattern is consistent when thermal safety margin is calculated with mean annual temperature.

may in fact have considerable negative impacts on performance.

In conclusion, the results of this study demonstrate that variation in environmental temperatures and variation in precipitation have had significant influences on two major components of reptile thermal performance curves. The influence of mean conditions on the third major variable of thermal performance curves, CT_{min} , may also help account for complex relationships among these performance

traits (Angilletta 2009; figures with these relationships are available in Dryad, <http://dx.doi.org/10.5061/dryad.8665>). Overall, these results show that the impacts of climate change on ectotherms will not be straightforward to predict. Spatially variable forecasts for changes in climate variables, the local effects of humans on these variables (Nair et al. 2003), and habitat structure (Zhou et al. 2009b), coupled with variation in the evolutionary responses of species (Kellermann et al. 2009), make this especially likely.

Recent smaller-scale studies of other groups (Helmuth et al. 2006; Mulholland et al. 2009; Zimmermann et al. 2009), have also demonstrated that biological responses to environmental change are not as straightforward as some earlier considerations might have suggested. Thus, current uncertainty regarding the biological consequences of climate change is perhaps larger than generally acknowledged, emphasizing that strategies for mitigation of climate change may be more effective for long-term conservation than those for assisting biodiversity to adapt, either through relocation or other interventions.

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Despite the high diversity of ecological and life-history characteristics among squamate reptiles, climate variables such as rainfall have had strong influences on the thermal performance of this group. Some exemplars: top left, Cape dwarf chameleon *Bradypodion pumilum*; top right, Southern rock agama *Agama atra*; bottom left, rock monitor *Varanus albigularis*; bottom right, Ovambo tree skink *Trachylepis binotata*. Photographs by Susana Clusella-Trullas.