

Short-term predicted extinction of Andean populations of the lizard *Stenocercus guentheri* (Iguanidae: Tropidurinae)

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ABSTRACT

We studied the thermal physiology of the Andean lizard *Stenocercus guentheri* in order to evaluate the possible effects of global warming on this species. We determined the preferred body temperature (T_{pref}), critical thermals (CTmin, CTmax), and hours of restriction and activity. T_{pref} was 32.14 ± 1.83 °C; CTmin was 8.31 °C in adults and 9.14 °C in juveniles, whereas CTmax was 43.28 °C in adults and 41.68 °C in juveniles. To assess extinction risk, we used the model created by Sinervo et al. (2010) and predicted that 16.7% of populations will have a high risk of extinction by 2020, with an increase to 26.7% by 2050. These results suggest that this species, despite being able to maintain its T_{pref} through behavioral thermoregulation and habitat selection, could be physiologically sensitive to climate warming; thus, the potential for local adaptation may be limited under a warmer climate. Further studies focusing on the ability of *S. guentheri* to evolve higher T_{pref} and thermal tolerances are needed to understand the ability of this species to respond to climate change.

1. Introduction

Global warming is one of the greatest threats to global biodiversity (Malcolm et al., 2006; Thomas et al., 2004; Vörösmarty et al., 2010). The global mean surface temperature increased by 0.85 °C (range: 0.65–1.06 °C) over the period 1880–2012. The decade 2003–2012 has been the warmest in the instrumental record. Climate projections indicate that in this century global mean surface air temperature could increase between 0.9 and 2.3 °C under the best emissions scenario, and between 3.2 and 5.4 °C under worse scenarios (IPCC, 2014).

Both yearly minimum and maximum temperatures have increased in South America, with the daily temperature amplitude (i.e., difference between the lowest and highest daily temperatures) dropping in some regions (Barry and Seimon, 2000). In Venezuela, Colombia, Ecuador, and Peru, the mean annual temperature has increased by 0.8 °C in the last century (Herzog et al., 2011), which has caused retreat of the tropical Andean glaciers at an increasing rate since the late 1970s (Rabatel et al., 2013). Projections of climate change in the tropical Andes indicate a trend of continuous warming throughout this century, with a higher temperature increase at higher altitudes (Herzog et al., 2011; Vuille et al., 2008). Further changes in hydrological cycles are also predicted, with increasing rainfall during the wet season and decreasing rainfall during the dry season (Vuille et al., 2008).

Climate change has an impact on different aspects of species natural histories, such as phenology, morphology, physiology, and behavior (Deutsch et al., 2008; Inouye, 2008; Przybylo et al., 2000). The vulnerability of species to climate change depends on their sensitivity to environmental changes, the degree of exposure to changes, their resilience, and their adaptive potential (Williams et al., 2008). In addition, the impact of climate change on species varies geographically (Thomas et al., 2004); for instance, thermal tolerance of many organisms is proportional to the magnitude of annual variation in temperature (Ghalambor et al., 2006), a feature of climate that increases with latitude. Therefore, those species with narrower thermal tolerances, such as tropical species, would be the most affected by climate change (Williams et al., 2007). Likewise, altitudinal patterns affect the operative temperature of an organism (Angilletta, 2009). Hence, organisms with the highest extinction risk are those with narrow thermal tolerance, limited acclimation ability, and reduced dispersal (Deutsch et al., 2008).

Most physiological processes in reptiles are temperature dependent and frequently optimal only within a narrow range of body temperatures, known as the optimal temperature range (Huey and Stevenson, 1979). Essentially, temperature affects all aspects of behavior and life history of reptiles, including locomotion, reproductive biology, sensory information, foraging ability, courtship, and feeding and growth rates

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(Angilletta et al., 2002; Boretto and Ibargüengoytia, 2009; Espinoza et al., 2004; Ibargüengoytia et al., 2010; Meiri et al., 2013; Sears, 2005; Zug et al., 2001). In addition, temperature is a determining factor for species distribution ranges (Andrews, 1998).

The thermo-physiological profile of a reptile species is essential to predict the effect that global warming will have on species range and survivorship. To visualize the effect of temperature increase on the fitness of a species, it is necessary to know how closely the body temperatures (T_b) experienced in nature relate to the optimal temperature of performance (T_o ; Angilletta, 2009), which generally coincides with the preferred temperature (T_{pref}) measured in the laboratory (Martin and Huey, 2008). Likewise, knowledge of critical thermal minimum and maximum temperatures is necessary to calculate the limits of thermal tolerance, rates and efficiencies of performance, and the relationship between latitude and the ranges of thermal tolerance (Grigg and Buckley, 2013; Huey et al., 2009; Huey et al., 2012). Another important factor in reptiles like lizards is the potential for behavioral thermoregulation. The effectiveness of lizards to thermoregulate depends on environmental sources of heat gain and loss (Zug et al., 2001). To evaluate this factor, it is necessary to know the hours of restriction and hours of activity. Hours of restriction are the daily number of hours a lizard must spend in a refuge due to excessive environmental heat; consequently, lizards have limited time available for foraging, dispersal and reproduction (Sinervo et al., 2010). Hours of activity are the daily number of hours that remain for lizards to fulfill their vital tasks. Global warming may increase the hours of restriction and decrease the hours of activity experienced by a population, reducing population growth rates and increasing extinction risk (Sinervo et al., 2010).

Studies of thermal physiology of tropical species of lizards are scarce (Jordán and Pérez, 2012; Sepúlveda et al., 2008; Van Berkum et al., 1986), and, to our knowledge, there are no published studies on species from the tropical Andes, one of Earth's hotspots (Myers et al., 2000) severely affected by climate warming (Rabatel et al., 2013). The purpose of this study is to determine the preferred body temperature, critical thermal temperatures, and hours of restriction and activity in the Andean lizard *Stenocercus guentheri*, and use these data to predict possible population-level effects of global warming. This species is an active thermoregulator that inhabits the northern Andes of Ecuador at an elevation range of 2135–3890 m (Carvajal-Campos, 2009; Torres-Carvajal and Mafía-Endara, 2013).

2. Materials and methods

2.1. Study area and field work data collection

This study was carried out in one of the last patches of Dry Andean Matorral and Dry Montane Forest in the Northern Andes. The study site lies in Parque Recreacional y Bosque Protector Jerusalem (00° 00' 19" –00° 00' 51" N, and 78° 21' 06" –78° 24' 08" W), a 1109 ha protected area with an elevation range of 2450–3000 m (Navarrete, 2010).

Five one-day sampling trips were conducted from 24 March to 21 April 2014, in which 39 specimens (13 males, 14 females, and 12 juveniles) were caught between 9:00–12:00 by noosing. We measured body temperature (T_b) of 22 of these individuals immediately after capture using a thermocouple (Omega 4-Channel Handheld Data Logger Thermometer) externally over the cloacal region. Additionally, we validated the data by performing a comparative test between temperature recorded externally and temperature recorded by introducing the thermocouple in the cloaca. We recorded these two data in 15 lizards simultaneously, every two minutes during ten minutes. Then we performed a Paired Samples *t*-test using the means of each individual, for each method. And no difference were found (*t*-test, $t=-1.311$, $P=0.211$).

We recorded the environmental temperature at the capture sites by

measuring substrate temperature and air temperature 1 cm above the ground. Body mass was recorded for each lizard using a precision digital scale (My Weigh I300), and reproductive status (Juvenile/Adult) and sex were determined by observation of phenotypic traits (Torres-Carvajal, 2007). Lizards were maintained at room temperature (22 °C) in plastic terrariums for four days during the experiments, and subsequently re-released at capture sites.

2.2. Thermal preference

T_{pref} was obtained in the laboratory (between 9:00–13:00) one day after capture. Lizards ($N=39$) were put directly into thermal gradients (substrate temperature range: 23–63 °C; air temperature range: 23.5–40 °C) that consisted of plywood board tracks that were each 1 m long, 12 cm wide and 20 cm high. The substrate was made of plywood as well. The thermal gradient was created along each channel by placing a 100 W light bulb as a heat source at one end. Body temperature was recorded in real time using a thermocouple that was placed anterior to the cloacal region and secured with medical cloth tape (Corbalán et al., 2013). Lizards were placed in individual channels for an hour and a half with an acclimation period of 15 min. Body temperature of each lizard was recorded every 30 s. Mean T_{pref} was calculated by averaging the recorded body temperatures of each lizard. Individual mean T_{pref} values were averaged among all lizards within age and sex classes to get the mean population T_{pref} (Angilletta and Werner, 1998).

We compared the data between groups (males, females, and juveniles) using One-Way-ANOVA. Assumptions of normality and variance-homogeneity were tested with the one-sample Kolmogorov-Smirnov and Levene tests, respectively. We also performed a Student's *t*-test to compare (1) T_{pref} and T_b of this species, as well as (2) both T_{pref} and T_b of *S. guentheri* with T_b of Tropidurinae (Tropiduridae in Sinervo et al. (2010)).

2.3. Critical thermal temperatures

Tolerance to low temperatures was measured using the critical thermal minima measurement (CTmin) 2 days after capture ($N=35$). CTmin was determined by placing each lizard in a transparent and dry glass chamber that was immersed in ice water; the chamber temperature was dropped at a rate of 0.8 °C/min from 22.8 °C to a minimum value of 0 °C. Body temperature was recorded in real time using a thermocouple that was placed anterior to the cloacal region and secured with medical cloth tape, every 30 s until the individual was unable to right itself after being placed on its back.

The tolerance to high temperatures was measured using the critical thermal maxima (CTmax) 3 days after capture ($N=35$). CTmax was determined using the same procedure as for the CTmin, but with a chamber immersed in water heated by a stove from 20.4 °C to a maximum temperature of 54.8 °C at approximately 1.8 °C/min.

Mean critical thermal temperatures were calculated averaging temperature values of all lizards in each group (males, females, and juveniles). We compared the data between groups using One-Way-ANCOVA, with body mass as covariate. Tukey test ($P>0.05$) was applied for means comparison. Assumptions of normality and variance-homogeneity were tested with the one-sample Kolmogorov-Smirnov and Levene tests, respectively.

2.4. Operative temperature (T_e)

The operative environmental temperature represents the internal T_b that a lizard may experience in its natural environment (Dzialoeski, 2005). Measurements of T_e are used to assess the availability of thermal microenvironments in the range of optimal physiological temperatures (Williams et al., 2008). In order to estimate T_e in the field, physical models of lizards were placed at five representative microhabitats used by *Stenocercus guentheri*.

Models were constructed using gray PVC pipes, 2 cm in diameter and 10 cm long, with the ends sealed with liquid silicone. The models were connected in pairs to V2-Pro HOBO data loggers, with one model on each of two probes. For each data logger, one model was placed in a shaded refuge site, whereas the other was placed in a sun-exposed site similar to where active lizards were observed. Data loggers were launched for five months between 23 March and 23 August 2014 to record T_e . T_e on each probe was recorded every 5 min. These models were calibrated using live specimens that were placed on the same microhabitats of models, and monitored in real time with a thermocouple taped to their bellies ($R^2=0.951$, $P < 0.001$).

We used the T_e recorded in the field to calculate the number of hours in which lizards must retreat to shelters to avoid overheating (H_r). According to the Sinervo et al. (2010) model, H_r is calculated as the number of hours per day in which the average T_e across all models is higher than the T_{pref} . Additionally, we calculated the hours of activity, H_a – hours that lizards are active outside their shelters performing various behaviors (Ibargüengoytia, 2005) – as the number of daily hours in which T_e is between the minimum temperature of activity and T_{pref} of the species. In accordance with Sinervo et al. (2010), we assumed that the minimum temperature of activity for thermoregulatory species is 25 °C.

To calculate the relationship between H_r and daily maximum air temperature (T_{max}), daily T_{max} records for the same days in which the lizard models were deployed were obtained from a weather station operated by Instituto Nacional de Meteorología e Hidrología (INAMHI) located 4-km-away (Guayllabamba).

A linear regression of H_r versus the difference between T_{max} and T_{pref} was performed to obtain the equation: $H_r = \text{slope} * (T_{max} - T_{pref}) + \text{intercept}$ for values measured in the field. This equation was then used to model extinction based on T_{max} values from global climate layers for the years 1975, 2010, 2020, 2050 and 2080.

2.5. Model of extinction prediction

The model introduced by Sinervo et al. (2010) was used to predict where extinctions of *S. guentheri* populations are likely to occur. This model integrates georeferenced points of species distribution, T_{pref} , global daily maximum temperature surfaces, and a predictive equation for hours of restriction (H_r), based on operative environmental temperature (T_e) and T_{max} for the years of 1975, 2010, 2020, 2050, and 2080. The model estimates the breakpoint at one of these specific decades in which the value of H_r is too high for a population to be viable according to the physiological model of local extinction (*sensu* Sinervo et al., 2010).

A total of 217 georeferenced localities (WGS84) of occurrence of *Stenocercus guentheri* were obtained from the collection database of Museo de Zoología QCAZ, Pontificia Universidad Católica del Ecuador. Of these, 30 localities representing distinct populations were included in the extinction model (Table A.1), because they were separated from each other by at least 1 km, a requirement to avoid pseudoreplication (Peterson et al., 2004).

We used R (R Core Team, 2014) to extract T_{max} values for each of the 30 chosen localities from global climate layers available at WorldClim (www.worldclim.org) for the year 1975 (climate database from 1950 to 2000), and the IPCC 4th Assessment, CCSM A2a scenario (10-arc minute resolution) predictions for T_{max} in the years 2010, 2020, 2050 and 2080. The T_{max} values for the 30 localities were applied to the linear equation in order to predict the average H_r experienced by each population year-round in order to predict local population extinctions throughout the range of *Stenocercus guentheri*. We constructed a map of predicted extinction sites by date of expected extinction using ArcGIS (ESRI, 2014).

To consider whether the 30 localities where *S. guentheri* occurs have different climatic properties, we conducted a Principal Component Analysis (PCA), using 19 temperature and precipitation-

Table 1

Thermal preference (T_{pref}), Body temperature (T_b), Critical thermal minima (CTmin) and maxima (CTmax) for juveniles and adults of *Stenocercus guentheri*. Mean, Standard Error (SE), and lower and upper bounds of a 95% confidence interval are given.

	Mean	SE	95% Confidence interval	
			Lower bound	upper bound
T_{pref} (N=39)	32.14	0.298	31.535	32.743
T_b (N=22)	31.93	0.506	30.879	32.985
CTmin				
Juveniles (N=12)	9.14	0.646	7.821	10.452
Adults (N=23)	8.31	0.423	7.446	9.168
CTmax				
Juveniles (N=12)	41.68	0.851	39.947	43.406
Adults (N=23)	43.28	0.520	42.227	44.339

based bioclimatic variables (BioClim) generated from climatic data provided by Ministerio del Ambiente de Ecuador (MAE, 2013).

3. Results

3.1. Preferred temperatures and critical thermals

T_{pref} , T_b , CTmin, and CTmax values are presented in Table 1. There were no differences in T_{pref} among males, females and juveniles (ANOVA, $F=1.262$, $P=0.295$). Consequently, the average T_{pref} for all individuals, 32.14 ± 1.83 °C ($N=39$), was pooled in other analyses. We found no differences in T_b measure in the field among groups (ANOVA, $F=1.913$, $P=0.175$), the average T_b was 31.93 ± 2.32 °C ($N=22$). Additionally, we found no difference between T_{pref} and T_b (*t*-test, $t=0.378$, $P=0.707$). By contrast, both T_{pref} and T_b of *S. guentheri* differed significantly from values proposed for the clade Tropidurinae (*t*-test, T_{pref} : $t=-3.520$, $P=0.001$ and T_b : $t=-3.037$, $P=0.003$).

CTmin was significantly different between males, females, and juveniles (ANCOVA, $F=4.73$, $P=0.008$) and the Tukey test ($P > 0.05$) showed differences between adults and juveniles. Hence, we established that CTmin is 8.31 °C in adults and 9.14 °C in juveniles (Table 1). Similarly, CTmax was significantly different among males, females and juveniles (ANCOVA, $F=7.317$, $P=0.001$), and the Tukey test ($P > 0.05$) showed differences between adults and juveniles. Hence we established that CTmax is 43.28 °C in adults and 41.68 °C in juveniles (Table 1).

3.2. H_r , H_a and extinction prediction

Fluctuations of H_r and H_a for *Stenocercus guentheri* as calculated from data loggers deployed April – August 2014 are shown in Fig. 1. During the five months evaluated, H_r ranged between 1.31 and 5.57 h,

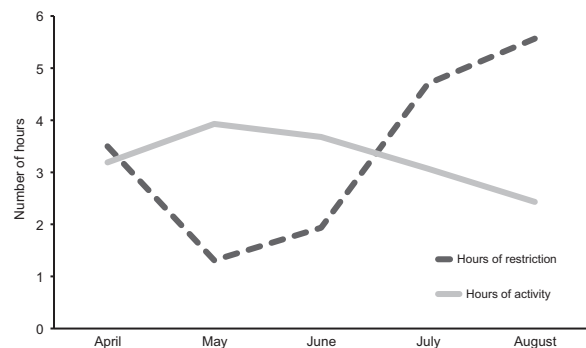


Fig. 1. Fluctuation of the hours of restriction (H_r) and hours of activity (H_a) at Parque Recreacional y Bosque Protector Jerusalem, Ecuador plotted by month (2014). The solid line shows the number of hours of activity, H_a , when T_e is between 25 °C and 32.14 °C (T_{pref}). The dotted line shows the number of hours of restriction, H_r , when T_e exceeds T_{pref} .

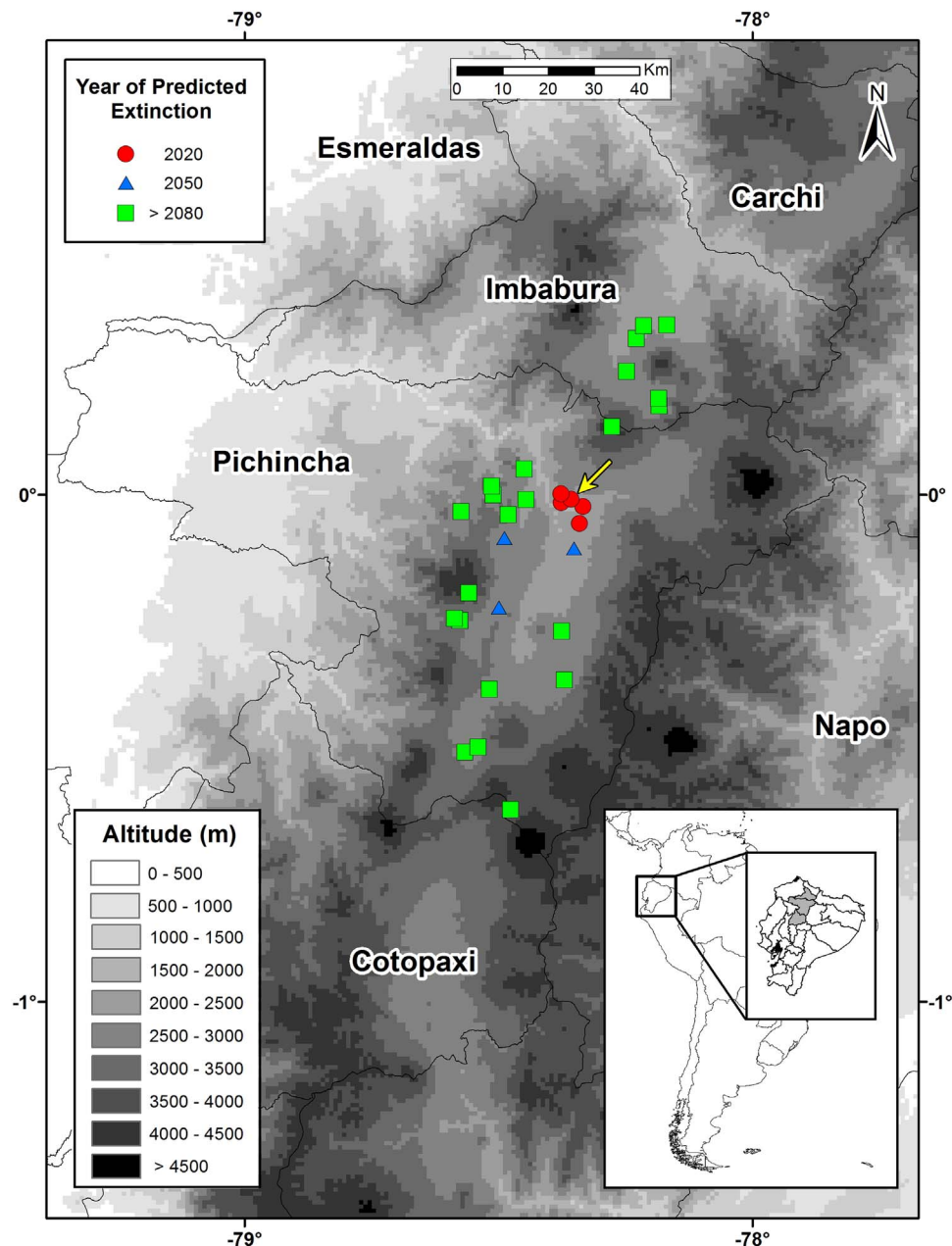


Fig. 2. Map of predicted extinction for 30 sampled populations of *Stenocercus guentheri* from northern Ecuador. The yellow arrow indicates our field site. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

while H_r ranged between 2.43 and 3.93 h. A significant and positive correlation between H_r and the difference between T_{\max} and T_{pref} was found (Pearson correlation, $R=0.738$, $N=143$, $P<0.001$). The linear equation describing this relationship was: $H_r = 1.02222*(T_{\max}-T_{\text{pref}}) + 10.113$.

Using georeferenced points of distribution, the T_{pref} obtained in the laboratory, global monthly T_{\max} surfaces, and the equation mentioned above, we estimated which decade the hours of restriction become too high for a population to be viable according to the physiological model of local extinction. We found that by 2020, 16.67% of the populations have a high risk of extinction, and this increases to 26.67% by 2050 (Fig. 2). The PCA shows that populations with high risk of extinction by 2020 occur in localities with similar climatic properties (Fig. 3). The first component explained 66% of the variance in the data, which represents the temperature-based bioclimatic variables. PC-2 explained 16.2% of variance, and also represents the temperature-based variables (Table 2).

4. Discussion

Many *Stenocercus guentheri* populations persist despite the threat of warming, even through 2080 (Fig. 2). These populations occur in environments with present-day temperatures (mean air temperature [T_a] range: 8.6–15.3 °C and mean T_{\max} range: 17.5–28.5 °C) that are lower than those areas containing populations at greater risk of extinction (mean T_a range: 14.1–17.3 °C; mean T_{\max} range: 27.5–28.6 °C), and that share temperature-based bioclimatic properties (Fig. 3; Table 2). These findings are disturbing because some of the populations predicted to go extinct five years from now currently have high population densities (MBA, personal observation). Populations that live in the coolest environments, such as at high altitudes, may even benefit from an increase in T_a if environmental temperatures are typically below the species' T_o (Buckley, 2008; Kearney and Porter, 2004; Kearney et al., 2009).

Thermoregulating lizards have behavioral or physiological mechan-

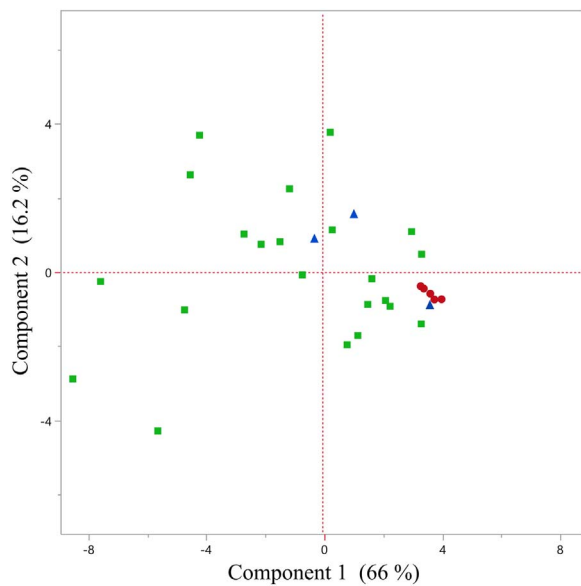


Fig. 3. Principal component analysis (PCA) showing variation in climate among 30 sampled localities of occurrence of *Stenocercus guentheri*. Red circles show localities with predicted extinction by 2020, blue triangles show localities with predicted extinction by 2050, green squares show localities with predicted extinction by 2080. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Table 2

PCA loadings, eigenvalues, and percent variance explained for the first two PCs for the 19 temperature and precipitation-based bioclimatic variables analyzed.

Variable	PC-1	PC-2
BIO1=Annual mean temperature	0.0902	0.0367
BIO2=Mean diurnal range	0.1583	0.1060
BIO3=Isothermality	−0.0560	0.0473
BIO4=Temperature seasonality	−0.0268	−0.0486
BIO5=Max temperature of warmest month	0.0696	0.0298
BIO6=Min temperature of coldest month	0.1344	0.0508
BIO7=Temperature annual range	0.1347	0.0649
BIO8=Mean temperature of wettest quarter	0.0909	0.0352
BIO9=Mean temperature of driest quarter	0.0876	0.0394
BIO10=Mean temperature of warmest quarter	0.0910	0.0356
BIO11=Mean temperature of coldest quarter	0.0877	0.0392
BIO12=Annual precipitation	−0.0010	0.0018
BIO13=Precipitation of wettest month	−0.0105	0.0329
BIO14=Precipitation of driest month	−0.0206	0.0087
BIO15=Precipitation seasonality	0.0234	−0.0082
BIO16=Precipitation of wettest quarter	−0.0020	0.0080
BIO17=Precipitation of driest quarter	−0.0065	0.0040
BIO18=Precipitation of warmest quarter	−0.0007	0.0038
BIO19=Precipitation of coldest quarter	−0.0024	0.0038
Eigenvalue	12.549	3.077
% Variance	66.050	16.195

isms to efficiently achieve T_b close to their T_{pref} (Díaz and Cabeza-Díaz, 2004; Ellis et al., 2006; Huey, 1982; Seebacher and Franklin, 2005). We found that in *Stenocercus guentheri* the T_{pref} measured in the laboratory (32.14 ± 1.83 °C) closely matches the active body temperature recorded in the field (31.93 ± 2.32 °C). Even though these lizards are able to maintain their T_{pref} through behavioral thermoregulation and habitat selection, T_b and thermal tolerances are phylogenetically conserved (Huey et al., 2009), rather than dependent on ecological filtering, dispersal, or local adaptation (Grigg and Buckley, 2013). These constraints limit the potential for local adaptation that might potentially soothe the impact of climate change (Angilletta, 2009), which has been predicted to be particularly severe for tropical species (Huey et al., 2009; Tewksbury et al., 2008). Moreover, although T_{pref} and T_b values of *Stenocercus guentheri* differ from the mean T_b value

reported for the clade Tropidurinae (33.7 ± 0.35 °C; $N=73$; Sinervo et al., 2010), *S. guentheri* could still be constrained by a low potential for evolution of thermal tolerances (Angilletta, 2009). The temperature values of Tropidurinae reported by Sinervo et al. (2010) are mostly from lowland species (elevation range: 1–2055 m; mean = 306 m); therefore they should be used with caution in comparisons with highland taxa, such as *S. guentheri* (elevation range: 2135–3890 m), because if we compare our data with species of Tropidurinae occurring above 1000 m (32.86 ± 0.63 °C; $N=8$; Sinervo et al., 2010), T_b values of *S. guentheri* are not different from Tropidurinae.

We found that adults had a larger thermal tolerance breadth ($CT_{min}-CT_{max}$: $8.31 - 43.28$ °C) than juveniles ($9.14 - 41.68$ °C). Because a narrow thermal tolerance breadth confers sensitivity to climate warming (Grigg and Buckley, 2013), juvenile *S. guentheri* are more at risk than adults. This may decrease the rates of recruitment into adulthood, thereby causing population declines. These ontogenetic differences in critical thermal tolerances suggest that the physiological systems underlying thermal tolerance change with age, possibly leading to differential use of microhabitats by juveniles and adults.

Although our analyses indicate that some populations of *Stenocercus guentheri* are at high extinction risk due to climate warming, these results should be interpreted with caution for three reasons. First, even though this species has low T_{pref} values, it could still be active at higher temperatures below CT_{max} . Second, the areas occupied by this species are complex, with several microhabitats available as resting or activity sites. However, climate change can also affect habitat structure (Holmgren et al., 2006; Salazar et al., 2007), potentially changing the thermal properties of the microhabitat (i.e., increased warming due to loss of vegetation cover) (Allen et al., 2010). Third, lizards in the most vulnerable localities (lower elevations) could disperse to more suitable (i.e., colder) areas at higher elevations.

Thermoregulation is a complex process that must integrate detection of temporal and spatial variation in the thermal environment with behavioral and physiological responses (Seebacher and Shine, 2004; Valdecantos et al., 2013). Thus, to better understand the efficiency in thermoregulation achieved by this species, it is important to collect additional information. For instance, we can incorporate physiological and microclimate variation data from other localities with different climatic properties where *S. guentheri* is known to occur (Clusella-Trullas and Chown, 2011). Present-day and short-term extinctions predicted by our model can be easily validated by visiting the corresponding localities, including our study site, after the time extinctions are predicted. The ability to validate and adjust the model is the major strength of this type of analysis.

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Appendix A

See Appendix Table A1.

Table A.1

Name, province, latitude, longitude and elevation (m) of 30 localities of occurrence of *Stenocercus guentheri* used in this study. Data were obtained from Museo de Zoología QCAZ, Pontificia Universidad Católica del Ecuador.

Locality	Province	Latitude	Longitude	Elevation
Limpipungo lake	Cotopaxi	−0.6208	−78.4762	3800
Machachi (around the Factory “Tesalia”)	Pichincha	−0.5074	−78.5659	2921
Machachi	Pichincha	−0.4973	−78.5403	2851
Uyumbicho	Pichincha	−0.3831	−78.5183	2663
Pintag	Pichincha	−0.3650	−78.3701	3000
Ilalo (ranch Chuspiyacu)	Pichincha	−0.2690	−78.3759	2576
Lloa	Pichincha	−0.2479	−78.5757	3086
Lloa (20 m from the main entrance)	Pichincha	−0.2441	−78.5866	3059
Quito (Itchimbia)	Pichincha	−0.2226	−78.4990	2894
Quito (brook Cóndor Huachana)	Pichincha	−0.1936	−78.5583	3783
Tababela	Pichincha	−0.1057	−78.3510	2297
Pusuquí	Pichincha	−0.0857	−78.4884	2653
Guayllabamba	Pichincha	−0.0564	−78.3406	2155
Casitagua (near Pomasqui)	Pichincha	−0.0390	−78.4810	3305
Alambi hill	Pichincha	−0.0330	−78.5740	2655
Road Pisque river – Parque Recreacional y Bosque Protector Jerusalem	Pichincha	−0.0234	−78.3337	2020
Parque Recreacional y Bosque Protector Jerusalem (1)	Pichincha	−0.0153	−78.3767	2600
San Antonio de Pichincha	Pichincha	−0.0091	−78.4458	2412
Parque Recreacional y Bosque Protector Jerusalem (detour to Malchingui)	Pichincha	−0.0087	−78.3573	2273
Calacali (stadium)	Pichincha	−0.0001	−78.5106	2833
Parque Recreacional y Bosque Protector Jerusalem (2)	Pichincha	0.0020	−78.3770	2380
Calacali (Simón Bolívar Street)	Pichincha	0.0171	−78.5135	3001
Quito (20.9 km N)	Pichincha	0.0510	−78.4500	2455
Tabacundo (Mojanda lake)	Imbabura	0.1349	−78.2771	3150
Itambi river	Imbabura	0.1757	−78.1839	2707
Otavalo (San Pablo, COUSIN hostel)	Imbabura	0.1904	−78.1847	2738
Otavalo (Jatunyacu river)	Imbabura	0.2435	−78.2482	2536
Ibarra (Panamericana 7.5 km N)	Imbabura	0.3080	−78.2290	2447
Atuntaqui	Imbabura	0.3331	−78.2140	2412
San Antonio de Ibarra	Imbabura	0.3351	−78.1688	2330

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