

PONTIFICIA UNIVERSIDAD CATÓLICA DEL ECUADOR
FACULTAD DE CIENCIAS EXACTAS Y NATURALES
ESCUELA DE CIENCIAS BIOLÓGICAS

Analysis of the thermal physiology of the Andean lizard *Stenocercus festae* (Squamata: Iguanidae: Tropidurinae) to predict possible extinctions in their populations due to climate change

Disertación previa a la obtención del
Título de Licenciada en Ciencias Biológicas

ESTEFANY SOFÍA GUERRA CORREA

QUITO, 2016

**Analysis of the thermal physiology of the Andean lizard *Stenocercus festae*
(Squamata: Iguanidae: Tropidurinae) to predict possible extinctions in their
populations due to climate change**

Estefany Guerra-Correa, Andrés Merino-Viteri, Omar Torres-Carvajal

Museo de Zoología, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Avenida 12 de Octubre y Roca, Apartado 17-02-2184, Quito, Ecuador.

ABSTRACT

We studied the thermal physiology of the Andean lizard *Stenocercus festae*, a thermoregulatory lizard that inhabits sub-Andean forests at southern Ecuador, to address the potential effects of climate change on its populations. Experimental data showed that the preferred body temperature (T_{pref}) was 21.79 °C, the minimum critical thermal (CT_{min}) was 6.20 °C, and the maximum critical thermal (CT_{max}) was 46.24 °C. We applied the model for thermoregulatory lizards proposed by Sinervo et al. (2010) that integrates georeferenced points of species distribution, the T_{pref} obtained in the field, the lowest temperature at which lizards are active (T_{act}), the operative temperature (T_e), and daily maximum air temperature to get the number of hours of restriction (H_r , the number of hours per day when T_e exceeded T_{pref}) and hours of activity (Because this model was not suitable for this species, we modified it by proposing three different scenarios of T_{pref} and T_{act} values, as well as by changing the way we predict extinctions from restriction hours. Both modifications predicted that on 2010, 13.8% of the populations had already gone extinct, including the population of study; by 2020, 60% of the populations that went extinct in 2010 will probably recover by recolonization. Warming tolerance (WT), compared with a closely related species, showed that *S. festae* tolerates higher

temperatures than *S. guentheri* because it presents a wider difference between its CT_{\max} and the average and maximum T_{air} , as well as a wider thermal tolerance breadth.

Key words: Climate change, critical thermals, extinction risks, lizard, warming tolerance.

1. INTRODUCTION

In the past century, an increase in temperature by about 0.6°C, the decrease of glaciers on earth's surface, and the rise of global sea level by about 20 cm have revealed serious environmental effects caused by climate change (King, 2004). The main factor that has triggered these climatic problems is attributed to the intense anthropogenic action on natural systems (Deutsch et al., 2008). Therefore, deforestation, pollution, and the increase of greenhouse emissions are contributing not only to alter the environment but also the ecology, abundance, and genetic diversity; as well as the phenology, physiology, morphology and behavior of organisms across all ecosystems (Deem, 2015; Kubisch, 2013).

For both flora and fauna, there are ecological impacts due to climate change. Some examples are the modification in timing of breeding (Parmesan, 2007), migration of birds, time of spawning in amphibians and timing of flowering of plants (Walther et al., 2002), and shifts on their spatial distribution (Azócar et al., 2013).

One of the greatest challenges for biologists is to understand how organisms are confronting such environmental variations (Travis, 2002). On one hand, some studies have shown that some organisms are able to move to different geographic areas with more favorable climate or adapt to new environmental conditions through behavioral adjustment, phenotypic plasticity or evolution (Buckley et al., 2013; Deem, 2015; Seebacher, 2005). These responses differ from one species to another by their sensitivity and grade of exposition to environmental changes, as well as their resilience and potential of adaptation (Williams et al., 2008). On the other hand, some organisms could fail to disperse, to adjust or adapt to changes, and hence its populations could culminate in a demographic collapse and local or total extinction (Sinervo et al., 2010). In this sense, species with low tolerance to heating, limited ability of acclimatization and reduced dispersion, such as terrestrial

organisms living in tropical montane forests, have a greater risk of extinction than other species (Williams et al., 2007; Forero-Medina et al., 2010).

Ectotherms, in particular, exhibit rapid and sensitive responses to environmental temperature and rainfall alterations because their basic physiological functions, metabolic rates, ecological fitness, and survival are closely related to environmental conditions (Deutsch et al., 2008; Lind, 2008). In fact, their ecological functionality is described by a curve of thermal performance that gradually increases from the critical thermal minimum (CT_{min}) until it reaches a maximal point of performance known as the thermal optimum or optimum temperature (T_{opt}), from which it falls rapidly to the critical thermal maximum (CT_{max}) (Deutsch, 2008). The optimum temperature of an organism is strongly correlationated with the preferred temperature (T_{pref}); which is the temperature selected by the organism when it is placed in artificial thermal gradients. However, is important to consider that a perfect match between the preferred temperature and the thermal optimum does not always occur (Angilleta, 2009).

Among reptiles, almost all behavioral and life history aspects, such as locomotion, reproductive biology, sensory input, foraging, courtship, feeding, and growth rates are influenced by environmental temperature (Angilleta et al., 2002; Ibarguengoytía et al., 2010). For instance, due to their limited dispersion capacity, lizards take advantage of microclimates created by the environmental heterogeneity to thermoregulate (Gutiérrez et al., 2010). The effectiveness of this behavior depends on the availability of suitable thermal microclimates that contribute to the establishment of activity patterns, habitat selection, and appropriate spatial distribution (Corbalán et al., 2013). However, thermoregulation sometimes may be maladaptive because it may impose costs on competing functions like feeding, reproduction, and avoidance of predators (Sears, 2005).

Given that temperature affects the physiological and behavioral performance of many ectotherms (Navas, 2003), it seems reasonable to think that species distributed along tropical altitudinal gradients, where thermal clines and daily thermal fluctuations are drastic, will be threatened by climate change. In the Andes, if the regional temperature increases 2°C in the next few decades as predicted, extinction cascades and extreme changes on ecosystems will be stronger than those with less elevation ranges (Raven, 2011).

Knowledge on the influence of climate change on species interactions is still very limited (Tiessen, 2011). However, mathematical models have been developed to estimate how climate change will affect local populations. These models will help to implement effective strategies to protect ecosystems in the future (Sinervo et al., 2010).

The present study aims to analyze the vulnerability of the Andean lizard *Stenocercus festae* by integrating thermal biology data with climate variables to assess possible extinction risks due to environmental warming. We hypothesize that Sinervo's et al. (2010) model for thermoregulatory lizards will help assessing the influence of climate change on the study species and thus its possible extinction risks in the future. We also compare our data with a previous study on the Andean lizard *Stenocercus guentheri*.

2. MATERIALS AND METHODS

2.1. Species and area of study

Stenocercus festae occurs in the Andes of southern Ecuador, between 2300–3200 m (Torres-Carvajal, 2007). It inhabits low dry montane, wet montane and humid sub-Andean forests and is frequently found at the base of small bushes or nags. This study was conducted in hacienda “El Gullán”, property of the University of Azuay, located about 70 km SE of Cuenca (3.3383, -79.1717). It has an elevation range between 3000-3200 m and

it is mainly covered by pine plantations, pastures, crops and areas of natural vegetation. Fog and cold winds are characteristic of the zone, where the temperature fluctuates between 10 and 15°C (Ansaloni y Chacón, 2003).

2.2. Field work and data collection

2.2.1. Specimen collection

Twenty-seven specimens (10 males, 11 females, and 6 juveniles) were collected by noosing in two field trips on February and May-June 2015. Sampling was carried out from 9:00 to 15:00, when lizards were observed to be active. Body temperature (T_b) of each individual was measured immediately after capture using a thermocouple (Omega 4-Channel Handheld Data Logger Thermometer).

2.2.2. Operative temperature (T_e) and air temperature (T_{air}) measurements

The operative environmental temperature (T_e) is the internal body temperature of lizards in equilibrium with the environment (Dzialoeski, 2005). To estimate T_e we used physical models that simulate a lizard's phenotype in size and color. Each model consisted of a 12 cm long segment of PVC pipe connected to V2-Pro HOBO data loggers that recorded temperature data through two different channels every 5 minutes over a 10-month period (October-December 2014, February-August 2015). Four models were placed randomly at four different microhabitats used by *Stenocercus festae*, recording temperatures of both shelters and sites exposed to direct sunlight. An additional data logger was placed at approximately 1.50 meters above the ground to record the air temperature (T_{air}) during the period of study.

2.3. Laboratory experiments

To reduce the stress of individuals, we recorded thermal physiology data (T_{pref} , CT_{min} , CT_{max}), snout-vent length (SVL), and body mass directly in the study area. Each individual was kept for two days after capture and then exposed to thermal physiology experiments.

2.3.1. Preferred temperature (T_{pref})

To determine T_{pref} we built an eight lane (1 m long x 12 cm wide x 20 cm high)-wooden track. In each lane we installed a 100-watt light bulb at one end to obtain a thermal gradient in which the lizard was free to move along. In laboratory conditions, the end with the bulb powered on reached 42,6 °C, whereas the opposite end of the lane reached 23,6 °C. Temperature data was recorded in the program Omega Logging Recorder every 30 seconds for 2 hours through a thermocouple placed on the cloacal area of each individual.

For five lizards collected on February 2015 we measured T_{pref} in the laboratory at Museo de Zoología (QCAZ) of the Pontificia Universidad Católica del Ecuador, Quito after two days of acclimatization at 23 °C (the average air temperature of the lab). The T_{pref} of the remaining 22 lizards, collected on May-June 2015, was measured in the field after the two days of acclimatization at 14 °C (the average air temperature of the field).

2.3.2. Critical temperatures

CT_{min} and CT_{max} were obtained by placing each lizard in a clear glass chamber immersed in water. We attempted to cool and heat water at an approximate rate of 1.0–1.5°C per minute. With a thermocouple attached to the cloacal area, we recorded the lowest and highest temperatures at which the individual was unable to incorporate itself if placed on its back (Kubisch, 2013). In addition, during CT_{max} experiments, we registered the temperature of panting, known as the temperature at which the respiration frequency of

the individual increases to a point where it opens its mouth for breathing (Schmidt-Nielsen, 2002).

2.4. Data analysis

2.4.1 Statistical analyses

A one-way ANOVA was used to compare the data of T_{pref} and T_{b} between groups (male, female, and juvenile). Student's t -tests were used to compare T_{pref} with T_{b} , as well as T_{pref} and T_{b} of *S. festae* with T_{b} of Tropidurinae ($33.7 \pm 0.35^{\circ}\text{C}$; $N= 73$; Sinervo et al., 2010). A t -test was also used to compare T_{pref} measured in the laboratory with T_{pref} measured in the field. Data of critical temperatures (maximum and minimum) were compared between groups (male, female, and juvenile) using a one-way ANCOVA, with the body weight and SVL as covariates. For all the analyses, we conducted Kolmogorov-Smirnov and Levene's tests to assess the normality and homogeneity of variances, respectively. Statistical analyses were performed in SPSS software (IBM Corporation, 2015).

2.4.2 Model of predicted extinctions

To predict possible local extinctions of heliothermic lizards, Sinervo et al. (2010) developed an extinction risk model that integrates georeferenced points of species distribution, the T_{pref} obtained in the field, the temperature of activity (T_{act} , defined in this study in particular as the lowest temperature at which lizards are active), the operative temperature (T_{e}), and daily maximum air temperature to get the number of hours of restriction (H_{r} , the number of hours per day when T_{e} exceeded T_{pref}) and the number of hours of activity (H_{a} , the number of hours per day when T_{e} is less than T_{pref} and more than T_{act}). Even though this model has been successfully used with other lizards (Ceia-Hasse et al., 2013; Corbalán et al., 2013) we noticed that the physiological data of *S. festae* did not

fit the model. Consequently, we modified the model by adjusting T_{pref} and T_{act} values, as well as the way we predict extinctions from restriction hours.

We used three different scenarios of T_{pref} and T_{act} . (A) $T_{act}=25^{\circ}\text{C}$, the minimum temperature of activity for thermoregulatory species proposed by Sinervo et al. (2010), and $T_{pref}=28.1^{\circ}\text{C}$, the average T_b of all individuals in this study. (B) $T_{act}=16^{\circ}\text{C}$, the minimum T_b of lizards when captured, and $T_{pref}=20.5^{\circ}\text{C}$, the average of the T_{pref} measured in the field (N=22). (C) $T_{act}=16^{\circ}\text{C}$, the minimum T_b of lizards when captured and $T_{pref}=28.1^{\circ}\text{C}$, the average T_b of all individuals.

After obtaining T_{pref} and T_{act} , we used T_e data to calculate the hours of restriction (Hr) and hours of activity (Ha). For Hr we established a function that calculated the hours per day in which the average T_e of all the models is higher than the T_{pref} . Meanwhile, another function was used to calculate the number of daily hours when T_e is between the T_{act} and the T_{pref} to get the Ha .

Of 90-georeferenced localities of *S. festae* obtained from the database of the Museo de Zoología (QCAZ) of the Pontificia Universidad Católica del Ecuador, only 36 were included in the extinction model because they were considered different populations by being separated by, at least, 1 km from each other (Peterson et al., 2004) (Table S1).

To predict which lizard populations were at major risk of extinction, we first performed a linear regression between hours of restriction (Hr) and $T_{max}-T_{pref}$ to get the values of slope and intercept used later to run the extinction model. Using the above-mentioned 36 populations we applied the equation $Hr = \text{slope} * (T_{max} - T_{pref}) + \text{intercept}$ to launch the extinction model based on T_{max} values from global climate layers for the years 1975, 2010, 2020, 2050 and 2080 (Sinervo et al., 2010). To obtain the localities and the year of possible extinction, we compared each of the Hr of the years in question with the maximum Hr of the year 1975, as the model establishes. We also ran the model comparing

each of the *Hr* of the years in question with the maximum *Hr* of the year before. Analyses were performed using R software (R Core Team, 2015).

For both results, we constructed the map of predicted extinction sites by year using ArcGIS (ESRI, 2014). We also conducted a Principal Component Analysis (PCA) with 19 temperature and precipitation-based bioclimatic variables (BioClim) generated from climatic data provided by Ministerio de Ambiente del Ecuador, to evaluate if the 36 localities used in this study have different climatic properties (Andrango, 2015). This analysis was performed using JMP software (SAS Institute Inc., 2010).

2.4.1. Warming tolerance

We conducted an analysis that quantifies the average amount of environmental warming an ectotherm can tolerate before its performance drops to fatal levels, known as warming tolerance (WT) (Deutsch et al., 2008). For this, we calculated the difference between the mean critical thermal maximum (CT_{max}), and both the average and maximum air temperature of the organism's habitat, separately. In the case of *S. festae*, we took the average and maximum T_{air} from the data logger placed at the study area to collect air temperature data. We also calculate the WT of *S. guentheri*, for comparison, by using air temperature data provided by the Instituto Nacional de Meteorología e Hidrología (INAMHI).

3. RESULTS

3.1. Preferred temperatures and critical thermals

There were no significant differences in T_{pref} among males, females and juveniles (ANOVA, $F=2.383$, $p=0.114$). The average T_{pref} for all individuals was 21.79 ± 4.87 °C ($N=27$), whereas the average T_b was 28.11 ± 5.47 °C ($N=27$) (Table 1). The *t*-test between

T_{pref} and T_b of *S. festae* showed highly significant differences (t -test, $t=-3.566$, $p=0.001$). We also found highly significant differences between T_{pref} of *S. festae* and T_b of the Tropidurinae clade (t -test, $t=12.152$, $p<0.0001$), as well as T_b of *S. festae* and T_b of the Tropidurinae clade (t -test, $t=5.018$, $p<0.0001$). T_b of Tropidurinae ($33.7 \pm 0.35^\circ\text{C}$; $N= 73$; Sinervo et al., 2010).

A Student's t -test between the T_{pref} measured in the laboratory and the T_{pref} measured in the field shows that they are significantly different (t -test, $t= 3,468$, $p=0.002$). The average T_{pref} measured in the lab was $27.51 \pm 3.96^\circ\text{C}$ whereas the average T_{pref} measured in the field was $20.5 \pm 4.11^\circ\text{C}$.

There were no significant differences in CT_{min} among males, females, and juveniles (ANCOVA, $F=0.074$, $p=0.929$); mean CT_{min} for this species is $6.195 \pm 2.56^\circ\text{C}$ ($N=27$) (Table 1). We also found no significant differences in CT_{max} among males, females and juveniles (ANCOVA, $F=0.963$, $p=0.397$); average CT_{max} is $46.239 \pm 1.56^\circ\text{C}$ ($N=27$) (Table 1).

3.2. H_r , H_a , and model of predicted extinctions

The pattern of fluctuations of the number of H_r and H_a (Fig. 1) was different among the three scenarios analyzed. In scenario (A), H_r varied from 0 to 0.933 and H_a varied from 0 to 1.06. For scenario (B), H_r varied from 1.13 to 5.13 and H_a varied from 2.17 to 11.92. Finally, for scenario (C), H_r varied from 0 to 0.933 and H_a varied from 3.33 to 13.92. In scenarios A and B, lizards had more hours of restriction during February, while hours of activity peaked in February and October (Fig. 1). The relationship between H_r and the difference between T_{max} and T_{pref} exhibited a significant and positive correlation in all scenarios (Fig. 2).

We found no differences in the results of predicted extinctions among the three scenarios for T_{pref} and T_{act} (Fig. 3). By 2010, 13.8% of the populations went, including the studied population. By 2020 no additional populations will go extinct, but on 2050 and 2080 the proportion of extinct populations will increase to 22.2% and 38.9%, respectively (Fig. 3A). However, we found a different extinction scenario after modifying the way we use restriction hours to predict extinctions. In 2010, as above, 13.8% of the populations have gone extinct, including the population of this study. By 2020, three populations (60% of the extinct populations in 2010) probably will get reestablished by recolonization, including the population of study. In 2050 the number of populations extinct will increase to 16.67% including the three populations that probably were recolonized on 2020. By 2080 no additional populations will go extinct (Fig. 3B).

The PCA analysis showed that the 19 climatic variables did not explain the occurrence of extinctions on different years (Fig. 4). Climatic variances among populations are explained principally by temperature in Principal Component 1 (51.2%) and precipitation in Principal Component 2 (20.3%).

3.2.1. Warming tolerance

The difference between CT_{max} and the average T_{air} for *S. festae* was 34.59 °C (WT = 46.42 °C – 11.83 °C = 34.59 °C), while *S. guentheri* showed a lower difference, 25.46°C (WT = 42.76°C – 17.3°C = 25.46°C). Similarly, the difference between CT_{max} and the maximum T_{air} was 18.52°C (WT = 46.42 °C – 27.90 °C = 18.52 °C) for *S. festae*, and 13.26 °C (WT = 42.76 °C – 29.5 °C = 13.26 °C) for *S. guentheri*.

4. DISCUSSION

Due to behavioral mechanisms, such as basking, thermoregulatory lizards tend to exhibit similar T_b and T_{pref} values (Huey, 1982). Nevertheless, we found that the T_{pref} of *S. festae* (21.79 °C) did not closely match the active body temperature recorded in the field (28.11 °C). This could be caused by an effect of the air temperature of the habitat, T_{air} , at the time we measured T_b and T_{pref} (Deutsch et al., 2008, in supporting information). The average T_{air} when we collected the individuals was 28.6 °C whereas the average T_{air} when we measured the T_{pref} of all individuals was 16.24 °C. The average T_b is higher because lizards were exposed directly to sunlight at the moment of capture; nevertheless we have to consider that we are not measuring all T_b values a lizard can have in its microhabitat. The same could happen when we measured the T_{pref} ; we are experimenting with only one gradient influenced by the T_{air} of the place. We also found highly significant differences between the T_{pref} measured in the laboratory and the T_{pref} measured in the field, presumably due to the same effect of air temperature. The laboratory air temperature when we measured the T_{pref} of lizards captured during the first field trip on February (N=5) was 22.94 °C, giving an average T_{pref} of 27.50 °C. The remaining lizards (N=22) had an average T_{pref} of 20.5 °C and the air temperature was lower, 14.72 °C. Thus, we can assume that body and preferred temperatures of these lizards are affected by the air temperature of their habitats, although this involves constraints in individual performance (Deutsch et al., 2008, supporting information).

Even though lizard's thermal physiology presents conservatism across the phylogeny (Huey et al., 2009), we found highly significant differences between both T_{pref} and T_b of *S. festae* and the T_b reported for the Tropidurinae clade (33.7; Sinervo et al., 2010). These differences could imply constraints in *S. festae* that are explained by a low potential for

evolution of thermal tolerances (Andrango, 2015; Angilleta, 2009; Tewksbury et al., 2008). Alternatively, differences in T_{pref} might be biased by T_{air} (see above).

In contrast to *S. guentheri*, we found no significant differences in critical thermals (CT_{min} and CT_{max}) between adults and juveniles of *S. festae*. This may be explained by juveniles and adults of *S. festae* sharing the same microhabitats, which differs from what has been reported for *S. guentheri* (Andrango, 2015). Additionally, there is the possibility that juveniles and adults were treated differently during the methodological process of experimentation. In this way, is subjective to the person who registered the critical temperature to determine the maximum and minimum point where each lizard can incorporate by itself.

Sinervo et al's (2010) model is a well-developed tool to predict extinction risks due to global warming. We found however some trouble applying this model to our data. First of all, it was not logic to calculate daily active hours when T_e is higher than the minimum temperature of activity of heliothermic lizards (25 °C as established by Sinervo et al., 2010) and lower than the T_{pref} obtained in the field for *S. festae* (20.5 °C). Also, we think that the model did not work out with this species because the average T_{air} was too cold at the moment we measured T_{pref} in the field. In order to correct for this possible bias, we ran the model under three different scenarios, but the results were similar to the uncorrected model (Fig. 3A). Our findings that 13.8% of the populations went extinct in 2010, including our population of study, are obviously misleading. After modifying the model, we obtained better results; although the population of study was predicted to have gone extinct in 2010, on 2020 lizards are predicted to have recolonized this locality, possibly because climate conditions will become less harsh and severe (Fig. 3B).

Another reason why Sinervo's model did not work might be that most temperature data used by Sinervo et al's (2010) belongs to lowland taxa. They analyzed species with an

elevation range between 1 and 2055 m that have an average T_b of 33.66 °C and a minimum T_b of 26.6 °C. However, those T_b data are too high for species that live above 2000 m as *S. festae*. The average T_b of *S. festae* was 28.11 °C while the minimum T_b was 16 °C. In this context, we believe we cannot assume there is a minimum temperature of activity (25°C as established by Sinervo et al., 2010) that fits all heliothermic lizards, at least if we study lizards adapted to live in colder environments.

Warming tolerance is a useful way to determine how detrimental climate warming is to a specific population. We found that *S. festae* could tolerate 9.13 °C more to local warming than *S. guentheri* when we calculate the difference between CT_{max} and the average T_{air} . Likewise, *S. festae* could tolerate 5.26 °C more to local warming than *S. guentheri* when we calculate the difference between CT_{max} and the maximum T_{air} . These analyses show that populations of Andean lizards living in environments at lower altitudes, as *S. guentheri* (2450- 3000 m; Andrango, 2015), may have more extinction risk than those from higher altitudes (*S. festae*, 3000- 3200 m, this study). Contrary to these results, the model of Sinervo et al (2010) showed that *S. festae* has more risk of extinction than *S. guentheri*. We consider that the model should be tested with more species living at high altitudes so we can certainly estate that this model cannot be applied to species living in cold zones as *S. festae*.

Additionally, *S. festae* has a wider thermal breadth (40 °C) than *S. guentheri* (34,97 °C for adults; 32,54 °C for juveniles, Andrango, 2015). Therefore, it seems reasonable to state that *S. guentheri* will be more sensitive to global warming than *S. festae* because it presents a narrower thermal tolerance breadth (Grigg and Buckley, 2013). Also, if we compare the fluctuation of air temperature of the habitat of *S. guentheri* and *S. festae*, we can see that our study site presents a lower minimum air temperature and a lower maximum air temperature (Fig. 5) than the site where *S. guentheri* was studied. Thus, populations living

at higher altitudes where air temperature is cooler have a better chance to survive longer than lowland species, as it will take longer for its habitat to reach the CT_{max} of the species.

ACKNOWLEDGMENTS

To Boris Tinoco from Universidad del Azuay for letting us stay in hacienda “El Gullán” to carry out this study. To María Belén Andrango for helping with the experiments and analyses, and to María José Navarrete, Andrés Mármol, Priscila Barragán, Keyko Cruz, Verónica Urgiles, Luis Sebastián Ruiz for their helpful work in the field. We are also grateful to Simón E. Lobos and Nadia B. Páez for helping with ArcGIS and JMP, respectively. We acknowledge Julio Sánchez-Otero for his statistical advice with SPSS. To Ministerio del Ambiente for providing temperature and precipitation data. Finally, to Pontificia Universidad Católica del Ecuador for financial support.

REFERENCES

- Andrango, M.B. 2015. Short-term predicted extinction of Andean populations of the lizard *Stenocercus guentheri*. Tesis de Licenciatura en Ciencias Biológicas de la Pontificia Universidad Católica del Ecuador.
- Angilletta, M.J. 2009. Thermal Adaptation. A theoretical and Empirical Synthesis. Oxford University Press Inc. New York.
- Angilletta, M.J., Niewiarowski, P.H., & Navas, C.A. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27: 249–268.
- Ansaloni, R., & Chacón, G.V. 2003. Interacción suelo, vegetación y agua: el efecto de las plantaciones de pino en ecosistemas alto andinos del Azuay y Cañar. *Revista de la Universidad del Azuay* 31-32: 166- 173.
- Araújo, M.B., Thuiller, W., & Pearson, R.G. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33: 1712-1728.
- Azócar, D.L., Vanhooydonck, B., Bonino, M.F., Perotti, M.G., Abdala, C.S., Schulte, J.A., & Cruz, F.B. 2013. Chasing the Patagonian sun: comparative thermal biology of *Liolaemus* lizards. *Oecologia* 171: 773-88.
- Buckley, L.B., Tewksbury, J.J., & Deutsch, C.A. 2013. Can terrestrial ectotherms escape the heat of climate change by moving? *Proceedings of The Royal Society B* 280: 1-6.
- Ceia-Hasse, A., Sinervo, B., Vicente, L., Pereira, H.M. 2013. Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. *Ecography* 37: 679-688.
- Corbalán, V., Debandi, G., & Kubisch, E. 2013. Thermal ecology of two sympatric saxicolous lizards of the genus *Phymaturus* from the Payunia región (Argentina). *Journal of Thermal Biology* 38: 384-389.

Deem, V. 2015. The effects of habitat fragmentation on the thermal plasticity of the aegean wall lizard (*Podarcis erhardii*, Lacertidae). Thesis for the degree of Master of Science (Natural Resources and Environment), University of Michigan.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D., & Martin P.R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105 (18): 6668-6672.

Dirzo, R., & Raven, P.H. 2003. Global state of biodiversity and loss. *Annual Review of Environmental Resources* 28:137-167.

ESRI. 2014. ArcGIS Desktop: Release 10.2. Redlands, CA: Environmental Systems Research Institute.

Forero-Medina, G., Joppa, L., & Pimm, S.L. 2010. Constraints to species' elevational range shifts as climate changes. *Conservation Biology* 25: 163-171.

Gutiérrez, J., Krenz, J.D., & Ibarquengoytía, N.R. 2010. Effect of altitude on thermal responses of *Liolaemus pictus argentinus* in Argentina. *Journal of Thermal Biology* 35: 332-337.

Ibarquengoytía, N.R., Medina, S.M., Fernández, J.B. Gutiérrez, J.A. Tappari, F., & Sclaro, A. 2010. Thermal biology of the southernmost lizards in the world: *Liolaemus sarmientoi* and *Liolaemus magellanicus* from Patagonia, Argentina. *Journal of Thermal Biology* 35: 21–27.

IBM Corporation. 2015. SPSS Statistics, Version 19.0.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

King, D. 2004. Climate Change Science: Adapt, Mitigate, or Ignore? *Science* 303: 176-77.

Kubisch, E. 2013. Efectos del cambio climático global en el crecimiento y aptitud de tres especies de lagartos. Trabajo de Tesis para optar al Título de Doctor en Biología, Universidad Nacional del Comahue Centro Regional Universitario Bariloche, Bariloche, Argentina.

Lind, A.J. 2008. Amphibians, Reptiles and Climate Change. Sierra Nevada Research Center, Pacific Southwest Research Station.

Navas, C. 2003. Herpetological diversity along Andean elevational gradients: links with physiological ecology and evolutionary physiology. *Comparative Biochemistry and Physiology* 133: 469 – 485.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13: 1860-1872.

Peterson, A.T., Navarro-Sigüenza, A.G., & Pereira, R.S. 2004. Detecting errors in biodiversity data based on collectors' itineraries. *Bulletin of the British Ornithologists' Club* 124: 143-151.

Raven, P. 2011. Foreword. En: Sebastian K. Herzog, Rodney Martínez, Peter M. Jørgensen, Holm Tiessen. 2011. *Climate Change and Biodiversity in the Tropical Andes*. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), 348 pp.

SAS Institute Inc. 2010. JMP, Version 9.0.1.

Schmidt-Nielsen, K. 2002. *Animal Physiology. Adaptation and environment*. Cambridge University Press, United States of America. (pp. 277).

Seebacher, F. (2005). A review of thermoregulation and physiological performance in reptiles: what is the role of phenotypic flexibility? *Journal of Comparative Physiology B: biochemical, systemic, and environmental physiology* 175: 453-461.

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Mezaláro, R.N., Gadsden, H., Ávila, L.J., Morando, M., De la Riva, I.J., Sepúlveda, P.V., Rocha, C.F.D., Ibarngüengoytía, N.R., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., & Sites Jr., J.W. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328: 894-899.

Tiessen, H. 2011. Introduction. In: Sebastian K. Herzog, Rodney Martínez, Peter M. Jørgensen, Holm Tiessen. 2011. *Climate Change and Biodiversity in the Tropical Andes*. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), 348 pp.

Torres-Carvajal, O. 2007. Phylogeny and biogeography of a large radiation of Andean lizards (Iguani, *Stenocercus*). *Zoologica Scripta* 36: 311-326.

Travis, J.M.J. 2002. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London B* 270: 467 – 473.

R Core Team. 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria. URL <https://www.R-project.org/>.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O., & Bairlein, F. 2002. Ecological responses to recent climate change. *Science* 416: 389 – 395.

Williams, J.W., Jackson, S.T., & Kutzbacht, J.E. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences* 104:5738–5742.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., & Langham, G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* 6: 2621-2626.

Zug, G.R., Vitt, L.J., & Caldwell, J.P. 2001. Herpetology. Academic Press, California, Estados Unidos.

FIGURES

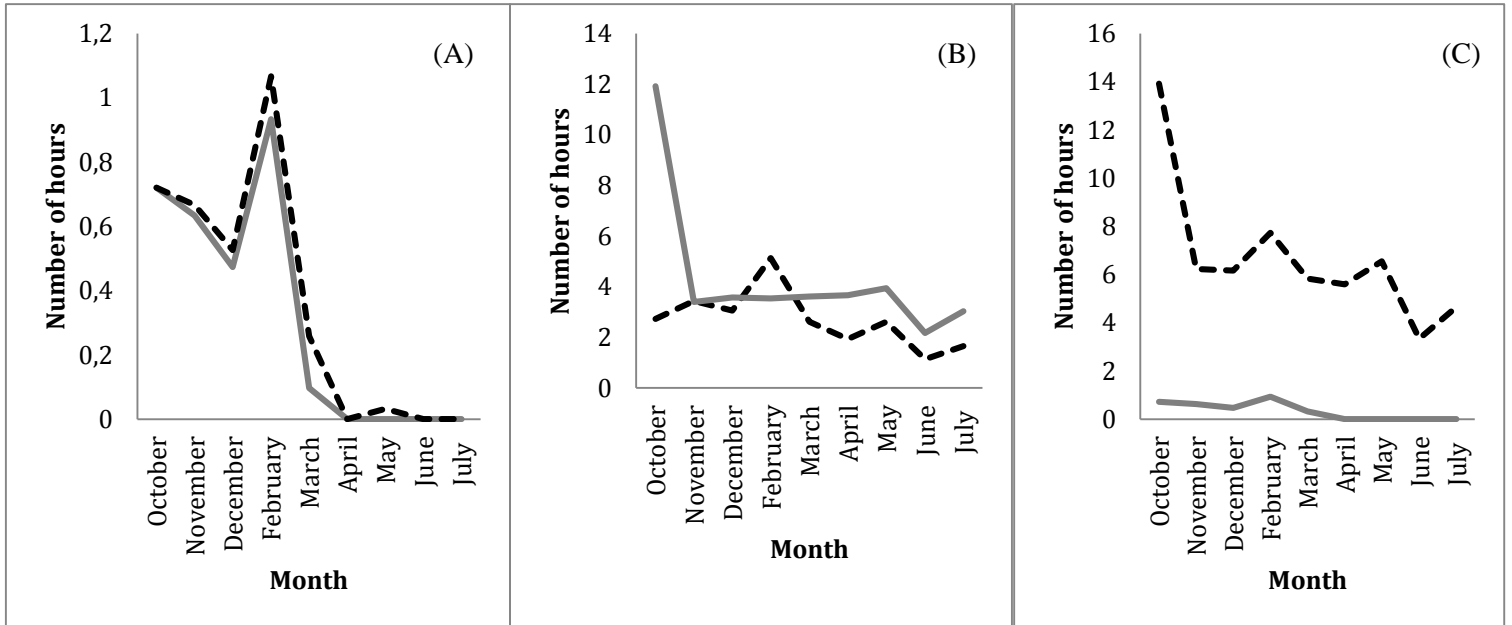


Figure 1. Fluctuation of the hours of restriction and activity by month (2014-2015) for the three scenarios. (A) $T_{act}=25^{\circ}C$, $T_{pref}=28.1^{\circ}C$. (B) $T_{act}=16^{\circ}C$, $T_{pref}=20.5^{\circ}C$. (C) $T_{act}=16^{\circ}C$, $T_{pref}=28.1^{\circ}C$. The solid line shows the number of hours of activity, H_a , between the T_{act} and T_{pref} . The dotted line shows the number of hours of restriction, H_r , when T_e exceeds T_{pref} .

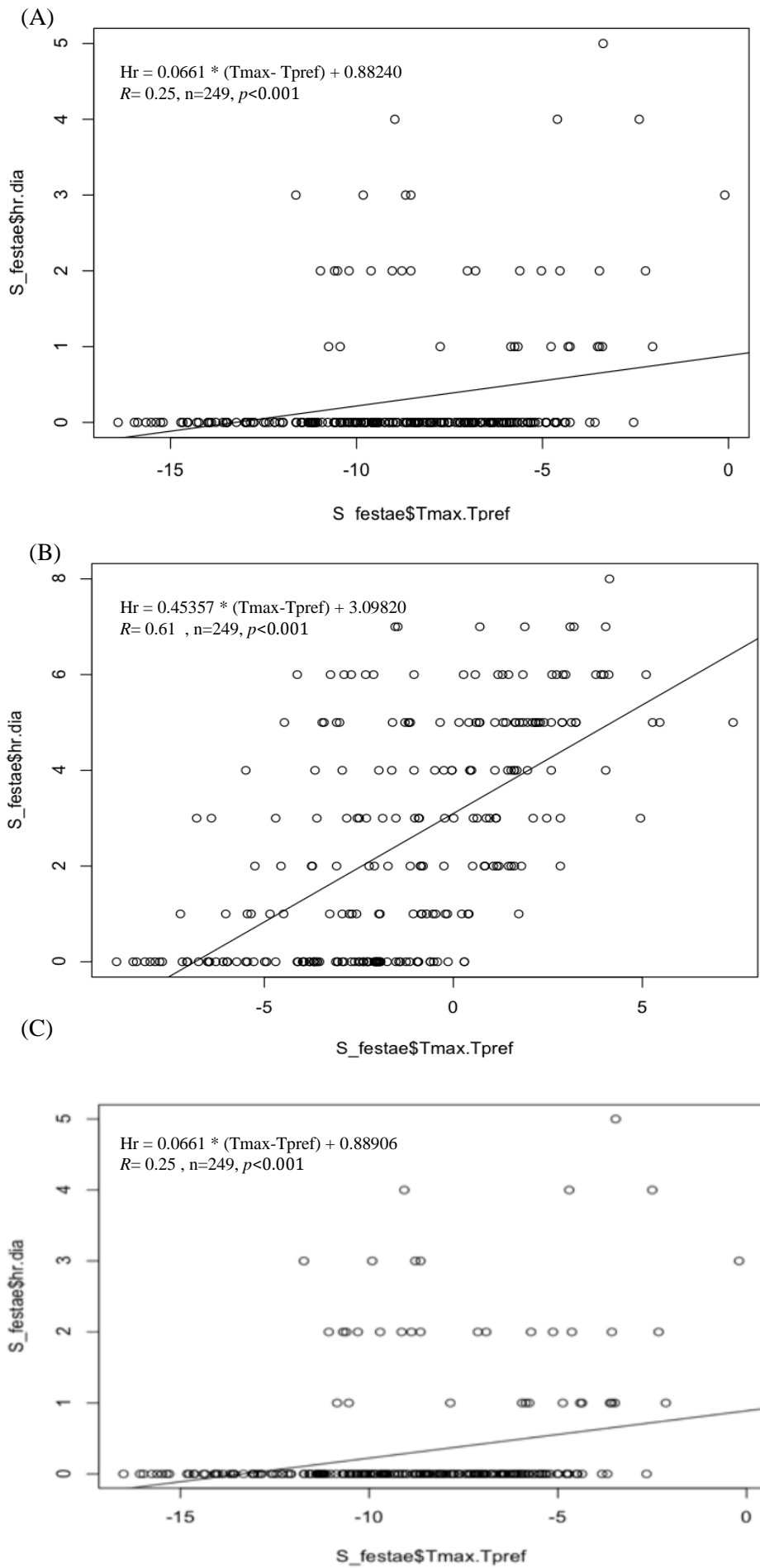


Figure 2. Linear and positive relationship between Hr and the difference between T_{max} and T_{pref} for the three scenarios. (A) $T_{act} = 25^{\circ}\text{C}$, $T_{pref} = 28.1^{\circ}\text{C}$. (B) $T_{act} = 16^{\circ}\text{C}$, $T_{pref} = 20.5^{\circ}\text{C}$. (C) $T_{act} = 16^{\circ}\text{C}$, $T_{pref} = 28.1^{\circ}\text{C}$

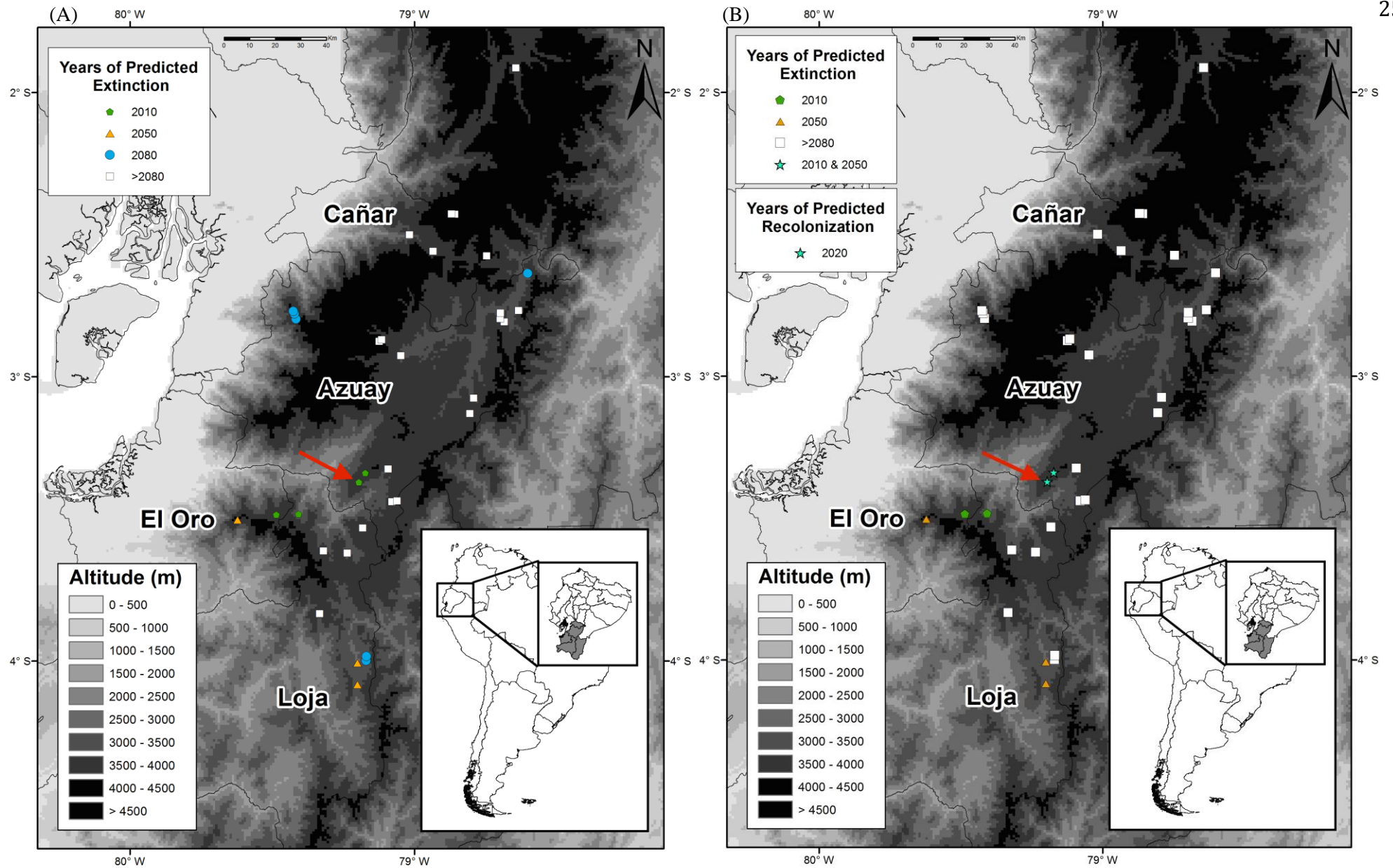


Figure 3. Map of predicted extinction for 36 sampled populations of *S. festae*. (A) Predicted extinctions by modifying T_{pref} and T_{act} values. (B) Predicted extinctions by modifying T_{pref} and T_{act} values as well as the way we predict extinctions from restriction hours. The red arrow shows the study area.

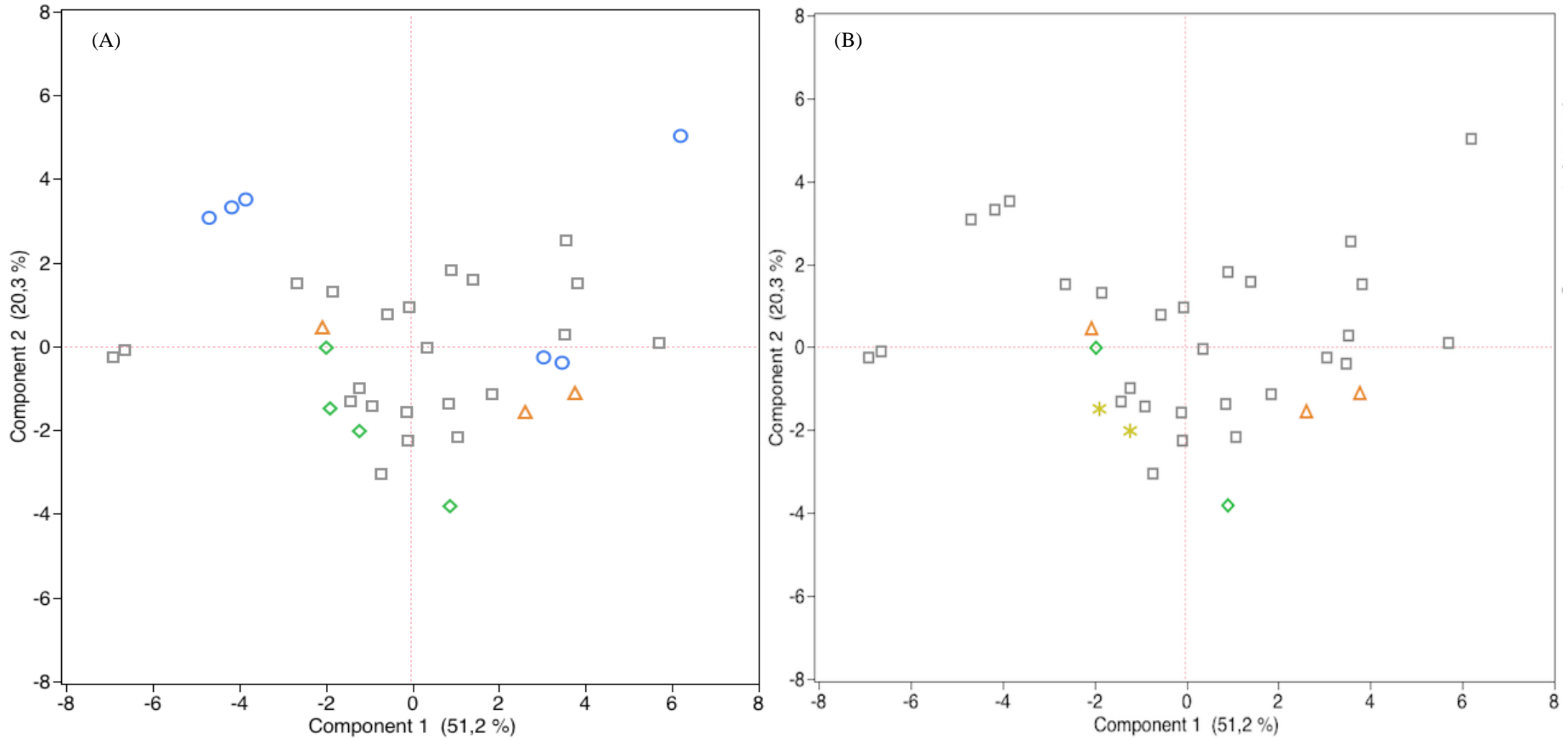


Figure 4. PCA showing climatic differences of the 36 localities used in this study. For (A) and (B), diamonds show populations extinctions on 2010, triangles show populations extinctions on 2050, circles show populations extinctions on 2080 and squares shows populations to be extinct over 2080. Asterisks on figure (B) are populations that recolonized.

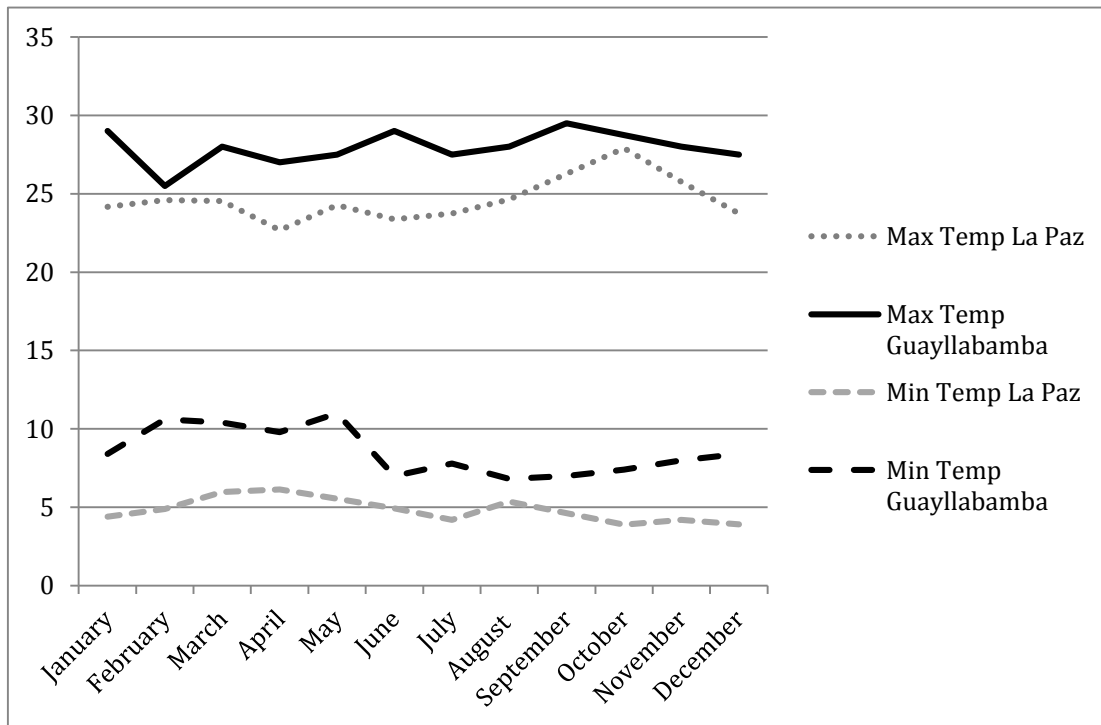


Figure 5. Fluctuation of air temperature of study sites for *Stenocercus festae* (La Paz) and *S. guentheri* (Guayllabamba). Curves show the maximum temperature and the minimum temperature at each station.

TABLES

Table 1. Experimental data of all the individuals collected in this study. Capture Date (CD), Capture Time (CT), Weight (WGT), Snout-Vent Length (SVL) and temperature data (CT_{min} , CT_{max} , $T_{panting}$, T_{pref} , T_b). Temperature of the air when the T_{pref} experiments were performed ($T_{pref-air}$). Reproductive status and sex are shown in parenthesis (M=male, F=female, J=juvenile).

	CD	CT	WGT (g)	SVL (mm)	CTmin (°C)	CTmax (°C)	Tpanting (°C)	Tpref (°C)	Tpref- air (°C)	Tb (°C)
N1 (F)	14/2/15	11:20	7.9	58.17	9.48	43.42	41.87	30.08	22.94	16
N2 (F)	14/2/15	12:09	7.2	55.02	11.23	44.7	40.3	31.86	22.94	17.9
N3 (F)	31/5/15	12:25	8.1	63.46	7.71	45.7	42.85	26.06	15.54	22.8
N4 (F)	31/5/15	12:15	8.1	62.1	4.8	46.4	45.34	23.18	15.54	
N5 (F)	31/5/15	13:13	5.7	56.31	6.58	46.3	43.7	16.99	15.47	19.9
N6 (F)	31/5/15	13:25	8.8	64.79	4.44	47.1	46.74	22.86	14.33	28.4
N7 (F)	1/6/15	11:30	8.4	61.84	6.02	48.02	44.19	27.67	15.24	25.4
N8 (F)	2/6/15	12:30	8.9	66.18	5.83	47.62	46.66	14.46	14.33	29.8
N9 (F)	2/6/15	12:32	9.3	59.03	3.44	48.12	47.35	22.62	13.86	24.5
N10 (F)	2/6/15	13:10	8.9	63.87	5.53	47.2	46.14	24.15	13.86	31.8
N11 (F)	2/6/15	13:15	6.9	55.97	4.18	45.94	45.13	22.03	14.33	30.9
N12 (J)	15/2/15	9:40	2	38.28	9.51	45.6	43.33	22.48	22.94	30.8
N13 (J)	30/5/15	13:00	3.8	51.77	8.7	46.44	41.46	18.62	14.96	33.4
N14 (J)	30/5/15	13:30	3.8	48.6	9.39	45.93	40.33	15.40	14.43	33.1
N15 (J)	31/5/15	10:35	1.9	38.14	12.18	43.81	43.02	22.95	14.96	31.7
N16 (J)	1/6/15	10:25	3.1	43.77	5.95	46.35	44.13	16.58	14.67	30.3
N17 (J)	4/6/15	15:00	3.9	48.16	3.78	43.3	42.11	16.43	14.02	27.2
N18 (M)	13/2/15	16:28	15.5	76	4.73	44.9	40.97	28.80	14.43	21.7
N19 (M)	15/2/15	13:00	20	82.42	6.72	45.7	44.5	24.32	15.47	30.7
N20 (M)	31/5/15	9:30	9.4	58.87	4.43	48.32	45.58	17.11	14.33	34.8
N21 (M)	31/5/15	12:50	15	76.03	4.38	47.07	45.15	18.56	15.24	31.4
N22 (M)	31/5/15	13:17	18.4	77.92	4.96	48.45	46.26	14.62	15.1	39.3
N23 (M)	31/5/15	13:55	17.6	66.96	2.62	47.2	46.31	24.85	15.1	29.6
N24 (M)	1/6/15	10:50	17.8	79.73	3.48	46.1	44.03	19.74	14.02	31.1
N25 (M)	2/6/15	10:00	8.7	58.47	8.7	48.76	48.01	16.85	22.94	30.1
N26 (M)	2/6/15	11:00	16.7	70.81	4.68	45.63	43.77	26.47	22.94	25.4
N27 (M)	2/6/15	13:30	20.4	79.69	3.66	49.18	45.22	22.63	14.67	22.9

SUPPLEMENTARY MATERIAL

Table S1. Locality, province, latitude and longitude of the 36 localities of occurrence of *Stenocercus festae* used in this study. Data were obtained from Museo de Zoología QCAZ, Pontificia Universidad Católica del Ecuador.

<i>Locality</i>	<i>Province</i>	<i>Latitude</i>	<i>Longitude</i>
El Gullán Hacienda, Azuay University	Azuay	-3.33833	-79.17167
Cerro El Mozo	Azuay	-3.43985	-79.07913
Cochapata, around Cerro El Mozo	Azuay	-3.43700	-79.06085
6 km South from La Paz over the Panamericana	Azuay	-3.37087	-79.19543
El Gullán Hacienda, between Susudel and Cuenca.	Azuay	-3.33829	-79.17178
Gulag	Azuay	-3.32425	-79.09200
Sigsig	Azuay	-3.12950	-78.80483
Santa Bárbara river	Azuay	-3.07500	-78.79100
Cuenca, south of the city	Azuay	-2.92566	-79.04720
Cuenca, Bosque Protector Mazan	Azuay	-2.87484	-79.12383
Cuenca, Bosque Protector Mazan	Azuay	-2.86891	-79.11478
Antennas way to San Vicente	Azuay	-2.80600	-78.68366
Cochapamba	Azuay	-2.79712	-79.41563
Antennas way to San Vicente	Azuay	-2.79531	-78.69811
Cochapamba	Azuay	-2.77773	-79.42167
Guablid, 2 km via Guachapala - Sevilla de Oro	Azuay	-2.77488	-78.69758
Yumate, Shoupshe	Azuay	-2.76961	-79.42543
Trail between Sevilla de Oro and Cerro Negro	Azuay	-2.76667	-78.63333
Sevilla de Oro	Azuay	-2.63605	-78.60097
Via from Zhoray to Mazar Reserve	Cañar	-2.57462	-78.74554
Cañar	Cañar	-2.55799	-78.93451
La Carbonería	Cañar	-2.50000	-79.01667
Tambo Real Sector	Cañar	-2.42805	-78.85817
Laguna Culebrillas Sector	Cañar	-2.42651	-78.86991
Cebadas	Chimborazo	-1.91269	-78.64285
Chillacocha	El Oro	-3.50317	-79.62159
Zaruma canton, Guanazan parish, Maije, Tacay river	El Oro	-3.48466	-79.48572
Cajanuma	Loja	-4.08333	-79.20000
Loja	Loja	-4.00669	-79.19953
Road Loja - Zamora	Loja	-3.99889	-79.16917
7,5 km from Loja (Road Loja – Zamora)	Loja	-3.98417	-79.16806
Saraguro	Loja	-3.62025	-79.23581
Saraguro, Selva Alegre	Loja	-3.61307	-79.31940
Carbonillo, 30 km from Oña	Loja	-3.53170	-79.18170
Manú	Loja	-3.48350	-79.40735
Chuquiribamba	Pichincha	-3.83333	-79.33333