INTRA AND INTERSPECIFIC VARIATION IN CRITICAL THERMAL MINIMUM AND MAXIMUM OF FOUR SPECIES OF ANOLE LIZARDS (REPTILIA: SQUAMATA: DACTYLOIDAE: *ANOLIS*)

JHAN CARLOS SALAZAR SALAZAR

UNIVERSIDAD ICESI

FACULTAD DE CIENCIAS NATURALES, DEPARTAMENTO DE CIENCIAS BIOLÓGICAS

BIOLOGÍA

SANTIAGO DE CALI

2017

INTRA AND INTERSPECIFIC VARIATION IN CRITICAL THERMAL MINIMUM AND MAXIMUM OF FOUR SPECIES OF ANOLE LIZARDS (REPTILIA: SQUAMATA: DACTYLOIDAE: *ANOLIS*)

JHAN CARLOS SALAZAR SALAZAR

TRABAJO DE GRADO PARA OPTAR AL TÍTULO DE

PREGRADO EN BIOLOGÍA

DIRECTORA: MARÍA DEL ROSARIO CASTAÑEDA, Ph. D.

DIRECTOR: GUSTAVO ADOLFO LONDOÑO, Ph. D.

TRABAJO DE GRADO PARA OPTAR AL TÍTULO DE PREGRADO EN BIOLOGÍA

SANTIAGO DE CALI

2017

UNIVERSIDAD
ICESI

APROBADO POR:

Juliana Rengifo

Juliana Rengifo Gomez, Ph.D.
Evaluador

Rosario Castañeda

María del Rosario Castañeda, Ph.D.
Tutora del Proyecto.

Gustavo Londoño

Gustavo Adolfo Londoño, Ph.D.
Tutor del Proyecto.

SANTIAGO DE CALI, MIÉRCOLES, 08 DE AGOSTO DE 2017

ACKNOWLEDGEMENT

I give my most sincere thanks to my parents and godparents for their unconditional support throughout the entire process of the completion of this Undergraduate Degree Project. Likewise, I thank my directors María del Rosario Castañeda, Ph.D. and Gustavo A. Londoño, Ph.D. for all their patience support and time they invested to help me, guide me and correct me throughout the process. In addition, I want to thank the Betty Cadena and her family, Don Juan, Gustavo from Parques Nacionales Naturales, Don Bertulfo from DAGMA and those people who made this project possible. Icesi University let us use the field station facilities. Also, I want to thank M. Loaiza and M. Sanchez for their help and guide in R. Finally, I want to thank M. F. Restrepo, C. Cárdenas, C. Estupiñán, S. Muñoz, N. Jimenez, S. Orozco, M. Cantero, L. Gonzales, P. Montes and J. Lizarazo for their help during the field work.

TABLE OF CONTENTS

TABLE INDEX

FIGURE INDEX

SUPPLEMENTARY MATERIAL

ABSTRACT

Critical thermal limits are thought to vary under different climatic regimes and ontogenetic stages. Although, tropical regions are recognized by their lower annual thermal fluctuation, important temperature changes can be observed in tropical mountains, which could be the mechanism limiting species distribution and generating the high Beta diversity observed in these areas. Here, we test whether the thermal limits of tropical *Anolis* lizards that are distributed in different locations along the montane gradient, coincide with their current thermal distribution and if they differ between sexes, ages, populations, elevation and species. In four species, we measured the Critical Thermal Maximum (CT_{max}) and Critical Thermal Minimum (CT_{min}) in four localities distributed along a 1700 m elevation gradient in the western cordillera of Colombia. We find that the interaction between elevation and body mass affect $CT_{max,}$ and that only the body mass affects CT_{min} along the montane gradient in the four species. We also find that the Thermal Limits do not change between, sexes, ages, and populations, but it changes between altitudes and among species. Nevertheless, there is a great variation in both CT_{max} and CT_{min} between lowland, and mid and highland species. Our findings suggest that the thermal limits for anole lizards are narrower in lowlands, than in mid and highland. And also, that those thermal limits of the continental anole species are narrower than the islands anole species (a study conducted in Caribbean islands). We discuss the implications of this narrow thermal limits under a climate change scenario, and how other factors aside from elevation, mass, or snout-vent length (SVL) can affect CT_{max} and CT_{min}.

Keywords: *Anolis,* Colombia, elevational gradient, thermal biology, thermal limits, thermal physiology

RESUMEN

Se cree que las temperaturas críticas varían en diferentes regímenes climáticos y etapas ontogenéticas. Aunque las regiones tropicales son reconocidas por una baja fluctuación térmica anual, hay cambios drásticos en la temperatura en las montañas tropicales, lo que podría ser un mecanismo que limite la distribución de especies, lo cual genera una alta diversidad Beta. En este estudio, probamos si los límites térmicos de lagartijas tropicales de género *Anolis* que están distribuidas en diferentes localidades a lo largo del gradiente montano coinciden con su distribución térmica actual y si difieren entre sexos, edades, poblaciones, elevaciones y especies. En cuatro especies, se midió la Temperatura Crítica Máxima (CT_{max}) y la Temperatura Crítica Mínima (CT_{min}) en cuatro localidades distribuidas a lo largo de un gradiente de elevación de 1700 m en la Cordillera Occidental de Colombia. Encontramos que la interacción entre la elevación y la masa corporal afectan a CT_{max}, y que sólo la masa corporal afecta a CT_{min} a lo largo del gradiente montano en las cuatro especies. También encontramos que los Límites Térmicos no cambian entre, los sexos, las edades y las poblaciones, pero cambia entre las altitudes y entre las especies. Sin embargo, hay una gran variación en CT_{max} y CT_{min} entre las tierras bajas, y las especies medianas y altas. Nuestros hallazgos sugieren que los límites térmicos para *Anolis* son más estrechos en las tierras bajas, que en las tierras medias y altas. Y también, que los límites térmicos de las especies continentales de *Anolis* son más estrechos que las especies de *Anolis* de islas (un estudio realizado en las islas del Caribe). Discutimos las implicaciones de estos límites térmicos estrechos en un escenario de cambio climático, y cómo otros factores diferentes de elevación, masa o longitud rostro-cloaca pueden afectar CT_{max} y CT_{min}.

Palabras clave: *Anolis*, Colombia, gradiente altitudinal, biología térmica, límites térmicos, fisiología térmica

1. INTRODUCTION

Temperature is one of the most important factors in nature, because it affects several groups of species, especially those whose internal temperature depends on the external temperature, i.e. poikilotherms (Janzen 1967, Holt 2003, Ghalambor et al 2006, Zamora-Camacho et al 2013). One of the ways to quantify those degrees of variation of the internal temperature is using the Critical Thermal Minimum (CT_{min}) and Maximum (CT_{max}). Cowles and Bogert (1994) defined CT_{min} and CT_{max} as the temperature in which an individual loses its motor ability. The lost the motor ability cause by the critical thermal is due to a change in the circulatory and ventilatory mechanism: For CT_{min}, the aerobic capacity of the mitochondria is limited, while for CT_{max}, there is an excessive demand of oxygen that cause an insufficient of oxygen in the body fluids (Pörtner 2002). The Critical Thermal parameter have been used to predict the thermal limits in several species, especially in ectotherms. However, not much information is available of the temperature ranges in the *Anolis* lizards found in continental zones, and the relation between altitude and temperature (Muñoz et al., 2013, Méndez-Galeano & Calderón-Espinosa 2017). Therefore, this project proposes to quantify the Critical Thermal Minimum (CT_{min}) and Maximum (CT_{max}) in four species of *Anolis* lizards that are found at three different altitudes in three regions of Valle del Cauca: *A. antonii, A. heterodermus, A. maculiventris* and *A. ventrimaculatus.* For this, we compared data between ages, sexes, and species.

We collected data in Anchicayá Hydroelectric (300-1100 m, lowlands), Bitaco Forest Reserve (1800-2000 m, midlands), Parque Nacional Natural (PNN) Tatamá, Pueblo Rico (1200-4200 m, midlands), and Parque Nacional Natural (PNN) Farallones de Cali (2300-2800 m, highlands). Performing manual capture during the night, which has been shown to be useful for capturing lizards (Doan 2003, Hoyos-Hoyos et al. 2012). Likewise, the capture site was marked with flagging tape for subsequent release of the individuals.

We measured the Critical Thermal using the technique described in Muñoz et al (2013) and Llewelyn et al. (2016). To obtain both, CT_{min} and CT_{max}, a thermocouple of 2x3 mm was installed in the cloaca of the adult individuals of large species, whereas for juveniles and for adult individuals of small species (e.g., less than 60mm) a 0.22 mm thermocouple was used. Plastic containers were used to measure each individual separately; the container was submerged in cold-water or hot water. The individual temperature was reduced or raised 1°C every 2:00min by adding ice or hot water. At the end of the experiment the individual was slowly returned (1°C every 1:00min) to its initial temperature by means of a hot-water bath or cold-water bath for CT_{min}

and CT_{max}, respectively. The following morning after taking the measurements the individuals were released at the capture site.

2. PROJECT DESCRIPTION

2.1 PROBLEM RESEARCH

Many factors affect organisms; these factors could be biotics and abiotic, as temperature (Janzen 1967, Holt 2003, Ghalambor et al 2006, Zamora-Camacho et al 2013). Organisms, as poikilotherms, depend on the external temperature to regulate their body temperature, and carry out their basic metabolic functions (Bogert 1949). Therefore, to understand how organisms are going to respond to changes in the global average temperature has been an important issue. To establish robust predictions, basic data is needed to build realistic models; several studies have focused in explaining how can poikilotherms maintain their optimal temperature, and which are their thermal limits (Holt 2003, Ghalambor et al 2006, Parmesan 2006, Corlett 2012, Huey et al 2012). Thus, in a climate change scenario, poikilotherms may change in their activities behavior, distribution, or face extinction, (Martin & Huey 2008, Deutsch et al 2008, Muñoz et al. 2013, Forham et al 2016). However, there is not much information available of the temperature ranges in the *Anolis* species found in continental zones, and the relation between the thermal limits and the elevation gradient that is the first approach to stablish the thermal tolerance for poikilotherms (Muñoz et al., 2013, Méndez-Galeano & Calderón-Espinosa 2017).

For this reason, this project proposes to establish the temperature range, Critical Thermal Minimum (CT_{min}) and Critical Thermal Maximum (CT_{max}), in four species of *Anolis* lizards that are found at different altitudes, in order to provide information about their thermal biology. This will provide information about its thermal biology for anole species found in the continental zone (Muñoz et al 2013, Piantioni et al 2015, Méndez & Calderón 2017). Therefore, this study will serve as a basis for making predictions about how climate change will affect the physiology, ecology and / or distribution of these continental species.

2.2 THEORETICAL FRAMEWORK AND STATE-OF-THE-ART

Many factors affect organisms; overall, these factors can be divided into biotic (e.g., parasitism, predation, and competition), and abiotic (e.g., latitude, altitude, humidity, and temperature) (Janzen 1967, Holt 2003, Ghalambor et al 2006, Zamora-Camacho et al 2013). Temperature has been one of the major subjects of research, especially in the last decade, because there is a worldwide interest to understand how climate change (i.e., temperature increase) will affect patterns of precipitation, flood and drought, and sea levels (Danin 2017, Iwami et al 2017, Nordvelle et al 2017). In addition, there is an interest to understand how organisms are going to respond to temperature variation. Organisms have different options: adjust their current climate (Stoks et al 2014, Andrango et al 2016), modify their thermal requirements (Tomanek 2008, Muñoz et al 2013) or become extinct (Sharma & Mishra 2011, Fordham et al 2016). Because poikilotherms depend on external resources to regulate body temperature and carry out basic metabolic functions (Bogert 1949), there is a consensus that they are currently (Thomas et al 2004, Brusch et al 2015) and will be strongly affected by climate change (Deutsch et al 2008, Fordham et al 2016). To establish robust predictions, basic data is needed to build realistic models; yet, these data are lacking for most poikilotherms from areas in which diversity is the highest: The tropics (Hulme & Viner 1998, Pounds et al 1999, Williams et al 2007, Deutsch et al 2008). Understanding poikilotherm thermal limits is the first step towards building robust models. Thermal limits can be obtained through the Critical Thermal Minimum (CT_{min}) and Maximum (CT_{max}) parameters. Cowles & Bogert (1994) defined critical thermal limits as the temperature in which an individual loses its motor ability. CT_{min} and CT_{max} have been used to predict the thermal limits in several species (Gunderson and Leal 2012, Muñoz et al 2013, Gunderson & Stillman 2015, Piantoni et al 2015, Andrango et al 2016, Gunderson et al 2016, Sinclair et al 2016). Here, we present the CT_{min} and CT_{max} in four species of mainland anoles to quantify and compare their thermal limits in different ontogenetic stages, sexes, populations, and among species.

The poikilotherms depend on the external temperature to regulate their body temperature, therefore any change in the temperature could significantly affect their survival (e.g., Bogert 1949, Gunderson & Stillman 2015, Ortega et al., 2016a, Sinclair et al., 2016). In general, tropical poikilotherms, compared to other geographic regions, have a greater sensitivity to changes in the temperature because they have narrower thermal limits (Ghalambor et al 2006, Williams et al 2007, Deutsch et al 2008, Muñoz et al 2013, Andrango et al 2016), making them more susceptible to temperature changes affecting their physiology (Andrango et al 2016), behavior (Deutsch et al 2008, Muñoz et al 2013) and natural history (Muñoz et al 2013, Piantoni et al 2015, Andrango et al 2016). Some of these studies have evaluated thermal sensitivity and plasticity of poikilotherms at different latitudes, but only a few show how the thermal limits change in altitudinal gradients (Muñoz et al 2013, May et al 2017). Janzen (1967) proposed that there is a difference in the annual temperature regimes between temperate and tropical regions, where the variation in temperate zones is greater compared to tropics. Something similar happens in the altitudinal gradient where in the highlands the variation in the annual temperature is greater than in the lowlands (Janzen 1967, Ghalambor et al 2006). Janzen (1967) also proposed that there is a difference between the thermal limit of organisms inhabiting high and low altitudes; those that live in highland populations should have a narrow tolerance for cooler temperatures; while the at low elevations, organisms show a narrow tolerance for warmer temperatures. Muñoz et al. (2013) showed that these thermal limits are not always narrower in lowland species compared to highland species, and can range from10.7°C to 40.3°C in lowland species, and from 7.2°C to 40.4°C in highland species. Despite these broader thermal limits, studies have shown that some species of the genera *Liolaemus, Sceloporus* and *Tropidurus*, would be highly affected by an increase in temperature and in a greater extent those at low elevations in tropical areas, because they have a reduction in the amount of hours of activity and their chances of overheating would increase (Hertz & Huey 1981, Huey et al 2009, Muñoz et al 2013, Piantoni et al 2015). In addition, species tend to increase their altitudinal distribution in search for their optimal temperature range, which would likely result in increased competition for resources; however, if they cannot go to upper elevation those species could become extinct (Hertz & Huey 1981, Huey et al 2009, Corlett 2012, Piantoni et al 2015). On the other hand, species such as the skink *Lampropholis coggeri*, which exhibits great plasticity when exposed to changes in temperature, probably would not be as affected in a climate change scenario because they would be able to survive in higher temperatures (Llewelyn et al. 2016).

For other lizard groups, like anoles, there is little information about their thermal limits, how those thermal limits change in an altitudinal gradient, and how they are going to respond to an increase in the global temperature. Muñoz et al. (2013) found that, in Caribbean *Anolis* species, an increase in temperature would have different effects for species in lowlands vs. highlands. Highland species would benefit because the temperature in these zones would approach their optimal temperatures, resulting in a decrease in the thermoregulation time and freeing time to be spent in other activities (Muñoz et al 2013). In contrast, lowland species would be affected, because they would be forced to change altitudinal distribution or face extinction (Muñoz et al 2013).

Recently, tropical mountains have been the focus of research, especially for studies interested in elevational gradients. For anole lizards, only a single study has been done in an elevation gradient; it shows that one possible effect of global warming is for lowlands species to migrate to higher elevations (a study conducted in Caribbean islands, Muñoz et al 2013). Regarding to preference temperatures, a single study has been done in a highland population of *Anolis heterodermus* in Colombia; it shows that this species changes in behavior during the dry and wet season to compensate the environmental thermal variation (Méndez & Calderón 2017). But no other information is available for *Anolis* in the continental lowland populations or in a highland altitudinal gradient.

In this study, we present the Critical Thermal Minimum (CT_{min}) and the Critical Thermal Maximum (CT_{max}) in four species of *Anolis* lizards found in the Colombian Andes from 500 to 2400m. We compared measurements between sexes, ages, populations, elevation, and species.

The species that were evaluated:

- *Anolis antonii:* this species has a range of altitudinal distribution from 800 to 2000m, and its conservation status is of less concern (LC; Morales-Betancourt et al. 2015).

- *Anolis heterodermus*: this species has a distribution range from 1800 to 3750m, this species has been considered a less concern in its conservation status (LC; Morena-Arias y Urbina-Cardona 2012, Morales-Betancourt et al. 2015).

- *Anolis maculiventris*: this species has a range of altitudinal distribution from 0 to 500m, in addition, this species is not considered in danger, in fact, its conservation status is of less concern (LC; Cardona-Botero et al. 2013, Morales-Betancourt et al. 2015).

- *Anolis ventrimaculatus*: this species has a range of altitudinal distribution that goes from 1300 to 2500m, and its state of conservation is of less concern (LC; Morales-Betancourt et al. 2015).

2.3 OBJECTIVES

2.3.1 General Objective

To quantify the Critical Thermal Minimum (CT_{min}) and Maximum (CT_{max}) in four species of *Anolis* lizards that are found at three different altitudes in three regions of Valle del Cauca: *A. antonii, A. heterodermus, A. maculiventris* and *A. ventrimaculatus.*

2.3.2 Specific Objectives

- Evaluate if there are differences in critical temperatures between the four *Anolis* species that are at different altitudes
- For each specie, evaluate the differences in critical temperatures between ages (juveniles and adults)
- For each specie, evaluate the differences in critical temperatures between sexes (males and females)

2.4 METHODOLOGY

2.4.1 Study sites and species

We collected data in four different localities from December 2016 to June 2017: 1) Anchicayá Hydroelectric (300-1100 m, lowlands), with an annual temperature between 25-42°C (3° 26' 27.12'' N, 76° 40' 0.13'' W); 2) Bitaco Forest Reserve (Chicoral; 1800-2000 m, midlands) with an annual temperature between 12-38°C (3° 33’ 9.95’’ N, 76° 35’ 1.52’’ W); 3) Parque Nacional Natural (PNN) Tatamá, Pueblo Rico (1200-4200 m, midlands), with an annual temperature between 10-29°C (5° 13' 47.96'' N, 76° 5' 1.51'' W); 4) Parque Nacional Natural (PNN) Farallones de Cali (2300-2800 m, highlands) with an annual temperature between 5-25°C (3° 24' 41.656" N, 76° 39' 5.364” W; Supplementary material 1). Four species were studied (altitudinal distribution in parentheses): *Anolis antonii* (800-2000 m), *A. heterodermus* (1800-3750 m), *A. maculiventris* (0-500 m) and *A. ventrimaculatus* (1300-2500 m; Supplementary material 2). Here, we considered lowlands below 1200m, midlands from 1200 to 2000m, and highlands above 2000m.

For two species, we measured different populations at different elevations: For *Anolis antonii* we measured two populations, PNN Farallones de Cali (2186m), and PNN Tatamá (1415m), and for *A. ventrimaculatus* we measured three populations, PNN Farallones de Cali (2220m), Bitaco Forest Reserve (RF; 1998m) and PNN Tatamá (1721m).

2.4.2 Measurement of CT_{min} and CT_{max}

Individuals were captured manually; sampling was done during the night (between 18:00 and 2:00) and occasionally during the day. Each capture site was marked with flagging tape and a GPS point was collected, for subsequent release of the individuals to the exact site of capture.

The sex, age (adult or juvenile), body (snout-vent length) and tail length, and body mass were recorded for each individual captured. A mark was made on the belly using a permanent black marker (i.e., Sharpie) to ensure each individual was only measured once. In order to minimize the stress of the individual, only one of the measurements (either CT_{min} or CT_{max}) was collected from each individual.

Temperature measurements were taken following the technique described in Muñoz et al (2013) and Llewelyn et al. (2016). To record instant body temperature, a thermocouple of 2x3 mm was installed in the cloaca of adult individuals of large species (SVL: 60mm – 115mm'), whereas for juveniles and for adult individuals of small species (SVL < 60mm) a 0.22 mm thermocouple was used. Plastic containers were used to maintain each individual separately. To measure CT_{min}, the container was submerged in a cold-water bath inside an icebox. The individual's temperature was reduced 1°C every 2:00 min by adding ice to the water bath. Each time the body temperature of the lizard dropped one degree the individual was turned, placing it on its back inside the container; if it returned by itself to its original position, we continued to reduce the temperature, one degree every 2:00min, until it was not able to turn by itself. At this point, the temperature was recorded as the CT_{min}. At the end of the experiment the individual was slowly returned (1°C every 1:00min) to its initial temperature by means of a hot water bath. The following morning after taking the measurements the individuals were released at the capture site. To obtain the Maximum Critical Temperature (CT_{max}), the procedure was the same as for CT_{min} measurements, but instead of using an ice bath, a hot water was used to heat the water bath. At the end of the experiment, the individual was slowly returned to its initial temperature using ice.

2.4.3 Data analysis

Kruskal-Wallis analysis of variance). For comparisons between populations (*A. antonii* and *A. ventrimaculatus*), we did a one-way ANOVA for CT_{min}, and a Kruskal-Wallis test for CT_{max}.

To test for the relative importance of mass, SVL, and elevation on CT_{min} and CT_{max}, we used a Generalized Least Square (GLS) and Generalized Linear Model (GLM), respectively, with the package nlme (Pinheiro et al 2013) in R v.3.3.3 (R Development Core Team, 2012). For the comparison of CT_{min} and CT_{max} between lowland and highland species, and among species we used one-way ANOVA for CT_{min} and a Tukey test, and for CT_{max} we did a Kruskal-Wallis test, and then a post-hoc, Duncan test.

2.5 RESULTS

All species combined, we measured CT_{min}, and CT_{max} on 237 individuals (94 for CT_{min} and 143 for CT_{max}), including 77 males (21 for CT_{min} and 56 for CT_{max}), 81 females (35 for CT_{min} and 46 for CT_{max}) and 79 juveniles (38 for CT_{min} and 41 for CT_{max}). Because the number of captures for *A. heterodermus* and *A. maculiventris* was too small, we were not able to conduct statistical analysis to these species.

2.5.1 Critical Thermal Minimum and Maximum analysis

When we analyzed CT_{min} for the four-species combined, we found that body mass is the primary factor affecting CT_{min} along the elevational gradient ($F_{1,81} = 15.5$, $p < 0.001$; Table 1), showing a negative relationship, in which larger individuals have the lower CT_{min} (Supplementary Material 3). In contrast, the interaction among elevation ($F_{1,126} = 53.2$, $p < 0.001$), mass ($F_{1,127} = 2.44$, $p < 0.12$) and SVL ($F_{1,125} = 0.30$, $p < 0.58$) is associated with CT_{max}, in which larger individuals at higher elevation have a lower CT_{max}. We also observed a strong interaction between elevation ($F_{1,127} = 39.7$, $p < 0.001$) and mass ($F_{1,126} = 16.4$, $p < 0.001$; Table 2) is associated with CT_{max}, in which larger species are commonly found at high elevation, and at low elevations species have higher CT_{max} (Table 2, Supplementary Material 4 and Supplementary Material 5).

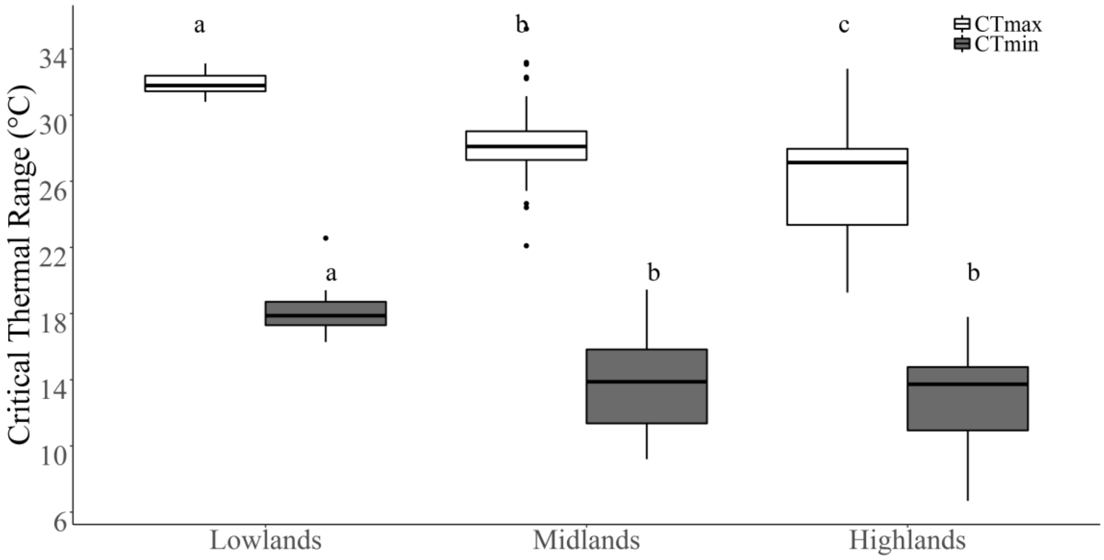


Figure 1. Box plots of CT_{max} and CT_{min} for low. mid and highland species. CT_{max} and CT_{min} values for lowland species (from 500m to 1200m; *A. maculiventris*), midland species (from 1200m to 2000m; *A. antonii* and *A. ventrimaculatus*) and highland species (above 2000m; *A. antonii, A. heterodermus* and *A. ventrimaculatus*). The box plots show the median (black bar), interquartile range (box), and 1.5 times the interquartile range (bars); the black circles represent outliers. CT_{min} ($F_{2, 80} = 13.7$, $p < 0.001$) and CT_{max} ($X^2 = 28.18$, $p < 0.001$) differ from lowland to highland. The small letters (a, b, c) show if the specie have or not similar Critical Thermal.

Table 1. Best models GLS analysis for CT_{min}. Effect of Elevation, Mass and SVL on CT_{min} analyzed using a Generalized Least Square (GLS). This analysis included the four anole lizards. Degree of freedom (d.f) are show with the *t* and *p* value, the AICc, and the delta of AIC (Δ) are shown.

Source	**CT_{min} (°C)**				
	d.f	*t*	*p*	AICc	Δ
Mass	3	24.4	<0.001	417.7	0.00
Elevation + Mass	4	17.2	<0.001	422.4	4.63
SVL + Mass	4	4.41	<0.001	422.6	4.82
SVL	3	11.3	<0.001	422.8	5.06
Elevation	3	16.8	<0.001	423.2	5.43

2.5.2 Interspecific variation in Critical Thermal Minimum and Maximum

When we compared the lowland anole species (*A. maculiventris*), midland species (*A. antonii* and *A. ventrimaculatus*) and highland species (*A. antonii, A. heterodermus* and *A. ventrimaculatus*) we found that CT_{min} for low elevation species (18.35°C ± 1.9°C; Fig. 1) was 25.01% higher compared to the 13.76°C ± 2.8°C observed in mid elevation species, and was 30.08% higher compared to the 12.83°C ± 2.8°C observed in high elevation species. When we compared midland and highland species we found that the difference between them only was 6.76%, in which midland species have a higher CT_{min} ($F_{2, 80} = 13.7$, $p < 0.001$). For $CT_{max,}$ we found that the CT_{max} for lowland species (31.90°C ± 0.8°C), was 11.07% higher than the midland species (28.37 ± 2.0C), and was 17.64% higher compared to the 26.27°C ± 3.0°C observed in high elevation species. ($X^2 = 28.18$, $p < 0.001$; Fig. 1). In addition, we found that the thermal range (the range from CT_{min} to CT_{max}) of lowland species is 13.5°C, while the thermal range of the midland species is 13.4°C, and for highland species is 1.6°C, the low and midland species has a narrower thermal range than the highland species.

When we did the comparison among species, we found that for CT_{min} ($F_{3,79} = 17.3$, $p < 0.001$) and CT_{max} ($X^2 = 13.8$, $p < 0.001$) there were significant difference among species, in which the lowland specie (*A. maculiventris*) has the highest thermal limits (Fig. 2).

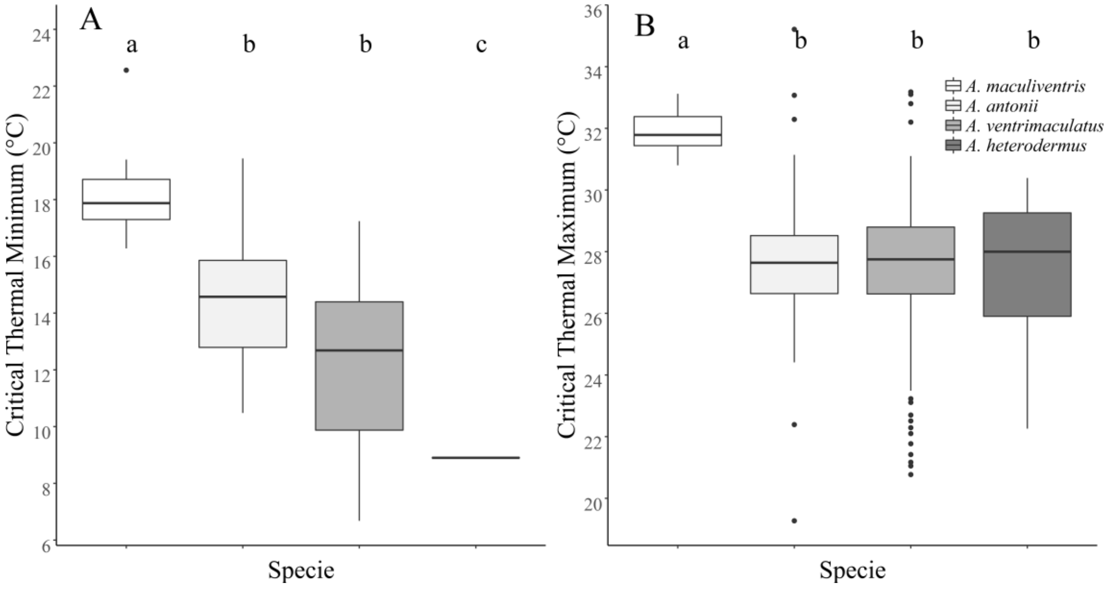


Figure 2. Box plots of CT_{max} and CT_{min} for *A. antonii, A. heterodermus, A. maculiventris A. ventrimaculatus*. CT_{min} (a) and CT_{max} (b) values for the four-anole species, *A. antonii, A. heterodermus, A. maculiventris* and *A. ventrimaculatus*. The box plots show the median (black bar), interquartile range (box), and 1.5 times the interquartile range (bars); the black circles represent outliers. The small letters

(a, b, c) show if the specie have or not similar Critical Thermal. CT_{min} ($F_{3,79} = 17.3$, $p < 0.001$) and CT_{max} ($X^2 = 13.8$, $p < 0.001$) among species, in which the lowland specie has the highest thermal limits.

Table 2. Best models GLM analysis for CT_{max}. Effect of Elevation, Mass, and SVL on CT_{max} analyzed using a Generalized Linear Model (GLM). This analysis included the four anole lizards. Degree of freedom (d.f) are show with the *t* value and the *p* value, the AICc, and the delta of AIC (Δ) are shown.

Source	**CT_{max} (°C)**				
	d.f	*t*	*p*	AICc	Δ
Elevation + Mass	4	108.7	<0.001	597.9	0.00
Elevation + SVL	4	81.1	<0.001	598.9	0.98
Elevation * Mass	5	56.1	<0.001	599.5	1.57
Elevation + Mass + SVL	5	48.9	<0.001	599.8	1.85
Elevation + SVL * Mass	6	44.7	<0.001	600.1	2.12

2.5.3 Intraspecific variation in Critical Thermal Minimum and Maximum

The thermal limits for *A. maculiventris* were: CT_{min} 18.4°C ± 1.9°C ($\bar{x}$ ± SD; range = 16.28–22.6°C; Table 3) and CT_{max} 31.9°C ± 0.83°C (range = 30.8-31.9°C; Table 1, Table 3). When we compared males versus females, for CT_{max}, we found that the males CT_{max}. was 0.9% smaller compared to the female (Fig. 3).

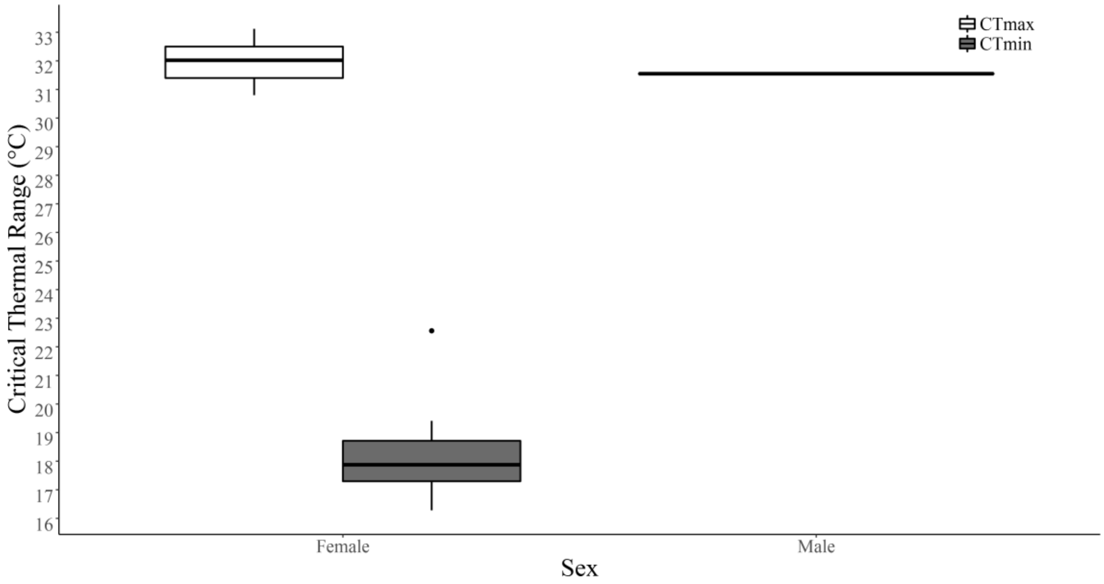


Figure 3. Box plots of CT_{max} and CT_{min} for sexes of *A. maculiventris.* CT_{max} and CT_{min} values for *A. maculiventris* by sex, we only measured one males for CT_{max}. The box plots show the median (black bar), interquartile range (box), and 1.5 times the interquartile range (bars); the black circles represent outliers.

When we compared the thermal limits between males vs. females of *Anolis antonii* we found that neither CT_{min} (t = 0.64, *p* = 0.52) or CT_{max} ($X^2 < 0.001$, *p* = 0.99) differ among sexes (Fig. 5a, Table 3). And, thermal limits do no differ between ages CT_{min} (t = 0.55, *p* = 0.59) or CT_{max} ($X^2 = 1.60$, *p* = 0.21; Fig. 4b, Table 3). The CT_{min} (*t* = 0.64, *p* = 0.52) and CT_{max} ($X^2 < 0.001$, p = 0.99) did not vary among the two *A. antonii* populations despite the 1000 m elevation and 2.5°C temperature differences (Fig. 5a, Table 4).

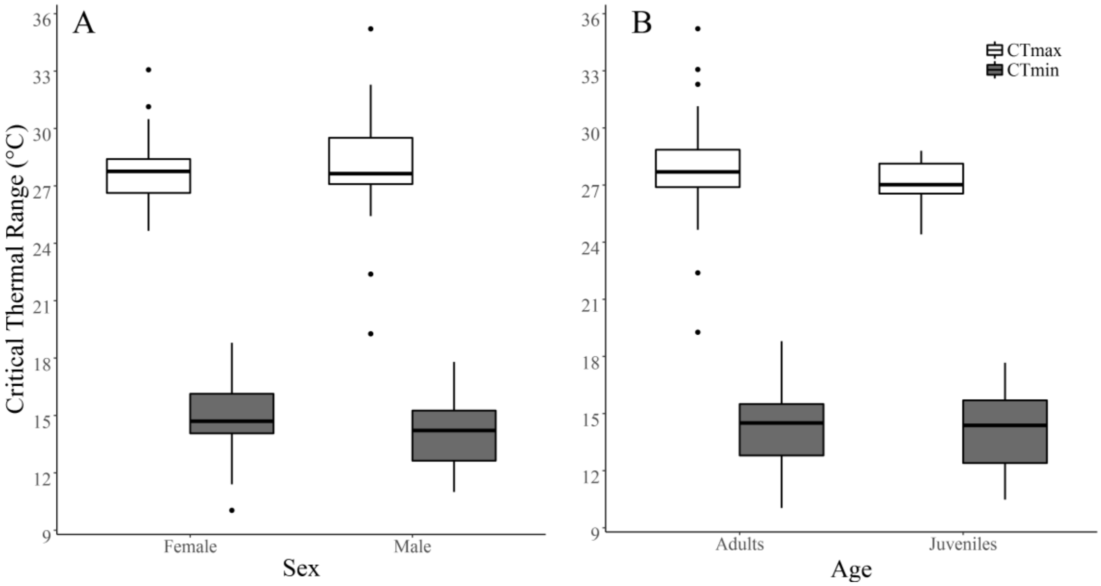


Figure 4. Box plots of CT_{max} and CT_{min} for sexes and ages of *A. antonii*. CT_{max} and CT_{min} values for *A. antonii* by sex (a), CT_{min} (t = 0.64, p = 0.52) and CT_{max} ($X^2 < 0.001$, p = 0.99). And age (b), CT_{min} (t = 0.55, p = 0.59) and CT_{max} (X^2 = 1.60, p = 0.21), neither CT_{min} or CT_{max} differ between age and sex. The box plots show the median (black bar), interquartile range (box), and 1.5 times the interquartile range (bars); the black circles represent outliers.

For *Anolis ventrimaculatus* the thermal limits did not differ between sexes, CT_{min} (t = 0.40, p = 0.69) and CT_{max} (X^2 = 3.01, p = 0.08) (Fig. 6a). Also, for adults versus juveniles comparison, both, CT_{min} (t = 1.31, p = 0.20) and CT_{max} (X^2 = 1.60, p = 0.21), not differ between age (Fig. 6b, Table 3). The CT_{min} ($F_{2, 27}$ = 1.55, p = 0.23) do not differ, but CT_{max} (X^2 = 16.6, $p < 0.001$) differ among populations among the three *A. ventrimaculatus* populations despite the 600m elevation and 2.5°C temperature differences (Fig. 5b, Table 4).

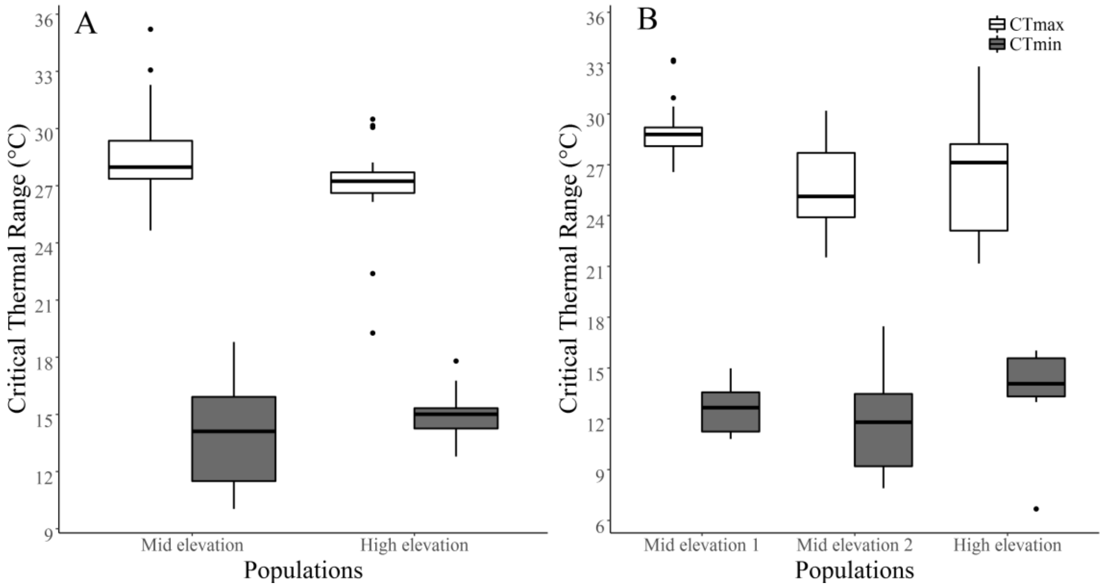


Figure 5. Box plots of CT_{max} and CT_{min} for populations of *A. antonii* and *A. ventrimaculatus.* CT_{max} and CT_{min} values for by *A. antonii* (a) for the two populations; PNN Tatamá (mid elevation) and PNN Farallones (high elevation), CT_{min} ($t = 0.64$, $p = 0.52$) and CT_{max} ($X^2 < 0.001$, $p = 0.99$) do not differ among populations. And *A. ventrimaculatus* (b) for each of its populations; PNN Tatamá (mid elevation 1), RF Bitaco (mid elevation 2) and PNN Farallones (high elevation), CT_{min} ($F_{2, 27} = 1.55$, $p = 0.23$) do not differ, but CT_{max} ($X^2 = 16.6$, $p < 0.001$) differ among populations.

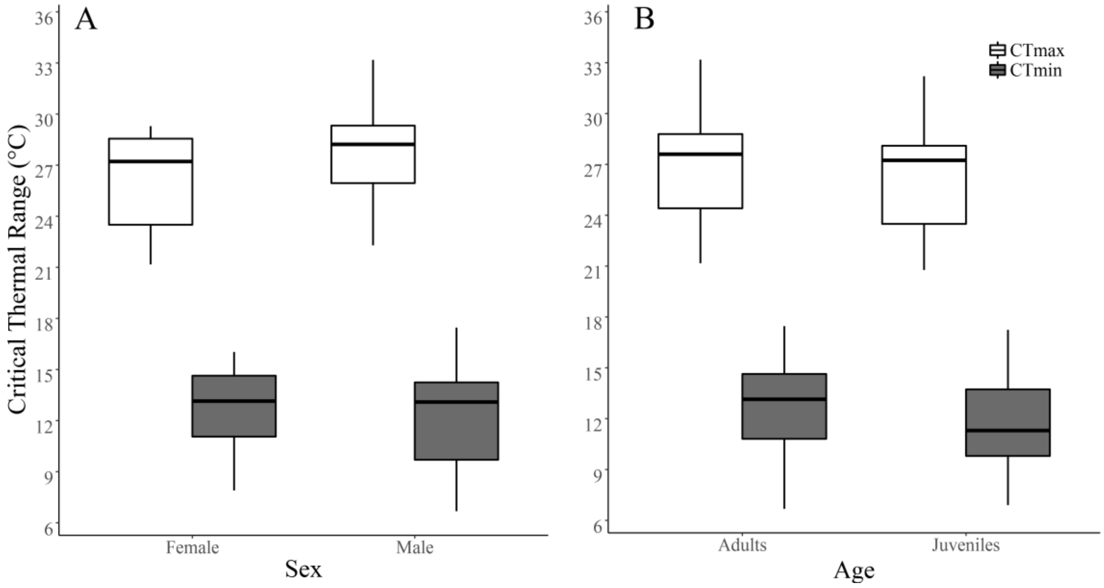


Figure 6. Box plots of CT_{max} and CT_{min} for sexes and ages of *A. ventrimaculatus.* CT_{max} and CT_{min} values for *A. ventrimaculatus* by sex (a), CT_{min} ($t = 0.40$, $p = 0.69$) and CT_{max} ($X^2 = 3.01$, $p = 0.08$). And age (b, CT_{min} ($t = 1.31$, $p = 0.20$) and CT_{max} ($X^2 = 1.60$, $p = 0.21$), neither CT_{min} or CT_{max} differ between age and sex. The box plots show the median (black bar), interquartile range (box), and 1.5 times the interquartile range (bars); the black circles represent outliers.

The thermal limits for *A. heterodermus* were: CT_{min} 8.9°C and CT_{max} 27.16°C ± 3.53°C (range = 22.26-30.39°C; Table 3). Adults versus juveniles' comparison (Table 3) showed that for the CT_{max} we observed that for adults was 29.6°C ± 1.1°C, that was 16.55% higher compared to the juveniles 24.7 ± 3.4°C.

Table 3. Quantification of Critical Thermal for the four each: males and females, adults and juveniles. Altitude, Critical Thermal Minimum (CT_{min}) and Maximum (CT_{max}) for males and females, and adults and juveniles of *Anolis maculiventris, Anolis antonii, Anolis ventrimaculatus.* and *Anolis heterodermus*. Mean, Standard Deviation, and in parenthesis sample size are shown.

Specie	Altitude (m)	CT_{min} (°C)	CT_{max} (°C)
A. maculiventris	587	18.4 ± 1.9 (9)	31.9 ± 0.8 (6)
Males	554	-	31.9 (1)
Females	598	18.35 ± 1.9 (9)	31.9 ± 0.9 (5)
Adults	587	18.4 ± 1.9 (9)	31.9 ± 0.8 (6)
A. antonii	1628	12.7 ± 3.4 (49)	27.7 ± 2.5 (63)
Males	1698	14.1 ± 2.2 (12)	27.9 ± 2.9 (27)
Females	1610	14.7 ± 2.4 (12)	27.9 ± 1.9 (20)
Adults	1553	14.4 ± 2.2 (24)	27.9± 2.5 (47)
Juveniles	1406	13.9 ± 2.3 (11)	27.2 ± 1.1 (15)
A. ventrimaculatus	2030	12.32 ± 2.6 (51)	26.7 ± 3.1 (74)
Males	2027	12.3 ± 3.5 (8)	27.8 ± 3.0 (27)
Females	2012	12.9 ± 2.3 (22)	26.2 ± 2.8 (26)
Adults	2019	12.7 ± 2.6 (30)	27.0 ± 2.9 (53)
Juveniles	2050	11.7 ± 2.6 (21)	26.1 ± 3.3 (21)
A. heterodermus	2227	8.9 (1)	27.16 ± 3.5 (4)
Males	2145	-	29.35 ± 1.1 (2)
Adults	2145	-	29.63 ± 1.1 (2)
Juveniles	2310	8.9 (1)	24.69 ± 3.4 (2)

Overall, we found that in both comparisons, females vs males, and adults vs juveniles, for each of the two species, females, males and juveniles have the almost the same CT_{min} and CT_{max}, i.e. similar thermal ranges (Fig. 3, Fig. 4), for the other two we cannot make any statistical analysis.

Table 4. Quantification of Critical Thermal for *A. antonii* and *A. ventrimaculatus* populations. Altitude, Critical thermal minimum (CT_{min}) and maximum (CT_{max}) for *Anolis antonii,* and *Anolis ventrimaculatus*, and their different populations. Mean, Standard Deviation, and in parenthesis sample size are shown.

Specie	Altitude (m)	CT_{min} (°C)	CT_{max} (°C)
A. antonii	1628	12.7 ± 3.4 (49)	27.7 ± 2.5 (63)
Farallones	2120	15.0 ± 1.5 (10)	27.0 ± 2.3 (18)
PNN Tatamá	1415	14.1 ± 2.7 (13)	28.5 ± 2.3 (28)
A. ventrimaculatus	2030	12.8 ± 2.6 (51)	26.7 ± 3.1 (74)
RF Bitaco	1998	11.9 ± 2.9 (13)	25.6 ± 2.6 (17)
Farallones	2192	13.3 ± 2.1 (11)	25.5 ± 3.3 (17)
PNN Tatamá	1721	12.6 ± 1.7 (6)	29.1 ± 1.8 (19)

2.6 DISCUSSION

In this study, we found that the thermal limits (the range from CT_{min} to CT_{max}) do not vary between, sexes, ages, and populations for each of the four species, except for one of the populations of *A. ventrimaculatus.* The CT_{max} of the population of *A. ventrimaculatus* in the PNN Tatamá (midland) is 11.1% higher than the populations from RF Bitaco (Chicoral) and Farallones (highlands; Fig. 2). Also, CT_{min} and CT_{max} differ between altitudes and species. Among low, mid, and highlands, our findings suggest that the thermal limits (from CT_{min} to CT_{max}) for anole lizards are narrower in lowlands, than mid and highlands. Also, thermal limits of the continental species are narrower than islands species (Muñoz et al 2013). Muñoz et al (2013) found that lowland island species thermal limits go from 10.7°C to 40.3°C and the highland island species from 7.2°C to 40.4°C, while in our study, the lowland continental species goes from 18.4°C to 31.9°C and the highland continental species from 8.9°C to 29.6°C. When we compared range of the thermal limits of lowland and highland species of continent and island we found that the thermal ranges of the island species are 54.45% and 37.7% higher than the mainland species, lowland and highland species, respectively. When we compared the thermal range of the low and highland continental species we found that this range is 34.8% higher in highland species than in lowland species. These results suggest that tropical continental anole species are highly sensitive to temperature, and that the continental anole species may be going to be more affected by an increase in the temperature than those anole species that inhabit in islands, especially those continental anoles species that inhabit lowlands (Deutsch et al 2008, Huey et al 2009, Muñoz et al 2013).

It is important to highlight that the high variability of our results in both CT_{min} and CT_{max} between low, mid and highland species supports that in an altitudinal gradient the low and midland species have narrower thermal limits than highland species (Janzen 1967, Ghalambor et al 2006; Fig. 3). The low and midland species continental anole species would be highly affect by climate warming due to they are living in habitats where the maximum annual temperature is close to their CT_{max} (Huey et al 2009).

2.6.1 Thermal behavior

We found that both elevation and mass affect CT_{min} and CT_{max}. CT_{min} is influenced by body mass, while CT_{max} by the elevation, body mass and SVL. There is a negative relation between CT_{min} and body mass, in which larger individuals at higher elevations would have cooler thermal limits. This suggests that mass could be a good predictor of cold thermal tolerance. In contrast, CT_{max} is influenced by elevation, mass and SVL; it has been shown in other poikilotherms that elevation can influence that species at lower elevation have higher thermal limit (Navas 2003, Muñoz et al 2013, May et al 2017). But we found that not only elevation, but mass and SVL, can affect $CT_{max.}$ This shows that this interaction could be a good predictor of CT_{max}. Despite elevation, body mass and SVL affecting the thermal limits of these four-anole species, there are other factors that could be affecting CT_{min} and CT_{max}. Those include biotic interactions, such as competition or predation, which can reduce the niche and the altitudinal range of different organisms, but also abiotic, such as changes in the annual temperature, humidity and rainfall, which can restrict these thermal limits (Terborgh & Weske 1975, Jankowski et al. 2013, May et al 2017).

The critical thermal temperature suggests that the thermal limits for *A. antonii* and *A. ventrimaculatus* do not vary among populations despite the 1000m and 600m elevational differences, respectively. And, for populations of *A. antonii* and *A. ventrimaculatus* that occur in sympatry. This suggest that species with difference sizes of anole lizards (*A. antonii* – SVL = 55mm and *A. ventrimaculatus* – SVL = 8mm) that occur in sympatry, their thermal limits may be similar among them.

Among specie we observed that there is not interspecific variation in CT_{min} in *A. antonii and A. ventrimaculatus*, but they differ from *A. maculiventris*, and *A. heterodermus*, in which *A. maculiventris* has a higher CT_{min} compared to *A. heterodermus*. And for CT_{max}, the mid and highland species (*A. antonii, A. heterodermus* and *A. ventrimaculatus*) do not differ in their CT_{max} compared to the lowland species (*A. maculiventris*; Fig. 2). This shows there is a little interspecific variation, in both CT_{min} and CT_{max} in continental anoles (van Berkum 1988, Bauwens et al 1995, Muñoz et al 2013, Valdecantos et al 2013).

We found that critical thermal limits for continental anole species are similar between sexes and ages, the thermal limits are not linked with the ontogenetic stage or sex, in agreement with the lack of differences observed by Tang et al (2013) between sexes thermal limits in *Eremias multiocellata*. But Tang et al. (2013) observed differences between adults and juveniles and we did not. These contrasting results can be explained by microhabitat use, which the no-random selection of microhabitat to avoid the intraspecific competition (e.g., perch sites, thermoregulation activities, hiding sites) that affect thermoregulatory behaviors and activities (Du et al 2000, Herczeg et al 2008, Tang et al 2013, Andrango et al 2016). Microhabitat segregation between adults and juveniles has been observed in other lizard groups, *Eumeces elegans* (Du et al 2000), *Zootoca vivipara* (Herczeg et al 2008), *Eremias multiocellata* (Tang et al 2013), however, this information is lacking for our continental anoles. More studies along montane gradients are needed to help to make predictions of how thermal limits could change among different sex, age, population and species, to estimate how they are going to respond in an increase of the global temperature. However, during the field work we saw that adults and juveniles of the four species were perching in almost the same types of perch (e.g., ferns or tree branches).

Another important factor that can be affecting thermal limits is the plastic capacity of the organisms. Plastic capacity is a rapid change in those traits that mediate climate sensitivity in an individual or population (Llewelyn et al 2016). Studies have been found that some species of different lizard genera and other poikilotherms could be overheated, because they do not have a plastic capacity (Hertz & Huey 1981, Huey et al 2009, Muñoz et al 2013, Gunderson & Stillman, 2015, Piantoni et al 2015). Our results suggest that the great variation in CT_{min} and CT_{max} of the highland population species maybe cause by the plastic capacity of the individuals that inhabit highlands (Fig. 1). Therefore, plastic capacity should be considered in future studies on tropical lizard groups, and how this capacity could change between low, mid and highland lizards.

2.6.2 Implications on climate change

Current climate models predict that an increment in temperature between 0.8-1.7°C would lead to the extinction of 23-40% of the tropical species (Thomas et al 2004, Sinervo et al 2010, Brusch et al 2015). Therefore, in a climate change scenario the possible responses of anoles lizards and other groups are: changes in their activities behavior, in their distribution, or face extinction, (Martin & Huey 2008, Deutsch et al 2008, Muñoz et al. 2013, Forham et al 2016), and it is going to affect more those species that inhabit the tropics and have narrow critical thermal ranges, the lowland species (Janzen 1967, van Berkum 1988, Angilletta 2006, Ghalambor et al 2006, Gunderson & Stillman 2015). Our findings show that the low and midland continental anole species have narrower thermal limits than those species than occur in highlands (Fig. 1). This support the idea that lowland anole species are going to be the most affected in a climate change scenario. Lowland anoles are living in habitats were the temperature is getting warmer, and in some periods of the year the temperature reaches above their optimal values (Colwell et al 2008, Huey et al 2009, Muñoz et al 2013).

An ongoing discussion is how organisms will face an increase in the global temperature, many studies have suggested that poikilotherms will have different responses to face the climate change. Some studies have shown in the hypothesis, that "*the hotter is better*", that means that individuals will have greater physical performance at the temperature increase (Angilleta et al 2010, Brusch et al 2015), some organism will improve their physiological performance (Angilletta et al 2010, Muñoz et al 2013, Brusch et al 2015). But what is going to happen with those lowland species than inhabit in the continent that have narrower thermal limits? The “*the hotter is better*” hypothesis fails to answer that question (Angilletta et al 2010, Muñoz et al 2013, Brusch et al 2015). Other studies suggest that several groups of animals are going to face the extinction (Wake & Vredenburg 2008, Sinervo et al 2010, Brusch et al 2015). And others, that is hard to predict what is going to happen to organisms in a climate change scenario, because the affection of temperature vary among taxa Frazier et al 2006). Our study is one of the first approaches to understand how thermal limits vary among low, mid and highland anole species, which can help to answer other questions such as how continental anole lizards are going to respond to a climate change, and how this increase in the global temperature is going to affect low and highland anole populations.

2.7 CONCLUSIONS

We found that there is a little interspecific variation in CT_{min} and CT_{max} among species, but when we compared low and highland species, we observed that the lowland species have narrower thermal limits than highland species.

The thermal limits for continental low and highland species are narrower compared to the thermal ranges found by Muñoz et al (2013) in low and highland anole species from islands. This finding suggest that tropical lowland continental anole species are highly sensitive to temperature (Deutsch et al 2008, Huey et al 2009, Muñoz et al 2013).

We observed that mass and elevation is affecting CT_{min} and CT_{max}, which suggest that that both factors, mass and elevation, can be good predictor the thermal limits for anole lizards. But we have to consider that many other biotic and abiotic factor can take places in the variation of CT_{min} and CT_{max}, such as plastic capacity, which can help poikilotherms to avoid overheating.

We also found that neither CT_{min} or CT_{max} change between ontogenetic stages or sexes, in agreement with the lack of differences observed by Tang et al (2013) between sexes thermal limits in *Eremias multiocellata*. But Tang et al. (2013) observed differences between adults and juveniles and we did not.

Our findings suggest that lowland anole species are going to be the most affected in a climate change scenario, because they inhabit in places where the temperature is getting warmer and warmer, and in some locations temperature reaches above their optimal values (Colwell et al 2008, Huey et al 2009, Muñoz et al 2013).

2.7 RECOMMENDATIONS

For future studies, we suggest that these studies should focus on understand which possible responds lowland anole species are going have to an increase in the global temperature. And other factors are affecting the thermal limits not just in lowland species but in low, mid and highland continental anole species such as plastic capacity.

We also suggest that behavioral studies should be carried out to see whether there is a special and / or temporal distribution in the microhabitat use by males and females, and adults and juveniles in continental *Anolis*.

Also, we conducted this study in the western cordillera of Colombia in an elevational gradient from 500m to 2400m, but we do not know if in other species with broader elevation gradient the similar pattern of CT_{min} and CT_{max} between ages, sexes, species populations and elevations are similar. Thus, we suggest to carry out this same experiment for species with a broader elevation range, and compare between ages, sexes, species, populations and elevations are similar.

3. REFERENCES

Andrango, M.B., Sette, C. & Torres-Carvajal, O. 2016. Short-term predicted extinction of Andean populations of the lizard *Stenocercus guentheri* (Iguanidae: Tropidurinae). Journal of Thermal Biology. 62(2016): 30-36.

Angilletta, M.J., Niewiarowski, P.H., & Navas, C.A., 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology. 27: 249–268.

Angilletta Jr, M.J., 2006. Estimating and comparing thermal performance curves. Journal of Thermal Biology. 31 (2006): 541–545.

Angilletta, M. J. Jr, Huey, R. B., & Frazier, M. R. 2010. Thermodynamic effects on organismal performance: is hotter better? Physiological and Biochemical Zoology. 83:197–206.

Bauwens, D., Garland Jr, T., Castilla, A. M. & van Damme, Raoul. 1995. Evolution of sprint speed in Lacertid lizards: morphological, physiological and behavioral covariation. 49(5): 848-863.

Bogert, C.M. 1949. Thermoregulation in Reptiles, A Factor in Evolution. Society of the Study of Evolution. 3(3): 195-211.

Brusch IV, G.A., Taylor, E.N. & Whitfield, S.M. 2015. Turn up the heat: thermal tolerances of lizards at La Selva, Costa Rica. Oecologia. 180(2): 325-334.

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C. & Longino, J. T. 2008. Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. Science. 322: 258-322.

Corlett, R.T., 2012. Climate change in the tropics: The end of the world as we know it? Biological Conservation. 151(1): 22-25.

Cowles, R.B. & Bogert, C.M. 1944. A preliminary study of thermal requirements of desert reptiles. Bulletin of the American Museum of Natural History. 83: 265- 296.

Danin, T. 2017. Projected Increases in Hurricane Damage in the United States: The Role of Climate Change and Coastal Development. Ecological Economics. 138(2017): 186-198.

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

Doan, T.M. 2003. Which Methods Are Most Effective for Surveying Rain Forest Herpetofauna? Journal of Herpetology. 37(1): 72-81.

Du, W.G., Yan, S.J., Ji, X., 2000. Selected body temperature, thermal tolerance and thermal dependence of food assimilation and locomotor performance in adult blue-tailed skinks, *Eumeces elegans*. Journal of Thermal Biology. 25: 197–202.

Forham, D.A., Brook, B.W., Hoskin, C.J., Pressey, R.L., VanDerWal, J. & Williams, S.E. 2016. Extinction debt from climate change for frogs in the wet tropics. Biology Letters. 12(10): 1-5.

Frazier, M.R., Huey, R.B. & Berrigan, D. 2006. Thermodynamics constrains the evolution of insect population growth rates: “warmer is better”. The American Naturalist. 168:512–520.

Ghalambor, C.K., Huey, R.B., Martín, P.R., Tewksbury, J.J. & Wang, G. 2006. Are mountain passes higher in the tropics? Janzen’s hypothesis revisited. The Society for Integrative and Comparative Biology. 46(1): 5-17.

Gunderson, A. R. & Leal, M. 2012. Geographic variation in vulnerability to climate warming in a tropical Caribbean lizard. Functional Ecology. 26: 783-793.

Gunderson, A.R. & Stillman, J.H., 2015. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. Proceedings of the Royal Society. 282(1808): 1-8.

Gunderson, A. R., Mahler, D. L. & Leal, M. 2016. A functional analysis of the contribution of climatic niche divergence to adaptive radiation. Unpublished.

Herczeg, G., Herrero, A., Saarikivi, J., Gonda, A., Jäntti, M., Merilä, J., 2008. Experimental support for the cost–benefit model of lizard thermoregulation: the effects of predation risk and food supply. Oecologia 155: 1–10.

Holt, R.D. 2003. On the evolutionary ecology of species’ ranges. Evolutionary Ecology Research. 5: 159-178.

Hoyos-Hoyos, J.M., Isaacs-Cubides, P., Devia, N., Galindo-Uribe, D.M. & Acosta-Galvis, A.R. 2012. An approach to the ecology of the herpetofauna in agroecosystems of the Colombian coffee zone. South American Journal of Herpetology. 7(1): 25-34.

Huey, R.B. & Slatkin, M., 1976. Cost and Benefits of Lizard Thermoregulation. The Quarterly Review of Biology. 51(3): 363-384.

Huey, R.B. & Webster, T.P., 1976. Thermal biology of Anolis lizards in a complex fauna: The *Cristatellus* group on Puerto Rico. Ecology. 57: 985-994.

Huey, R.B., Deutsch, C., Tewksbury, J.J., Herzt, P.E., Alvarez Perez, H.J. & Garland Jr., T. 2009. Why tropical forest lizards are vulnerable to climate warming. Proceedings of the Royal Society. 276(1664):19391948.

Hulme, M. y Viner, D. 1998. A climate change scenario for the tropics. Climatic Change. 39(2): 145-176.

Irschick, D.J., Vanhooydonck, B., Herrel, A. & Meyers, J. 2005. Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. Biological Journal of the Linnean Society. 85: 211-221.

Iwami, Y., Hasegawa, A., Miyamoto, M., Kudo, S., Yamazaki, Y., Ushiyama, T. & Koike, T. 2017. Comparative study on climate change impact on precipitation and floods in Asian river basins. 11(1): 24-30.

Jankowski, J. E., Londoño, G. A., Robinson, S. K., & Chappell, M. A. 2013. Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. Ecography. 36: 001-012.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. The American Naturalist. 101: 233–249.

Kour, E.L. & Hutchison, V.H. 1970. Critical thermal tolerance and heating and cooling rates of lizards from diverse habitat. Copeia 1970: 219-229.

Lailvaux, S. P., 2007. Interactive effects of sex and temperature on locomotion in reptiles. Integrative and Comparative Biology 47(2): 189-199.

Llewelyn, J., Macdonald, S.L., Hatcher, A., Morits, C. & Philips, B.L. 2016. Intraspecific variation in climate-relevant traits in a tropical rainforest lizard. Diversity and Distributions: A Journal of Conservation Biogeography. 1-13.

Martin, T.L. & Huey, R.B. 2008. Why “Suboptimal” Is Optimal: Jensen’s Inequality and Ectotherm Thermal Preferences. 171(3): E102-E118.

May R., Catenazzi, A., Corl, A., Santa-Cruz, R., Carnaval, A.C. & Moritz, C. 2017. Divergence of thermal physiological traits in terrestrial breeding frogs along a tropical elevational gradient. Ecology and Evolution. 7(9): 3257-3267.

Méndez-Galeano, M.A. & Calderón-Espinosa, M.L. 2017. Thermoregulation in the Andean lizard *Anolis heterodermus* (Squamata: Dactyloidae) at high elevation in the Eastern Cordillera of Colombia. Iheringia, Série Zoologia. 107: e2017018.

Muñoz, M.M., Stimola, M.A., Algar, A.C., Conover, A., Rodriguez, A.J., Landestoy, M.A., Bakken, G.S. & Losos, J.B. 2013. Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. Proceedings of the Royal Society. 281(1778): 1-9.

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

Nordkvelle, J., Rustad, S.A. & Salmivalli, M. 2017. Identifying the effect of climate variability on communal conflict through randomization. Climate Change. 141: 627-639.

Ortega, Z., Mencía, A. & Peréz-Mellado, V. 2016a. Are mountain habitats becoming more suitable for generalist than cold-adapted lizards thermoregulation? PeerJ. 4: e2085.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology and Evolution. 37: 637-669.

Piantoni, C., Navas. C.A. & Ibargüengoytía N. R., 2015. Vulnerability to climate warming of four genera of New World iguanians based on their thermal ecology. Animal Conservation. 19(4): 391-400.

Pinheiro J, Bates D, DebRoy S, Sarkar D, Development Core Team R. 2013. nlme: linear and onlinear mixed effects models. R package version 3:1–110.

Pörtner, H.O. 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comparative Biochemistry and Physiology. 132 (2002): 739-761.

Pounds, J.A., L. Fogden, M.P. & Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. Nature. 398:611-615.

R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Sharma, D. K. & Mishra, J. K. 2011. Impact of environmental changes on biodiversity. IndianJ.Sci.Res. 2(4): 137-139.

Sinclair B.J., Marshall, K.E., Sewell, M.A., Levesque, D.L., Willett, C.S., Slotsbo, S., Dong, Y., Harley, C.D. G., Marshall, D.J., Helmuth, B.S. & Huey, R.B. 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? Ecology Letters. 16(11): 1372-1385.

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., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Duarte-Rocha, C. F., Ibargüengyotía, N., Aguilar-Puntriano, C., 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.

Stevenson, R.D., 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. American Zoologist. 19: 357-366.

Stoks, R., Geerts, A. N. & De Meester, L. 2013. Evolutionary and plastic responses of freshwater invertebrates to climate change: realized patterns and future potential. Evolutionary Applications. 7(2014): 42-55.

Terborgh, J. & Weske, J. S. 1975. The role of competition in the distribution of Andean birds. Ecology. 56: 23-40.

Thomas, C.D., Camero, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., N. Erasmus, B.F., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, E. 2004. Extinction risk from climate change. Nature. 427: 145-148.

Tomanek, L. 2008. The Importance of Physiological Limits in Determining Biogeographical Range Shifts due to Global Climate Change: The Heat-Shock Response. Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches. 81(6) 709-717.

Valdecantos, S., Martínez, V., Lobo, F. & Cruz, F. B. 2013. Thermal biology of *Liolaemus* lizards from the high Andes: Being efficient despite adversity. Journal of Thermal Biology. 38(2013): 126-134.

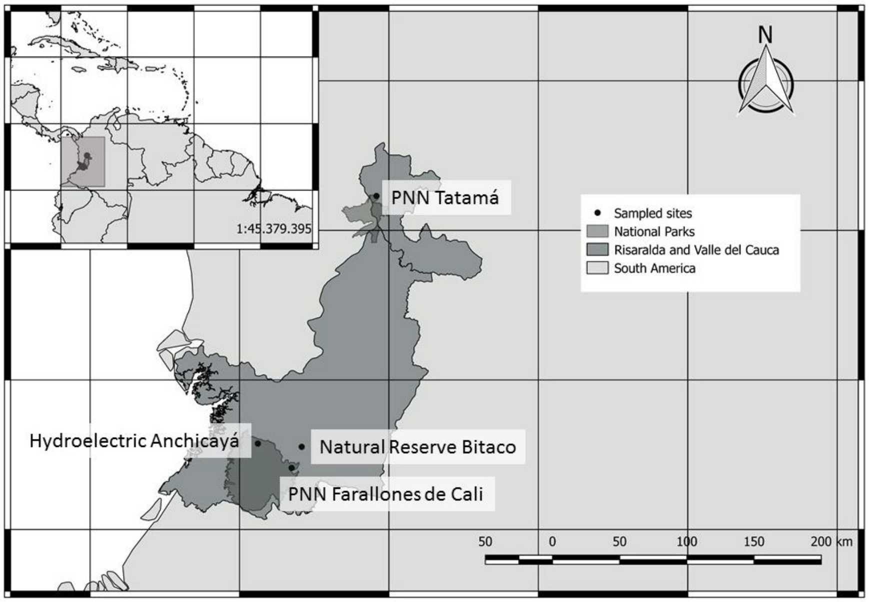
Van Berkum, F.H., 1988. Latitudinal pattern of the thermal sensitivity of sprint speed in lizards. The American Naturalist. 132(3): 327-344.

Wake, D.B. & Vredenburg, V. T. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences of the United States of America.105:11466–11473.

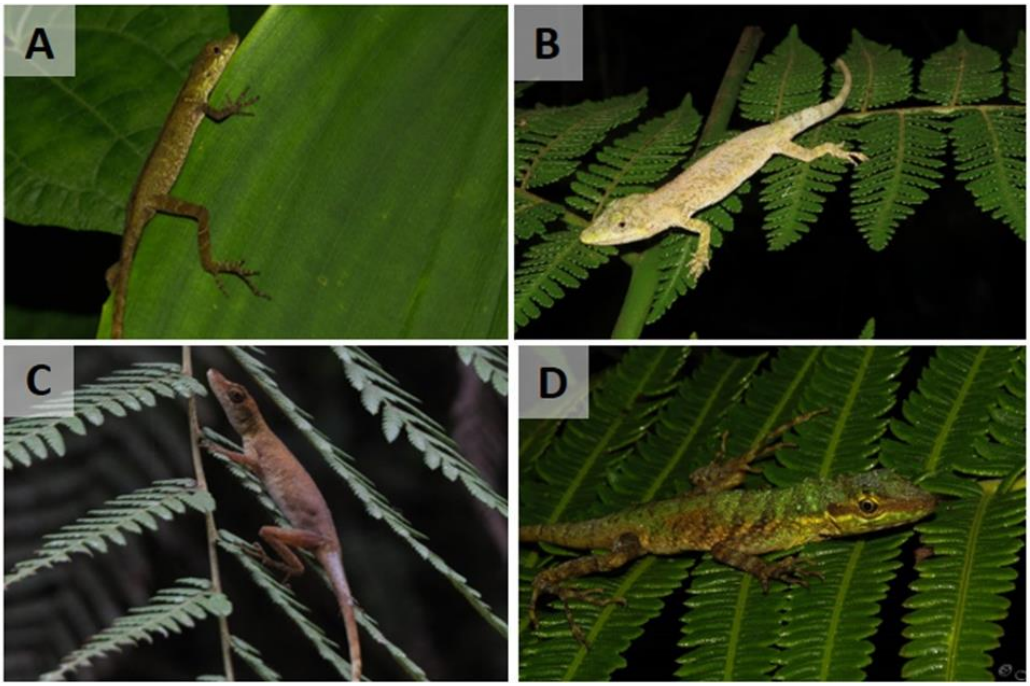
Williams, J.W., Jackson, S.T., & Kutzbacht, J.E., 2007. Projected distributions of novel and disappearing climates by 2100 CE Proceedings of the National Academy of Sciences. 104: 5738–5742.

Zamora-Camacho, F.J., Reguera, S., Moreno-Rueda, G. & Pleguezuelos, J.M. 2013. Patterns of seasonal activity in a Mediterranean lizard along a 2200 m altitudinal gradient. Journal of Thermal Biology. 38(2013): 64-69.

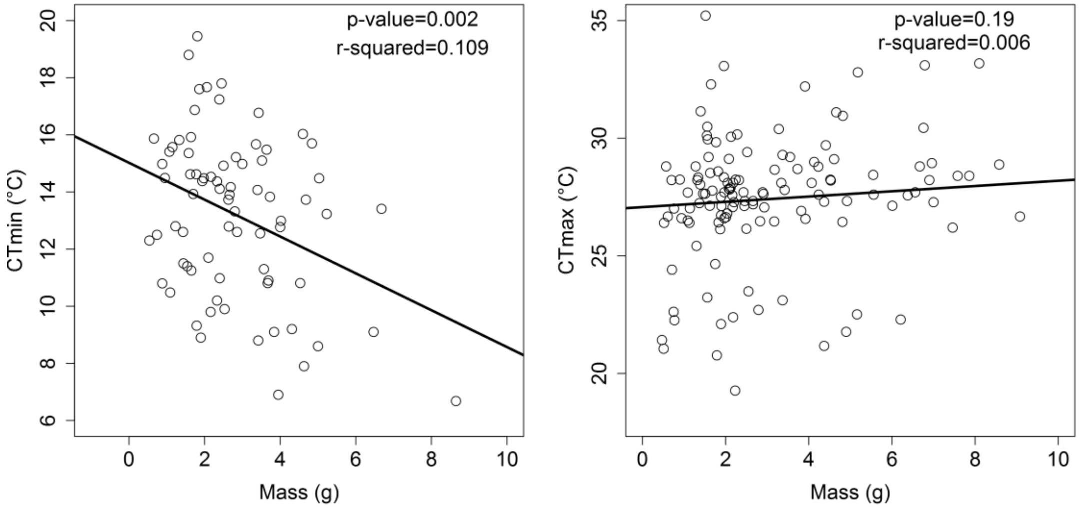
SUPPLEMENTARY MATERIAL



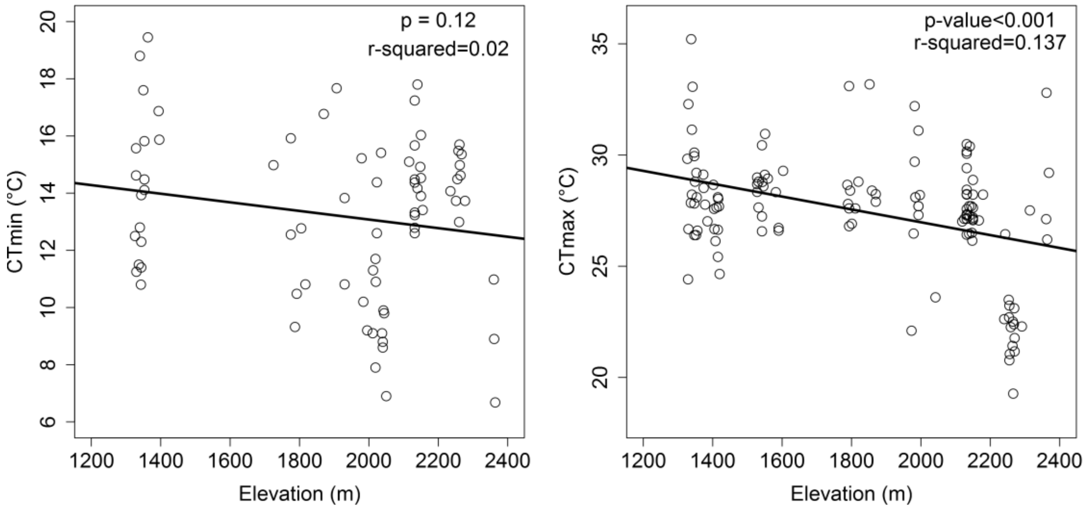
Supplementary material 1. Map with the localities where study was conducted. Map showing the localities for each anole lizard sampled in the study. The localities that are shown correspond to the northwestern of Colombia in South America.



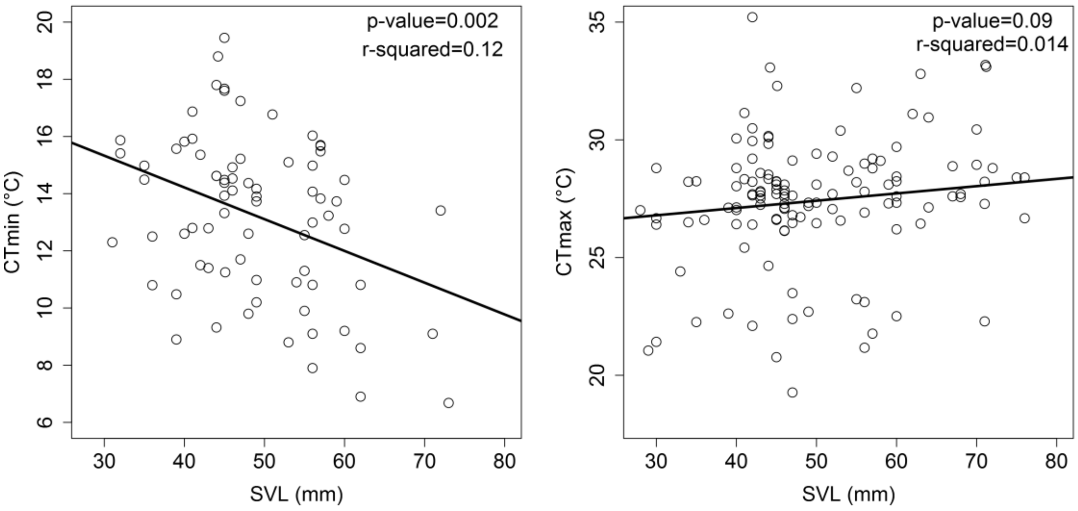
Supplementary material 2. *Anolis* species sampled in the study. Anole species that were sample during the study. *Anolis antonii* (A), *Anolis heterodermus* (B), *Anolis maculiventris* (C) and *Anolis ventrimaculatus* (D).



Supplementary material 3. CT$_{min}$ or CT$_{max}$, and mass correlation. Correlation between Critical Thermal Minimum (CT$_{min}$; for the four-species combined), Critical Thermal Maximum, CT$_{max}$, and mass (g). Showing the *p*-value, and r^2.



Supplementary material 4. CT$_{min}$ or CT$_{max}$, and elevation correlation Correlation between Critical Thermal Minimum (CT$_{min}$; for the four-species combined), Critical Thermal Maximum, CT$_{max}$, and elevation (m). Showing the *p*-value, and r^2.



Supplementary material 5. CT_{min} or CT_{max}, and SVL correlation. Correlation between Critical Thermal Minimum (CT_{min}; for the four-species combined), Critical Thermal Maximum, CT_{max}, and snout-vent length (SVL; mm). Showing the *p*-value, and r^2.