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ARTICLE

Living in a cold tropical mountain: do the microhabitat use and activity pattern change with elevation in the high-Andean lizard *Stenocercus trachycephalus* (Squamata: Tropiduridae)?

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Abstract. The high mountain environment is a tough habitat that imposes many challenges to reptiles. As temperature decreases with altitude and has a dramatic variation throughout the day in the tropical mountains, ectotherms must cope with these harsh conditions. We studied the use of microhabitat and activity patterns of *Stenocercus trachycephalus* in the eastern Andes mountain range of Colombia. Three localities were sampled across the wide altitudinal distribution of this lizard species, in a range from 2,670 to 3,950 m a.s.l. The initial hypothesis was that these natural history traits would change with altitude but instead, we found that they remained roughly consistent, showing the great plasticity of this species. The results support that this lizard is a microhabitat-generalist using principally herb across the gradient, rarely shifting to specific plants or microhabitats such as rocks depending on availability. Regarding the activity pattern, this species was active throughout the day from 8:00 to 16:00 with a similar pattern along the gradient. Nevertheless, some differences were detected across localities. The activity pattern shifted from bimodal in the lower locality to unimodal in the higher ones. As expected, a correlation between temperature and activity patterns was found in one of the study sites. However, this was not the case for the lower and mid-elevation localities, where there was no correlation between these variables. The mid-elevation study site was the most interesting locality as the use of microhabitat relied virtually just on the herb stratum and the activity was constrained to the morning hours. These findings may be the result of the synergic effects of other ecological variables (weather variability, human impact, predation, population structure, or reproductive season). Our study gives the basis for a better understanding of how behavior (microhabitat choice and hours of activity) of ectotherms can help to counter thermal constraints in the neotropics when facing an altitudinal gradient. Further studies should focus on the thermal biology of this species, considering the influence of anthropic impact on these lizards' populations.

Keywords. Altitudinal gradient; Lizard; Ecology; Natural history; Neotropical mountain.

INTRODUCTION

Elevation shapes the ecology of species and populations by determining its habitat temperature, humidity, radiation, pressure, and vegetation (Heatwole, 2009; Buckley *et al.,* 2013; Siliceo-Cantero *et al.,* 2016). For example, the temperature is typically lower at higher elevations due to increased cloud cover and adiabatic cooling (McCullough & Porter, 1971; Hertz & Huey, 1981; Buckley *et al.,* 2013; Iraeta *et al.,* 2013). Altitudinal thermal changes are particularly important for ectotherms like lizards since they heavily depend on environmental temperature to grant adequate

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thermal conditions for performance, reproduction, and physiology (Hertz & Huey, 1981; Dunham *et al.,* 1989; Adolph & Porter, 1993).

Tropical mountains are a more stable region than temperate zones (Körner, 2003); however, the altitude difference promotes the existence of diverse ecosystems that may not be optimal for ectothermic animals (Navas, 2002). This is the case of high Andean ecosystems where the environmental temperature is highly fluctuating during the day, and night temperatures can reach 0°C or less (Sarmiento, 1986; Méndez-Galeano & Calderón-Espinosa, 2017). Altitudinal changes can modulate adaptation of ecological traits of species (Hertz & Huey, 1981; Ballinger, 1983; Adolph & Porter, 1993; Fierro-Estrada *et al.,* 2019) or promote the expansion of their physiological tolerance and the scope of thermal plasticity (Van Sluys *et al.,* 2004; Méndez-Galeano *et al.,* 2020). Both hypotheses have been previously tested in different studies demonstrating the importance of evaluating ecological variables in different populations along gradients (Grant & Dunham, 1990; Adolph & Porter, 1993; Vitt *et al.,* 2007; Fierro-Estrada *et al.,* 2019; Gilbert & Miles, 2019).

Lizards adopt different thermoregulatory strategies to deal with these Andean harsh conditions and to reach optimal or nearly optimal temperatures such as choosing microhabitats with adequate thermal qualities (Berk & Heath, 1975; Hertz & Huey, 1981; Bauwens *et al.,* 1996) or shifting their activity period (Hertz, 1992; Adolph & Porter, 1993). However, the existence of spatio-temporal ecological gradients limits the distribution of species depending on their capacity to adjust physiologically to the environment (Parsons, 1990). Therefore, it is harder for reptiles to colonize harsh thermic environments.

As a result, it is intriguing to study how populations at different altitudes of the Andean mountains face these ecological challenges. In addition to thermoregulatory advantages, various microhabitats supply other resources like preys, shelter, mating sites, oviposition sites, and general conditions that allow populations to persist on a specific location (Lott, 1991; Hodder *et al.,* 1998; Smith & Ballinger, 2001; Van Sluys *et al.,* 2004). Understanding the role of microhabitat use in lizard's ecology allows to assess the potential impacts of environmental changes and to suggest conservation measures (Smith & Ballinger, 2001). As resources are not equally available for lizards to exploit, time and energy budget become relevant factors as activity patterns may enhance or constrain the use of resources, and therefore alter population or community dynamics (Lima & Dill, 1990; Morgan, 2004). If activity periods are restricted to a few hours of the day and lizards do not have enough time for daily activities, a population's survivability could be at risk (Smith & Ballinger, 2001; Sinervo *et al.,* 2010; Andrango *et al.,* 2016).

The genus *Stenocercus* comprises species widely distributed in South America occurring from sea level up to 4,000 m a.s.l. and occupying a wide variety of habitats (Torres-Carvajal, 2007, 2009). *Stenocercus trachycephalus* is an endemic species of the Eastern Colombian Andes mountain range, distributed between 1,749 and 3,800 m a.s.l. It inhabits transitional areas between cloud forests and páramos, boundaries of native forests and forest plantations (Rodríguez-Barbosa *et al.,* 2017). One of the main concerns about this lizard is that the anthropogenic activities on Andean ecosystems have driven to changes in land cover over the years (Armenteras *et al.,* 2017; Rodríguez-Barbosa *et al.,* 2017). This leads to habitat loss and fragmentation of ecosystems which has proved to have negative impacts on the populations of this lizard (Moreno-Arias *et al.,* 2010).

Given the wide altitudinal range of this species and the variable abiotic conditions that provide the Andes in the tropics, our objective was: to describe the use of microhabitat and activity pattern of *S. trachycephalus* on three localities of different altitude in the eastern Andes mountain range. Then evaluate the effect of the altitudinal gradient (1,280 meters) over these two natural history traits. Additionally, we assess the relation between environmental temperature (that has variation along the gradient) and activity patterns. We expected that altitude would progressively modify these natural history traits.

MATERIAL AND METHODS

Study area

Fieldwork was carried out on the western flank of eastern Andes mountain range of Colombia along an altitude gradient between 2,670-3,950 m a.s.l. at three distinct locations in Cundinamarca, Boyacá, and Santander departments. Our choice of localities was determined by the difference in altitude among them, ease of access to each place, and different vegetation formations given by elevational changes (Fig. 1):

(1) The Santuario de Flora y Fauna Guanentá Alto Rio Fonce (Guanentá), a National Natural Park protected area of Colombia and its buffer area, located between Boyacá and Santander departments [05°58′39.90″N, 73°05′02.22″W]. The rainy season occurs from April to June from September to December with a precipitation of 1,216 mm and a mean temperature of 7.02°C (IDEAM, 2017). The dry season occurs from January to February, and from July to August with annual precipitation of 213 mm and a mean temperature of 6,73°C (IDEAM, 2017). We surveyed during September 2018 and February and April 2019, between 3,700-3,950 m a.s.l. This location presents abrupt topography with high mountains and valleys, several lakes, swamps, and streams. The surveyed habitat was a páramo ecosystem, around open high-Andean grasslands with several shrub patches and rocky outcrops. The main vegetation consisted of grasses (*Calamagrostis* sp.) and several species of *Espeletia* spp. (Asteraceae) along with a high diversity of plants in both herbaceous and shrub stratum.
(2) Las Moyas páramo is at the east of Bogotá [04°39′22.26″N, 74°01′33.72″W]. The rainy season

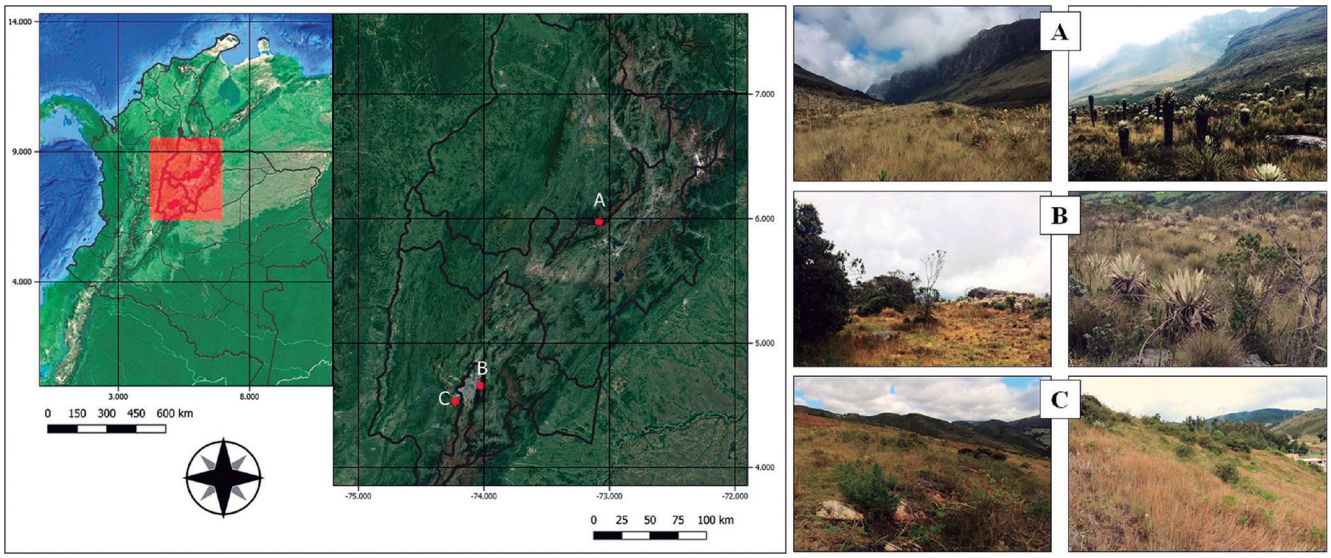

Figure 1. Study locations in the Andes eastern mountain range. (A) Guanentá, 3,750-3,950 m; (B) Las Moyas Páramo, 3,200 m; (C) La Chacua, 2,670 m.

happens from April to May and from October to November with precipitation of 444 mm and a mean temperature of 8.5°C (IDEAM, 2017). The dry season is in January and February and from July to August with precipitation of 256 mm and a mean temperature of 8.3°C (IDEAM, 2017). We surveyed in August 2018 at 3,270 m a.s.l. (average). Las Moyas presents natural páramo vegetation with anthropic degradation. The habitat is diverse and heterogeneous like most páramos but with some introduced vegetation (*Pinus* sp.). It consisted of high-Andean grasslands and shrublands with big rocky outcrops. The herbaceous stratum was mainly composed of *Calamagrostis* sp. (Poaceae) and several *Puya* spp. (Bromeliaceae). The shrub stratum consists of *Arcytophyllum* sp. (Rubiaceae), *Hypericum* spp. (Hypericaceae), *Espeletia* sp. and several other species of Asteraceae, Melastomataceae, and Ericaceae.

(3) La Chacua is in Soacha municipality of Cundinamarca department, at the south of Bogotá D.C., [04°31'55.02"N, 74°13'42.48"W]. The rainy season occurs from April to May and from October to November with a precipitation of 376 mm and a mean temperature of 9.15°C (IDEAM, 2017). The dry season occurs from January to February, and from July to August with a precipitation of 778 mm and a mean temperature of 11.60°C (IDEAM, 2017). We surveyed from May to June (when the dry season started) 2014 at 2,670 m a.s.l. This study site had soft hills with open habitats, having mostly herbaceous vegetation, mainly *Cenchrus clandestinum* (Chiov.) Morrone, *Calamagrostis* sp (Poaceae), small rocky outcrops, and human-made rock walls. Most of the vegetation is a product of disturbances by anthropic activities. However, some natural vegetation represented in several isolated shrub patches is still present in the zone which consists mostly of Asteraceae, Ericaceae spp., *Monnina* sp. (Polygalaceae), *Dodonaea* sp. (Sapindaceae) and *Miconia* spp. (Melastomataceae).

Data collection

We conducted sampling using visual encounter surveys (VES) (Heyer *et al.,* 1994; Angulo *et al.,* 2006). Surveys took place during the day from 8:00 to 16:00 and we did 146 hours/researcher per surveyed locality. The surveys consisted of searching carefully all microhabitats occupied by the species in the páramo grasslands.

For the lizards observed or captured, we recorded date, hour, GPS coordinates (with GARMIN GPS eTrex 10), and microhabitat type: ground, rock, shrub (> 1 m) and herb (< 1 m), based on páramo vegetation structure (Lozano-Contreras & Schnetter, 1976; Rangel-Ch. *et al.,* 1997). A handling permit only was required for the work at Guanentá, it was granted by the Ministerio de Ambiente y Desarrollo Sostenible by Resolution No. 205 of December 21 of 2018.

For the estimation of environmental temperature there are two approaches usually used, dataloggers (Monasterio *et al.,* 2009; Méndez-Galeano & Calderón-Espinosa, 2017) and weather station data (Fischer & Lindenmayer, 2005; Iraeta *et al.,* 2006; Pincheira-Donoso *et al.,* 2007). We used the second as it is a common approach in ecological studies along environmental gradients (Graae *et al.,* 2012). Although it has some limitations due to the potential difference between the station and the microsite of study due to altitude, wind, and slope (Graae *et al.,* 2012; Suggitt *et al.,* 2017; Bütikofer *et al.,* 2020), we considered the most optimal station to get the smaller possible difference (Table 1). Additionally, for La Chacua station that had a 130 m altitude difference with the study site we adjusted weather station data to the elevation equivalent using a rate of -0.55°C/100 m based in extensive analysis of global climate records (Körner, 2007; Graae *et al.,* 2012; Yan *et al.,* 2020). As extreme operative temperatures are better descriptors of the thermal environment than mean temperatures (Camacho *et al.,* 2015), we used for our analysis the mean and standard deviation of temperature data, to account for the extreme temperatures and central tendency measures.

Table 1. Weather stations of reference for each locality. Supplementary data in Appendix I.

Locality	Station	Coordinates	Altitude	Distance	Frequency
Guanentá	Lagunas Encantadas	05°58′07.1″N, 73°05′07.5″W	3,850	1.5 km	Half hour to Hour
Las Moyas	Cerro Los Cazadores	04°39′57.7″N, 74°01′43.1″W	3,180	1.0 km	Minute
La Chacua	Colegio Sierra Morena	04°34′28.7″N, 74°10′12.2″W	2,800	8.0 km	Minute

The weather stations used were: Instituto Distrital de Riesgos y Cambio Climático (IDIGER, 2020) for La Chacua and Las Moyas, and Parques Nacionales Naturales de Colombia (PNN) for Guanentá. We gathered the temperature data for the days we sampled in each locality, during the interval of fieldwork. We then averaged temperatures for the IDIGER station to get half-hour data for each station on the sampled days. PNN data was already in half-hour averages of temperature. Each station is listed in Table 1, and the data used is available in Appendix I (Table S1-S3).

Statistical analyses

A Pearson's chi-square test was used to assess whether there was differential use of microhabitat between locations. To establish if one microhabitat was used more than others, a Chi-squared test for given probabilities was used for data on each site.

To estimate activity patterns, density curves were used to avoid biases that might appear choosing hour intervals (Ávila-Nájera *et al.,* 2016; Hernández Hernández *et al.,* 2018). This approach is often used to describe activity patterns in mammals, and it allows to analyze data as circular probabilities (Oliveira-Santos *et al.,* 2013; Oberosler *et al.,* 2017). We used the Multimode R package to test for modality (Ameijeiras-Alonso *et al.,* 2019). Besides, a Chi-squared test for given probabilities was used to evaluate if there was a preference for the morning vs the afternoon in each locality. Since activity patterns data did not follow a Von Mises normal distribution (Watson's U^2 test: $p < 0.05$), the Rao's test was applied to assess uniformity, and the Watson-Wheeler test was performed to address differences in activity patterns across locations. Also, overlap coefficients were calculated for each paired-locality comparison.

For environmental temperatures, the Levene's test addressed differences in the temperatures among days for each site (taking every hour temperature average). For each locality, a normality (Shapiro-Wilks) test was performed for the environmental temperatures and lizard's activity (taken as hour probability values of Kernell density curves). Then, Pearson's or Spearman's correlation tests were performed to assess the correlation between environmental temperature and lizard's activity for each locality. As weather station data might differ from the real temperature of the microhabitat (Graae *et al.,* 2012) of the lizard, we did not expect a perfect match with this variable.

The same tests were performed to assess differences between the rainy and the dry seasons in La Chacua and Guanentá. Pearson's Chi squared was applied to test if the use of microhabitat was different between seasons. Fisher's exact test was used when data did not meet the assumptions for the Chi-squared test. Rao's test was used to assess for uniformity in circular data in both seasons, and the Watson-Wheeler test was applied to evaluate differences in activity patterns given by seasonality. This was made to test if seasons were influencing our studied variables and whether the localities could be compared. Most of the statistical tests were performed with R-Studio 3.6 (RStudio Team, 2018), except for the Watson-Wheeler test performed in PAST 4.0 (Hammer, 2001).

RESULTS

Neither the use of microhabitat nor the activity pattern changed due to seasonality for La Chacua and Guanentá (see below). In other words, these ecological traits stayed consistent through the seasons in these two localities. For this reason, we could compare the results for the three sampled localities, even though Las Moyas was not sampled during the rainy season.

Use of microhabitat

A total of 111 individuals of *S. trachycephalus* were observed across the three study sites. The abundance was higher at Guanentá (n = 44) and La Chacua (n = 40), and lower at Las Moyas (n = 27). Among all microhabitats available, *S. trachycephalus* was found mainly in herb (n = 69, 62.16%), followed by bare ground (n = 28, 25.22%), and rocks (n = 10, 9.0%), being shrubs the least frequently used microhabitat (n = 2, 1.8%). There was a statistical difference on the use of microhabitat through localities (Pearson's Chi-squared test: $X^2 = 25.612$, df = 6, $P < 0.001$). A significant association was detected between the herb microhabitat and lizard's abundance along all three locations (Chi-squared test for given probabilities: Guanentá: $X^2 = 34.116$, df = 3, $P < 0.001$; Las Moyas: $X^2 = 66.185$, df = 3, $P < 0.001$; La Chacua: $X^2 = 18.6$, df = 3, $P < 0.001$; Fig. 2).

Variation in microhabitat use among the study sites is shown in Fig. 2. Lizards used exclusively herb, and avoided almost all the other microhabitats in Las Moyas, even though they were available. For the herbaceous stratum in this locality, the lizards were found in *Calamagrostis* sp. (n = 17, 63%) and *Puya* sp. (n = 8, 29.6%), both resources were abundant in this study site (*pers. obs.*). At La Chacua and Guanentá there were *Puya* spp. and other similar bromeliads, but any *S. trachycephalus* was recorded using the leaves of those plants. Besides herb, rock and ground were also often used in La Chacua (Fig. 2). On the other hand, in Guanentá the species showed a broader use of microhabitat being recorded in all types, with a higher abundance of lizards in herb and ground (Fig. 2). No differences were found for this variable between seasons in

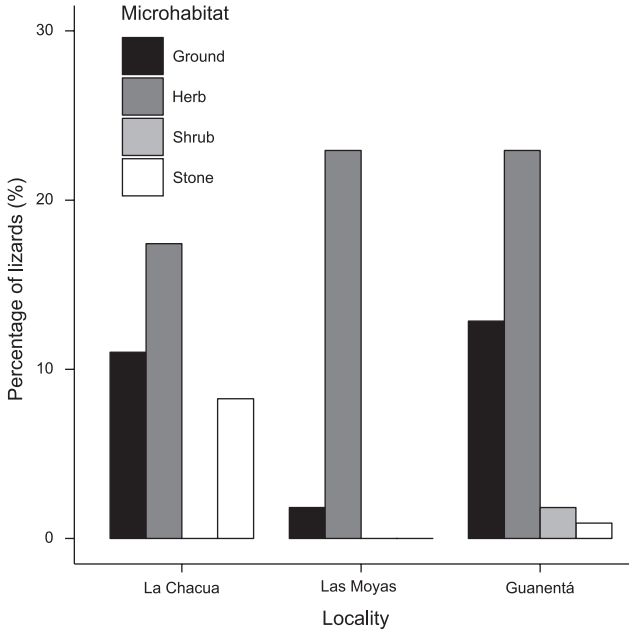

Figure 2. Frequency of individuals of *Stenocercus trachycephalus* on each microhabitat by locality.

Guanentá (Pearson's Chi-squared test: $X^2 = 4.1829$, df = 3, P > 0.05) or in La Chacua (Fisher's exact test: P > 0.05).

Activity pattens

Regarding the activity pattern, *S. trachycephalus* was active throughout the day from 8:00 to 16:00 h with a similar pattern along the gradient. Support was found for unimodal activity pattern in Guanentá (Excess mass = 0.09706, p = 0.342) and Las Moyas (Excess mass = 0.12606, p = 0.21); in contrast, la Chacua had a bimodal activity pattern (Excess mass = 0.18537, p < 2.2e-16). The peaks of activity were at: 11:39 on Guanentá, 10:26 on Moyas, and 11:28 and 14:07 on La Chacua (Fig. 3). There was not a preference for the morning or the afternoon in most of the study sites (Chi-squared test for given probabilities, La Chacua: $X^2 = 1.6$, df = 1, P > 0.05, Guanentá: $X^2 = 1.6$, df = 1, P > 0.05), except for Las Moyas in the morning (Chi-squared test for given probabilities

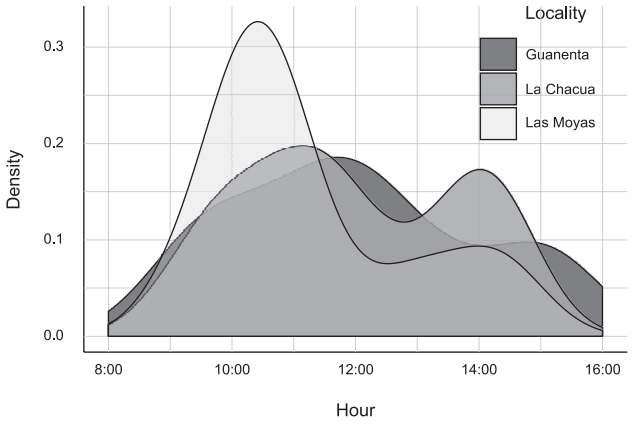

Figure 3. Activity patterns density curve along the three localities. Guanentá in dark gray, Las Moyas in light gray and La Chacua in gray.

$X^2 = 6.2593$, df = 1, P < 0.05; Fig. 3). Different probabilities of encounter for the lizards were obtained along the day across study sites. In particular, the activity started earlier in Las Moyas and ended later in the afternoon in Guanentá (Fig. 3). Rao's test rejected uniformity for each locality ($U_{La\ Chacua} = 271.3$, $p < 0.05$; $U_{Las\ Moyas} = 261.6$, $p < 0.05$; $U_{Guanentá} = 251.4$; $p < 0.05$), and for seasonal data for Chacua ($U_{Dry} = 267.4$, $p < 0.05$; $U_{Rainy} = 263$, $p < 0.05$) and Guanentá ($U_{Dry} = 257.2$, $p < 0.05$; $U_{Rainy} = 262.5$, $p < 0.05$). Activity patterns remained seasonally constant in both La Chacua (W = 1.114, p = 0.57) and Guanenta (W = 0.355, p = 0.84). Additionally, the activity patterns of *S. trachycephalus* did not varied between Guanentá and La Chacua (W = 0.136, p = 0.935). Nor between Guanentá and Las Moyas (but presents a considerable marginal significance: W = 5.775, p = 0.056). Yet it differed from Las Moyas and La Chacua (W = 6.359, p = 0.04). This agrees with overlap coefficients (La Chacua-Las Moyas = 78.6; La Chacua-Guanenta: 91.6; Las Moyas-Guanenta: 79.9).

There was disparity regarding the environmental temperature variation among localities as Levene's test showed differences in the variance of the sampled day temperatures at each site: $\sigma^2_{La\ Chacua} = 1.099$, $\sigma^2_{Las\ Moyas} = 4.736$, and $\sigma^2_{Guanentá} = 4.442$, ($F_{[2,235]} = 14.794$, $P < 0.001$). Nevertheless, variance was significantly different only between La Chacua and Las Moyas ($F_{[1,140]} = 30.326$, $P < 0.001$, Appendix II: Fig. S1, S2) and between La Chacua and Guanenta ($F_{[1,158]} = 24.548$, $P < 0.001$, Appendix II: Fig. S1, S3), but not between Las Moyas and Guanentá ($F_{[1,172]} = 0.2524$, P = 0.616, Appendix II: Fig. S2, S3). This means that temperature fluctuates more through the day at higher altitudes (Appendix II: Fig. S2, S3). Furthermore, lower mean day temperatures were found at higher altitudes, (La Chacua = 18.07 ± 1.04°C, Las Moyas = 11.49 ± 2.17°C, and Guanenta = 10.96 ± 2.10°C) (Appendix I: Table S1-S3). Additionally, we found significant positive correlations between environmental temperatures and probability of detecting lizards at Guanentá ($R^2 = 0.723$, $P < 0.001$) but no correlation was found for Las Moyas (rho = 0.254, P = 0.322) neither for La Chacua ($R^2 = 0,515$, P = 0.07).

DISCUSSION

Environmental factors and their variation on an altitudinal gradient can have deep consequences over lizards' ecological traits (Hertz & Huey, 1981; Smith & Ballinger, 2001; Gilbert & Miles, 2019). There are few studies that assess this potential variability on lizards in the Neotropics. Here we supply new information on how the use of microhabitat and activity patterns are influenced by a 1,280 m altitudinal gradient. Contrary to expected, there were no conspicuous differences in the use of microhabitat and activity patterns along this altitudinal gradient.

Our results support that herb was the most used microhabitat by *Stenocercus trachycephalus* across the altitudinal gradient. Therefore, it must supply thermal or ecological advantages over other microhabitats also available at different elevations (Adolph, 1990; Peñalver-

Alcázar *et al.,* 2016; Ortega *et al.,* 2019). In general, areas with open vegetation like grasses supply sunny patches that increases the availability of thermally heterogeneous microhabitats that can be used for thermoregulation (Scheffers *et al.,* 2017; Guerra-Correa *et al.,* 2020). Besides, studies on the composition of arthropod fauna in the lower vegetation strata of high-Andean ecosystems match the stomach contents found in *S. trachycephalus* (Rodríguez-Barbosa *et al.,* 2017), indicating that herb and bare ground offer suitable resources for foraging. In this sense, this single microhabitat offers several useful resources for this species. Although, lizard's abundance for this microhabitat was consistent, most of the differences observed along the gradient can be explained by the conditions of the locality rather than altitude.

On the other hand, the higher abundance of the lizards in herb at Las Moyas may be linked to records of *S. trachycephalus* using medium-sized *Puya* sp. rosettes. In these bromeliads there are spinose-serrate margins on the leaves, and some authors have suggested that this kind of vegetation may be useful as a refuge for the species (Rodríguez-Barbosa *et al.,* 2017). In addition, the increasing loss of natural habitat due to urbanization near Las Moyas may be favoring the loss of refuges and increased predation rates in this peri-urban area (Anderson & Burgin, 2008). Moreover, domestic animals are also pushing these lizards to use rosettes more often to avoid predation or injuries considering the increasing presence of these animals (Loss & Marra, 2017; Woinarski *et al.,* 2018). In fact, we recorded several *S. trachycephalus* with a regenerated tail, indicating predation events. The threats over Andean mountain environments (Alarcon & Pabón, 2013; Rodríguez Eraso *et al.,* 2013; Correa-Ayram *et al.,* 2020) highlight the need of addressing the anthropic effect and apply conservation actions to maintain refuges and thermoregulation sites for these lizards, enabling populations to persist (Moreno-Arias *et al.,* 2010).

Despite herb stratum's overall association, localities supplied heterogeneous microhabitats for lizards such as several rocks, shrubs, and bare ground. In both Guanentá and Las Moyas, there were small to big rocky outcrops that were rarely used. In contrast, in La Chacua there was an artificial rock wall where most of the lizards using rocks were found. This observation is interesting as the anthropic transformation of the habitat has been linked with a reduction in the abundance of this species (Moreno-Arias *et al.,* 2010; Cortés-Suárez, 2011). As La Chacua had a similar number of observations to Guanentá (the protected area), we propose that these stone structures have helped to mitigate the loss of natural habitat providing shelter and thermoregulation sites, differing in this way from other natural rock microhabitats (Avery, 1978; Van Sluys *et al.,* 2004; Ribeiro *et al.,* 2009). This finding reveals the importance of maintaining heterogenous microhabitats as *S. trachycephalus* takes advantage of conditions given by microhabitat and resource availability.

According to several studies in the natural history of tropidurid lizards, there are species with a restrained microhabitat use (specialist) and species with a varied use of microhabitats (generalist) (Van Sluys *et al.,* 2004; Ribeiro *et al.,* 2009; Daza & Castillo, 2011). For generalist *Tropidurus,* the use of microhabitat shifts towards the most abundant microhabitat available, although a wide variety of microhabitats is present along its environment (Van Sluys *et al.,* 2004; Ribeiro *et al.,* 2009). Daza & Castillo (2011) observed *Stenocercus santander,* a lizard distributed close to our focal species, using open ecosystems where rocks and soil microhabitat were preferred. By contrast *S. trachycephalus* used mostly herbaceous vegetation and rarely other microhabitats. As we recorded this lizard using several microhabitats along its distribution, we consider that it is a microhabitat-generalist. Given the high diversity on the ecology of tropidurids, further studies on other species that occupy broad ecological gradients will allow to identify patterns in the responses in this family and genus.

Regarding the overall activity pattern of *Stenocercus trachycephalus,* the lizards were active throughout most of the daylight period, with higher activity in the morning. This pattern was roughly consistent through the altitudinal gradient; hence, we rejected our hypothesis. A similar activity during the day is common among other tropidurids (Van Sluys *et al.,* 2004) that present a single peak (Vitt *et al.,* 1997; Ribeiro *et al.,* 2009). In *Tropidurus* such as *T. torquatus, T. itambere* and *T. oreadicus,* it have been reported a similar activity pattern, but only during the rainy season (Faria & Araujo, 2004; Ribeiro *et al.,* 2009; Velasquez & Gonzalez, 2010). Instead, *S. santander* is also active during the day but it has a more consistent activity from 7:30-15:30 (Daza & Castillo, 2011). There are not previous studies showing the differences in activity patterns along an altitudinal gradient in any tropidurid species.

The higher activity in the morning was especially pronounced in Las Moyas, where activity started earlier. In general, lizards are cool after night in the early morning and as they emerge from their refuges, they use the sun to warm up (Paulissen, 2001; Ibargüengoytía, 2005; Vidal *et al.,* 2010). This is especially important in high-Andean ecosystems as the environment presents temperatures close to 0°C during the night across all the year (Sarmiento, 1986; Navas, 2002). The higher activity early in the morning at Las Moyas must be a consequence of the strong effect of a continuous cloud cover observed only in this locality (*pers. obs.*), that decreases the incidence of solar radiation leading to less opportunities for thermoregulation (Howland *et al.,* 1990; Vitt, 1991; Perez-Mellado & de la Riva, 1993; Vitt & Zani, 1996; Vitt *et al.,* 1997; Rangel-Ch., 2000). Moreover, the cold and fluctuating temperatures presented at this locality constrain the activity during the day (Fig. 3.; Appendix I: Table S2; Appendix II: Fig. S2) (Hertz, 1981; Hertz & Huey, 1981; Méndez-Galeano & Calderon-Espinosa, 2017). Therefore, to avoid losing opportunities to reproduce or forage, lizards need to optimize their time investing their activity in the morning, especially at this locality.

On the other hand, there was a unimodal activity pattern at higher elevations (Las Moyas and Guanentá) and a bimodal one in the lower elevation (La Chacua). A bimodal activity pattern has been associated with higher

midday temperatures in the lower altitudes of some species (Appendix II: Fig. S1) (Huey *et al.,* 1977; Marquet *et al.,* 1989; Zamora-Camacho *et al.,* 2013). This pattern is also expected in high-mountain species such as *S. guentheri* where lizards may find temperatures over the maximum critical temperatures across their habitat (Guerra-Correa *et al.,* 2020). Thus, it is not a surprise that a bimodal activity pattern was found at La Chacua, which had a higher mean and midday temperatures (Appendix I: Table S1).

Despite the mentioned variation of the activity peaks along the altitudinal gradient, we could not detect differences in activity patterns between Chacua and Guanentá. This is explained by the fact that activity patterns resembled in all localities, as the overlap coefficients proves. Therefore, it can be said that activity patterns of *S. trachycephalus* are similar along the altitudinal gradient with few changes caused by the specific characteristics of each site. This supports that lizards have their capabilities to counter thermal constraints along the gradient (Bauwens *et al.,* 1996; Gilbert & Miles, 2019). In contrast to our results, other lizards like *Psammodromus algirus* do present pronounce differences on its activity pattern along an altitudinal gradient (Zamora-Camacho *et al.,* 2013). However, we observed differences in the activity pattern between Las Moyas and La Chacua and a marginal difference between Las Moyas and Guanentá, explained by the particular weather conditions observed for Las Moyas.

We did not find a correlation between temperature and probability of encounter of the lizards at Las Moyas and La Chacua. Thermoregulatory behaviors might explain this as microhabitat selection (herb) that allow individuals to compensate the particular thermal regime of Las Moyas (Appendix II: Fig. S2 (Bauwens *et al.,* 1996; Fierro-Estrada *et al.,* 2019), which also explains the absence of these lizards on rocks and ground at this locality, and the use of *Puya* sp. rosette plants in addition to its use as a refuge (Guerra-Correa *et al.,* 2020). Several other ecological factors might explain the lack of association of activity patterns with temperature in this locality. For example, exposition to predator cues (Downes, 2001), reproductive season (Ribeiro *et al.,* 2009), sex proportion in a population (Vidal *et al.,* 2010) or the activity schedule of their prey (Huey, 1974; Díaz & Cabezas-Díaz, 2004). Finally, as we explained before we did not except perfect match between weather station temperatures and microsite temperatures, so this result can be linked to this fact (Suggitt *et al.,* 2017).

CONCLUSION

We studied two natural history traits of *S. trachycephalus* across a 1,280 m elevation gradient, as it shapes multiple ecological variables of this lizard's habitats. We expected that microhabitat use and activity patterns changed among the studied sites due to differences in altitude. However, our study proved that the use of microhabitat and activity pattern of *S. trachycephalus* was rather similar along the altitudinal gradient, so we rejected our hypothesis. We conclude that *S. trachycephalus* is a microhabitat generalist lizard influenced by resource availability, principally using herb stratum in all the study sites. The use of microhabitat and activity patterns may shift depending on specific conditions of each site, for example, availability of *Puya rosettes,* human-made rock walls, anthropic disturbance or a combined effect of low temperatures and cloud cover. On the other hand, this lizard's activity patterns ranged from 8:00 to 16:00 with higher activity in the morning hours. Some differences along the gradient were found such as changes from bimodal to unimodal pattern as altitude increased. This plasticity helps them to face thermal and ecological constraints that come with an environmental gradient.

We highlight the importance of studying high-mountain lizards, as they are interesting models and ecological information about them is scarce, especially in the Neotropics. Further studies should focus on understanding the thermal biology of this lizard. Besides, Las Moyas is an interesting locality for further studies as the microhabitat use and activity pattern were more constrained. It was also the locality with the lowest abundance of lizards. Finally, the anthropic impact and its relationship to populations dynamics should be considered in future works.

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AUTHORS' CONTRIBUTIONS

All the authors actively participated in the design, fieldwork, analysis and writing of the manuscript for this study.

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APPENDIX I. SUPPLEMENTARY TABLES

Table S1. Environmental temperature (°C) throughout the day for the sampled days in La Chacua.

Hour/Date	31/05/14	08/06/14	14/06/14	21/06/14
0:00	15.59	14.89	14.85	14.74
0:30	15.35	15.24	14.80	14.47
1:00	15.43	15.53	14.71	14.72
1:30	15.50	14.66	14.60	14.54
2:00	15.05	14.56	14.37	14.52
2:30	14.39	14.54	14.43	14.56
3:00	14.58	14.47	14.63	14.54
3:30	14.61	14.47	14.81	14.71
4:00	14.72	14.32	14.85	14.71
4:30	14.83	14.17	14.74	14.85
5:00	14.78	14.17	14.70	14.71
5:30	14.70	14.35	14.87	14.72
6:00	14.75	14.99	14.96	14.81
6:30	15.05	16.06	15.21	14.42
7:00	15.42	16.65	15.40	15.08
7:30	15.85	16.43	15.65	15.62
8:00	16.53	17.35	15.69	15.69
8:30	16.95	17.42	16.05	15.98
9:00	17.25	17.71	16.72	17.08
9:30	17.74	18.05	16.72	17.99
10:00	17.66	18.64	17.18	17.85
10:30	17.81	18.24	17.97	18.64
11:00	18.51	18.08	19.09	19.17
11:30	18.68	19.18	19.41	19.14
12:00	18.24	18.76	19.09	19.00
12:30	17.61	18.42	19.09	19.02
13:00	19.23	18.44	18.43	19.12
13:30	18.67	18.60	19.80	18.45
14:00	18.48	19.12	18.99	19.05
14:30	18.13	18.54	17.57	19.12
15:00	19.17	18.42	15.82	18.39
15:30	19.33	17.15	15.66	17.82
16:00	18.99	17.34	15.70	17.09
16:30	17.68	17.07	15.60	17.00
17:00	17.73	16.72	15.37	16.70
17:30	17.20	16.45	15.34	16.40
18:00	16.80	16.05	14.94	16.14
18:30	16.69	15.95	14.90	15.98
19:00	16.51	15.86	15.02	15.92
19:30	16.14	15.68	15.00	15.87
20:00	16.19	15.56	14.92	15.86
20:30	16.27	15.48	14.90	15.94
21:00	16.20	15.53	15.05	16.01
21:30	16.12	15.55	14.97	15.83
22:00	16.00	15.41	14.79	15.57
22:30	15.85	15.33	14.88	15.38
23:00	15.81	15.35	14.66	15.27
23:30	15.65	15.18	14.52	15.34

Table S2. Environmental temperature (°C) throughout the day for the sampled days in Las Moyas.

Hour/Date	07/08/18	08/08/18	11/08/19	19/08/19	20/08/18
0:00	7.32	7.50			8.31
0:30	7.15	7.35			8.47
1:00	7.41	7.03			8.53
1:30	7.32	7.04			8.52
2:00	7.63	7.18			8.40
2:30	7.81	7.18			8.37
3:00	7.76	7.10			8.22
3:30	8.05	6.99			8.04
4:00	7.95	6.77			7.97
4:30	7.58	7.14		8.43	8.02
5:00	7.64	7.48		8.35	8.03
5:30	7.76	7.52		8.28	7.85
6:00	7.96	7.60		8.29	8.04
6:30	8.12	7.81		8.27	8.31
7:00	8.73	8.18		8.23	8.66
7:30	9.48	8.68		7.94	10.12
8:00	10.24	8.97		7.98	10.47
8:30	10.52	9.13		7.94	10.52
9:00	11.25	9.39	11.48	8.02	10.24
9:30	13.90	10.28	13.22	7.96	10.37
10:00	15.01	11.19	12.43	8.06	10.87
10:30	15.09	11.20	13.45	8.03	11.46
11:00	12.75	12.23	14.82	8.23	12.43
11:30	11.43	12.45	15.10	8.35	12.62
12:00	10.33	11.13	14.76	8.41	12.87
12:30	9.96	11.14	14.73	9.04	15.41
13:00	10.08	10.45	15.03	9.45	14.38
13:30	9.95	11.12	16.61	10.08	13.40
14:00	10.42	12.97	16.05	10.24	12.26
14:30	10.26	12.66	14.31	10.69	12.07
15:00	10.18	12.06	13.61	11.99	13.04
15:30	8.80	11.31	12.79	11.24	12.18
16:00	8.33	11.43	14.57	11.20	12.84
16:30	8.36	10.47	11.56	10.40	12.34
17:00	9.02	9.71	10.01	10.24	13.73
17:30	9.89	9.08	9.03	10.97	11.79
18:00	9.99	8.80	8.89	9.87	9.49
18:30	8.88	8.60	8.87	8.37	8.92
19:00	9.62	8.67	8.33	8.39	8.94
19:30	9.04	8.47	8.49	8.86	9.19
20:00	8.75	8.34	8.52	9.00	8.95
20:30	8.60	7.69	8.45	9.01	8.74
21:00	8.05	7.57	8.46	9.05	8.59
21:30	8.08	7.71	8.48	8.56	8.51
22:00	7.87	7.66	8.52	8.46	8.37
22:30	7.61	7.59	8.39	8.62	8.25
23:00	7.55	7.64	8.39	8.50	8.42
23:30	7.48	7.55	8.33	8.91	8.37

Table S3. Environmental temperature (°C) throughout the day for the sampled days in Guanentá.

Hour/Date	20/09/18	21/09/18	22/09/18	23/09/18	15/02/19	16/02/19	17/02/19	07/04/19
0:00	5	4.3	5.5	4.3	5.6	5.8	4.5	5.8
0:30	5.1	4.4	5.7	4.3				
1:00	5	4.6	5.7	5.1	6.2	4.6	4.5	5.3
1:30	5.2	4.5	5.6	5.3				
2:00	5.2	4.8	5.6	5.8	5.2	5.4	4.3	5.5
2:30	5.2	5.2	5.7	4.8				
3:00	5.2	4.4	5.5	5.3	4.7	3.1	5.8	4.8
3:30	5.2	4.4	5.2	5				
4:00	4.9	5.2	5.2	5.2	5.8	4.4	6.2	2.8
4:30	4.5	4.6	4.9	5.1				
5:00	4.5	4.1	4.6	4.9	6.4	5.1	4.1	2.9
5:30	4.2	4	4.3	4.8				
6:00	3.8	4.3	4.6	4.7	5.2	2.8	5.8	3
6:30	3.8	4.6	5	4.7				
7:00	4.2	4.9	5.5	4.8	6.3	3.1	6.9	4.4
7:30	6.1	6.7	6.2	5.3				
8:00	7.5	8.1	7.3	5.8	11.2	7.8	9.2	6.1
8:30	8.8	9.3	8.4	6.4				
9:00	9.3	9.9	9.1	6.6	14.2	11.5	12	8.9
9:30	10.5	11.2	9.2	7.3				
10:00	11.3	11.2	10.1	8.1	14.6	9.4	13.5	10.6
10:30	11.4	11.9	11.2	9.4				
11:00	11.9	12.6	10.4	10.3	12.9	9.7	15.2	11.1
11:30	12.3	13.7	10.4	9.3				
12:00	13.1	14.6	10.6	9.9	14.6	11	12.1	13.3
12:30	13.1	13.1	13	9.3				
13:00	12.6	15.1	13.8	9	14.7	11.9	12.1	11.9
13:30	12.9	13.5	12.5	8.3				
14:00	12.6	13	11.4	9.6	11.3	13.2	11	10.6
14:30	13.2	12.1	11.1	10.1				
15:00	11.4	12.4	10.6	10.4	11.6	10.9	9.5	10.4
15:30	11.8	11	10.4	8.8				
16:00	11.4	10.1	10.6	8.8	10.8	8.7	7.5	8.4
16:30	11.2	9.5	10.6	9.3				
17:00	9.2	9.6	9.9	8.2	9.7	7.2	7.6	8.8
17:30	8.6	8.8	8.9	7.3				
18:00	6.1	7.6	6.7	6.4	9.1	6.4	6.8	7.4
18:30	5.4	7	5.3	6				
19:00	5.2	6.1	4.9	6.3	6.2	6.3	6.6	6.8
19:30	4.9	5.8	5.2	6.4				
20:00	4.2	5.9	6	6.3	4.7	6.5	6.4	7.1
20:30	4.7	5.7	6	6.1				
21:00	5.2	5.9	5.9	5.8	4.3	6.7	6.5	6.2
21:30	5.4	6	5.7	5.2				
22:00	5.3	5.9	5.9	4.8	4.7	6.6	6.4	6
22:30	4.9	6.1	5	5.2				
23:00	4.1	5.9	5.4	4.8	4.2	5.9	6.1	6.3
23:30	3.9	5.9	5	4.6				

APPENDIX II. SUPLEMENTARY FIGURES

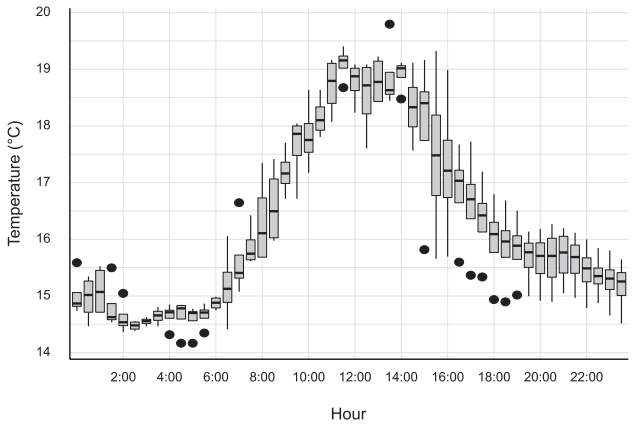

Figure S1. Environmental temperature fluctuation throughout the day in La Chacua.

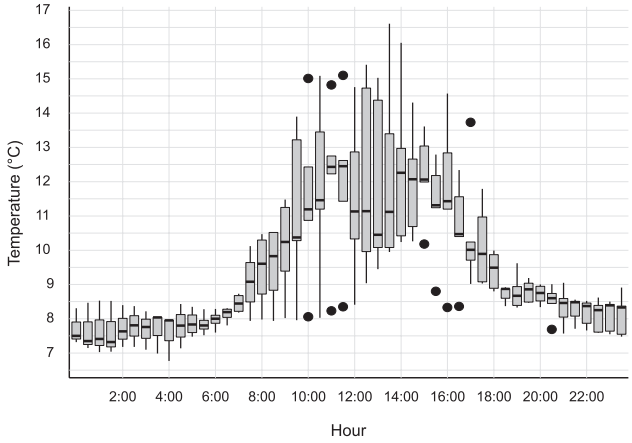

Figure S2. Environmental temperature fluctuation throughout the day at Las Moyas.

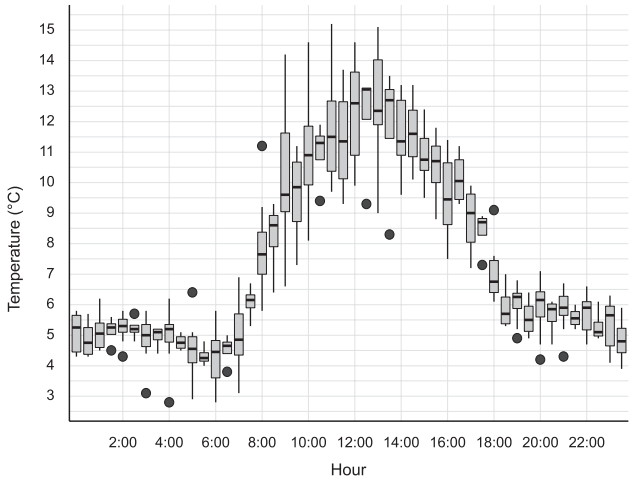

Figure S3. Environmental temperature fluctuation throughout the day in Guanentá.

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