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Limited ecophysiological variation in the Canary Island lizard *Gallotia galloti* (Oudart, 1839) across an elevational range of over 3500 m (Squamata: Lacertidae)

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Abstract. The lacertid lizard *Gallotia galloti* inhabits drastically different environments on the island of Tenerife, from sea level to > 3500 m, encompassing mesic as well as extremely arid sites. To obtain a first exploratory overview of the thermophysiology of lizards in this range of environments, we experimentally inferred preferred temperature (T_{pref}) and instant evaporative water loss (IWL) in 63 individuals from five bioclimatically distinct sites. We found statistically significant but weak differences between individual median T_{pref} values across sites, without an obvious relationship to bioclimate. Considering only adult male lizards, the highest T_{pref} values were found at one mesic and one very arid site. IWL differences were also significantly different across sites, and this variable was positively correlated with rainfall if analysed at the level of individual lizards, a hypothesis that requires testing against more extensive data sets. It appears that *G. galloti* occupies an extensive range of bioclimates without heavily adjusting its thermal physiology to local conditions.

Keywords. Canary Islands, Tenerife, endemic lizard, thermoregulation, behaviour, temperature preference, evaporative water loss.

Introduction

Elevation gradients on mountains are excellent models to improve our understanding of fundamental ecological and evolutionary processes. On steep mountain slopes, drastic changes in climatic conditions lead to differences in turnover of biological communities. These climatic gradients can trigger reproductive isolation (Keller and Seehausen, 2012) through selection against maladapted genotypes (Nosil, 2012), promoting community specialization to certain elevational ranges. Research on elevation-restricted species can provide information about the effects of climate warming (i.e., persistence through adaptation or phenotypic plasticity; Porcelli et al., 2015; Stillman and Armstrong, 2015), upslope movement (e.g., Kéry et al., 2009; Freeman and Freeman, 2014), or extinction. Additionally, studying organisms distributed across a large elevational gradient can enable us to understand the variation of morphological, behavioural, and ecophysiological traits that allow them to cope with drastically different climatic conditions.

Diurnal lizards as a group are an excellent model for studying adaptation to temperature and humidity regimes due to their dynamic thermoregulatory behaviour. This is further facilitated by the ease of experimentally assessing temperature optima and temperature-specific physiological performance in these animals and incorporating these data into mechanistic niche models (e.g., Sinervo et al., 2010; García-Muñoz and Carretero, 2013; Clusella-Trullas and Chown, 2014). In a prominent group of lizards, Caribbean anoles, cold tolerance was found to evolve faster than heat tolerance, probably because cold can be more easily alleviated by thermoregulatory behaviour (Muñoz et al., 2014). Recent evidence suggests that many lizard species are threatened with extinction, with global increases in temperature playing an important role (Sinervo et al., 2010). In Europe, the most prominent lizard group is the family Lacertidae, which comprises about 325 species distributed across a wide range of habitats, from hot desert regions to high mountains and subarctic zones. Lacertids have been the subject of numerous ecophysiological studies (e.g., Díaz, 1994; García-Muñoz and Carretero, 2013; Belasen et al., 2016; Carretero et al., 2016; Carneiro et al., 2017; S'khifa et al., 2020). Recently, it was found that an increasing disparity accompanied their evolution among occupied bioclimatic niches, and their ecophysiology is correlated

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with bioclimatic parameters indicating physiological adaptations to climate (Garcia-Porta et al., 2019).

Two extant lacertid species, *Gallotia galloti* (Oudart, 1839) and *G. intermedia* Hernández et al., 2000 are found on Tenerife, one of the Canary Islands located in the Atlantic Ocean off Africa's northwest coast. *Gallotia galloti* is distributed across the entire island in two morphologically distinct subspecies, *G. g. galloti* and *G. g. eisentrauti* Bischoff, 1982 (Fig. 1B). Tenerife is dominated by the Pico del Teide stratovolcano, which rises to 3715 m above sea level and is the highest point in Spanish territory. Recent studies suggest that Tenerife's current relief was formed by two smaller shield volcanos on the flanks of a large central shield (Carracedo et al., 2007). Major debris avalanches on both slopes of the island have further structured its present-day geography (Cantagrel et al., 1999). This topography, its volcanic history, and the predominantly northwesterly trade winds

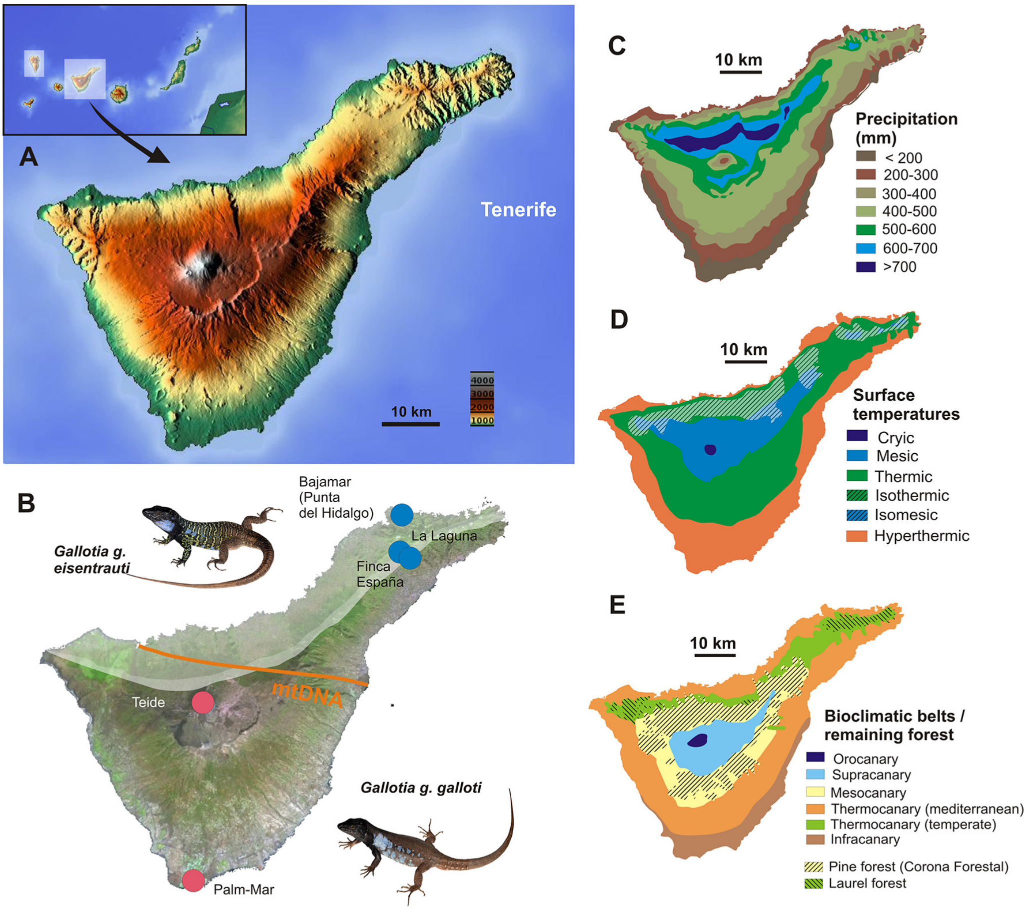

Figure 1. Sampling sites of *Gallotia galloti*, geography and bioclimatology of Tenerife, Canary Islands, Spain. (A) Elevational profile of Tenerife with an inset showing the location of Tenerife among the Canary Islands and in relation to the African mainland (https://maps-for-free.com). (B) Sampling locations used in this study, relative to the distribution of the main *G. galloti* morphs on Tenerife (redrawn from Brown et al., 2016), corresponding to the subspecies *G. g. eisentrauti* (blue circles), and the nominal subspecies (red circles). Note that the boundary of the distribution of mtDNA haplotypes (orange line) does not correspond to the morphotype boundary. (C) Annual precipitation on Tenerife (redrawn from http://www.seos-project.eu). (D) Spatial distribution of soil temperature regimes on Tenerife (after Rodríguez et al., 2010; see Soil Survey Staff, 2014, for a description of regimes). Note that the coastal strip was found mostly hyperthermic but isohyperthermic in some study years by Rodríguez et al. (2010). (E) Main bioclimatic zones for Tenerife proposed by Rivas-Martínez (1987). Shaded areas represent the approximate current extent of pine and laurel forest associated with the Mesocanary and Thermocanary zones, respectively. For a more detailed description of the bioclimatic areas and potential vegetation, see Del Arco et al. (2006).

provide an extensive range of habitats, with cool moist air currents producing cloud formations on the north-facing slopes. As a consequence, the island has five main natural biomes: (1) xerophytic endemic coastal scrub; (2) thermosclerophyllous woodlands of diverse formations, largely of Mediterranean origin; (3) laurel forest in high-humidity zones linked to the trade winds; (4) open pine forest, basically composed of *Pinus canariensis*; and (5) high-mountain scrub and endemic legume shrubland. A wide variety of soil types also accompanies this distinct zonation of vegetation types along elevational bands around Pico del Teide. Rodríguez et al. (2010) reported that seven of the nine temperature regimes used in soil taxonomy (hyperthermic, thermic, mesic, isohyperthermic [only in certain years], isothermic, isomesic, and cryic; Fig. 1D) are found on the island, emphasizing its extraordinary heterogeneity. Furthermore, precipitation regimes differ widely, from > 700 mm per year in areas dominated by laurel forest, to < 200 mm per year in dry coastal regions and on Pico del Teide.

Thus, it can be argued that *G. galloti* populations on Tenerife are exceptionally well suited to study environmental adaptation. It has been the subject of numerous pioneering studies (e.g., Thorpe and Baez, 1987; Thorpe and Brown, 1989a; Thorpe, 1991; Thorpe et al., 1996; Thorpe and Richard 2001; Brown et al., 2016), encompassing aspects of morphology, colouration, sexual selection, parasites, chemical signals, environmental stress tolerance, locomotion, activity, thermoregulation, and digestive ecology (e.g., Díaz, 1994; Vanhooydonck et al., 2001; Valido and Nogales, 2003; Font and Molina-Borja, 2004; Huyghe et al., 2005; Bohórquez-Alonso et al., 2011; Megía Palma et al., 2016, 2020; García-Roa et al., 2017). Furthermore, genetic variation within the species is complex, and while one of its components appears to have arisen during historical allopatry (possibly associated with volcanism), a second is related to xeric/mesic habitat differences and shows signatures to be expected under divergent selection between these areas (Brown et al., 2016).

Here, we present the results of an exploratory ecophysiological study carried out on five *G. galloti* populations. We experimentally assessed preferred temperature (T_{pref}) and instantaneous evaporative water loss (IWL) of lizards from very different environments, including an arid site near sea level, more mesic sites in the north of the island, and a population living at an elevation of 3500 m near the summit of Pico del Teide. This study was primarily carried out to obtain data for this species within a large meta-analysis of lacertid lizards' thermal and hydric physiology (Garcia-Porta et al., 2019). Consequently, the sampling design was not optimized for hypothesis testing, which would have required a standardized transect with a higher number of sampling locations. Instead, we rely on data from a relatively small number of drastically different environments, scattered across Tenerife and encompassing the two distinct subspecies of *G. galloti.* We here provide a descriptive account of the physiological differences among these populations in the hope to stimulate discussion and provide a baseline for future studies aimed at testing specific hypotheses.

Materials and Methods

Experiments were carried out on *Gallotia galloti* specimens collected at five sites with strong differences in elevation, temperature, water regime, and vegetation: (1) Palm-Mar, a residential-touristic estate located between the protected nature areas of Malpaís de la Rasca and Guaza Mountain in Arona Municipality (28.0226°N, 16.688°W, elevation 54 m); (2) near the summit of Pico de Teide (28.271°N, 16.640°W, 3560 m); (3) Bajamar, a coastal area near Punta del Hidalgo (28.560°N, 16.317°W, 30 m); (4) the Anchieta Campus of La Laguna University (28.474°N, 16.319°W, 838 m); and (5) an agricultural area near Finca España (28.474°N, 16.300°W, 548 m). Active lizards were captured either by pitfall trapping or noosing (e.g., Angeli, 2017), using a noose created with a thin filament and fixed to the tip of a fishing pole, from 12–17 June 2016, during the main activity period of the species. Experiments were carried out from 13–18 June 2016. Data were obtained from 63 individuals (29 males, 32 females), of which one and six individuals, respectively, were possibly subadult, plus two unsexed subadults. The females did not include individuals in an obvious advanced stage of gravidity (as recognizable externally by increased body volume), but they were not checked systematically for gravidity and thus may have included some in early gravidity. Data from most of these individuals were used for analysis, with extreme and obviously artefactual outliers or incomplete measurements were removed from the analysis, as explained below.

As a proxy estimate of the preferred temperatures (T_{pref}) of the lizards, we measured their body temperature in a thermal gradient consisting of five individual tracks, each of which was ca. 120 cm in length and 20 cm in width, corresponding to a surface of ca. 2400 cm², as specified by Garcia-Porta et al. (2019). An incandescent 100-W light bulb (full spectrum) was suspended 30 cm above one end of a track to create a photothermal gradient of approximately 20–55°C at ground level. This gradient ranged from ca. 15°C in its coldest part to very hot temperatures (> 50°C) near the heat source. We measured body temperature every minute using ultra-thin T-type thermocouples (Omega 5SCTT-T-40-72; diameter 0.076 mm, Norwalk, Connecticut, USA) affixed with medical tape to the lizards' venter and connected to an 8-Channel USB Thermocouple Data Acquisition Module (Omega TC-08; resolution < 0.1°C). Lizards were allowed unrestricted movement within their individual gradient. To mirror their regular activity period, experiments started at 08:30 h in the morning, and again at 14:30 h in the afternoon. Treatments lasted up to a maximum of 2 h. Before the experiments, lizards were kept for 24–72 h at an air temperature of 15–20°C (natural temperature range in the shade) and were provided water and food ad libitum. Lizards were released at the initial capture site after completion of the experiments. When animals showed signs of fatigue (non-natural behaviour), experiments were stopped, and they were released after recovery. Individuals who remained inactive at the gradient's cold end for more than 50 min were not included in the final analysis under the assumption that they were not actively thermoregulating. Temporarily entangled or detached thermocouples were repaired and reattached, the respective data points were discarded, and the experiment was continued. The experiment's initial 30 min were discarded as acclimation time, resulting in a maximum of 100 individual measurements (≈ 1:30 h). From the total of 63 lizards tested in the T_{pref} experiments, a subset of 41 (22 females and 19 males) was included in the final analysis. Data of lizards for which < 60 valid observations were taken (equivalent to an experimental duration of 60 min) were discarded, together with those animals that showed erratic thermoregulation curves. The latter were usually caused by thermocouple malfunction or because the animals tried to escape from their thermal gradient tracks. For some lizards, experiments were interrupted before the time limit. Due to this, the number of observations per individual ranged from 71–100.

Instant evaporative water loss (IWL) was measured in lizards housed individually in plastic boxes with holes in their top, bottom, and sides, to ensure airflow (García-Muñoz and Carretero, 2013). Each box was placed within a second box containing silica gel on the bottom. All individual boxes were placed in a large container with sufficient silica gel to maintain humidity values of 10–20%. This container was then placed in the dark at a constant temperature of 20–22°C. Lizards were weighed once every hour for 12 h, and instantaneous evaporative water loss (IWL) was calculated as the amount of hourly weight loss, averaged over all measurements per individual. Water loss is dependent on body surface, which decreases disproportionally with mass. Therefore, we calculated lizard body surface as ln[surface area] = 2.36 + (0.69 * ln[mass]) according to Grigg et al. (1979), then regressed IWL against ln[surface area]. The residuals of this regression were used as surface-corrected IWL. Following the rationale of Garcia-Porta et al. (2019), we quality-checked the IWL data set and (1) excluded weights preceding and following verified instances of defecation or urination; (2) interpreted negative values of IWL (i.e., a weight increase over time), as a measurement error and deleted the respective value; (3) excluded IWL outlier values > 3 SD above the mean, assuming these corresponded to unnoticed defecation or urination events; and (4) excluded values corresponding to the 11th and 12th hours because these were not available for all individuals. A total of 55 lizards were used for the IWL experiment (25 males, 29 females), including one individual not classifiable as either an adult female or male whose data were discarded from the final analysis. These were largely the same individuals as used for T_{pref} assessments, and as before females were not checked for gravidity except for a tentative external evaluation. The number of IWL readings per individual varied, as only 11 individuals completed the experiment without any invalid IWL reads (i.e., with eight usable IWL measurements). For most individuals, some measurements had to be excluded and the observations ranged from 3–7 per lizard, mostly being 6 (in 23 lizards).

We summarized values per individual for both T_{pref} and IWL, using medians to circumvent non-normality of values. We also summarized per-population data for all individuals per population, again as medians. Despite this, T_{pref} medians of individuals were not normally distributed (Shapiro-Wilk tests, $p < 0.05$), even after log-transformation. We instead used a Kruskal-Wallis rank sum test and a pairwise Wilcoxon rank-sum test to assess the influences of each population and specimen sex on the summarized T_{pref} values. In the case of IWL, once corrections for body-surface area were applied, individual medians were normally distributed (Shapiro-Wilk tests, $p > 0.05$). We then used a two-way ANOVA and a Tukey's HSD (honestly significant difference) test to analyse the effects of population and sex on lizard IWL. All analyses were performed using the statistical software R version 4.0.2. (R Core Team, 2020) for the entire data set, and also separately for males and females. The secondary analysis was to account for intersexual differences and especially for potential biases in the female data caused by the possible inclusion of gravid individuals, which are known to differ in their temperature and humidity preferences (Carretero et al., 2005).

To identify possible correlations between ecophysiology and bioclimatic variables, we first extracted the original 19 bioclimatic variables from the Worldclim database layers Version 2.1 (www.worldclim.org; Fick and Hijmans, 2017) for each of the study sites using the *raster* R package Version 3.3-13 (Hijmans, 2020). Subsequently, we assessed the correlation strength of various predictors with the response of interest by response screening in JMP 13.0 (SAS Institute), correcting for the effect of multiple testing. All 19 bioclimatic variables were analysed simultaneously.

Results

The Kruskal-Wallis test results showed differences in T_{pref} medians among lizard populations ($\chi^2 = 10.397$; $df = 4$; $p = 0.034$; Fig. 2A). Pairwise comparisons revealed statistically significant differences between Pico del Teide and La Laguna *G. galloti* populations ($p = 0.008$), between La Laguna and Palm-Mar ($p = 0.031$), and La Laguna and Bajamar ($p = 0.005$; Fig. 2A). Additional Kruskal-Wallis tests, using the data subsets of males and females, respectively, revealed significant differences among populations for males ($\chi^2 = 10.99$; $df = 4$; $p = 0.026$; Fig. 2B) but not for females ($\chi^2 = 2.35$; $df = 4$; $p = 0.67$; Fig. 2C). Subsequent Wilcoxon rank-sum tests showed that males from the Palm-Mar and Bajamar, Pico del Teide and La Laguna, and Teide and Palm-Mar populations had statistically different median T_{pref} values ($p = 0.016$, 0.036, and 0.016, respectively), with differences between males from La Laguna and Bajamar close to significance ($p = 0.05$; Fig. 2B).

For IWL, median values differed between lizard populations (two-way ANOVA, $F(4,2) = 6.87$; $p = 0.0002$). Tukey pairwise comparisons showed statistically significant differences between the specimens from Palm-Mar and Bajamar ($p = 0.015$; Fig. 3A) and La Laguna and Palm-Mar ($p = 0.0001$; Fig. 3A). This same two-way ANOVA showed no differences between males and females among populations ($F(4,2) = 0.72$; $p = 0.48$) or within populations ($F(4,2) = 1.35$; $p = 0.26$; Fig. 3B, C). However, further pairwise-comparisons revealed statistically significant IWL differences between the male lizards from La Laguna and Palm-Mar ($p = 0.005$; Fig. 3B). Our data set includes values from only five collection sites. Therefore, a correlation analysis of ecophysiological versus environmental variables is not reliably possible at the level of populations (with only five data points). Response screening at the level of individuals – the median value for each individual corresponding to one data point – revealed no significant correlation of T_{pref} with any bioclimatic variable. However, IWL was correlated with all of the precipitation-related variables (bio12-bio19; FDR-corrected $p < 0.01$ for all variables), with the highest effect size (0.523) for bio17 (precipitation in the driest quarter; $p = 0.0001$). IWL values per site arranged by bio12 (annual mean precipitation) correlated almost equally strongly ($p = 0.0004$; effect size = 0.477; Fig. 4) with a positive slope.

Discussion

The *Gallotia* system in Tenerife is unique in a global context. Few systems exist where the same lizard, and the same genetic lineage within a species (in this case the nominal subspecies *G. g. galloti*), occupies a comparably wide elevational range (sea level to > 3500 m) in such a limited geographical setting. Some Andean *Liolaemus* lizards (family Liolaemidae) reach elevations up to 5000 m and maximum elevational ranges of around 3000 m (e.g., *L. bibroni* and *L. nitidus*; Pincheira-Donoso et al., 2008) and on Hispaniola, *Anolis cybotes* occurs from sea level to at least 2700 m (Boronow et al., 2018). In the Himalayas, some agamid species occur up to elevations of 5300 m, but with a range of < 3000 m (Yang et al., 2014). Indeed, *G. galloti* might well be the lizard species with the widest elevational range worldwide. Another lizard species with a wide elevational range is *Psammodromus algirus*, a representative of the sister genus of *Gallotia* that occurs from sea level to 2600 m in the Sierra Nevada region of southern Spain (Martín et al., 2017).

Our data set provides an exploratory assessment of the thermal and humidity preferences of *G. galloti* populations from different environments. Our results suggest that significant differences between populations may occur, especially for lizards from the arid lowland site Palm-Mar, which differ distinctly in their lower IWL from those collected at other sites. This and several other patterns (see below) were particularly obvious in males, whose data we consider to be more reliably comparable among populations than female data, which show less distinct inter-populational differences in our physiological experiments and which were not checked in detail for gravidity. Given that gravid females of squamates can differ in their thermal and hydric preferences (Castilla et al., 1999; Carretero et al., 2005; Lourdais et al., 2017), we cannot exclude a bias in female results related to this factor, especially in the case of inter-populational differences in female reproductive period.

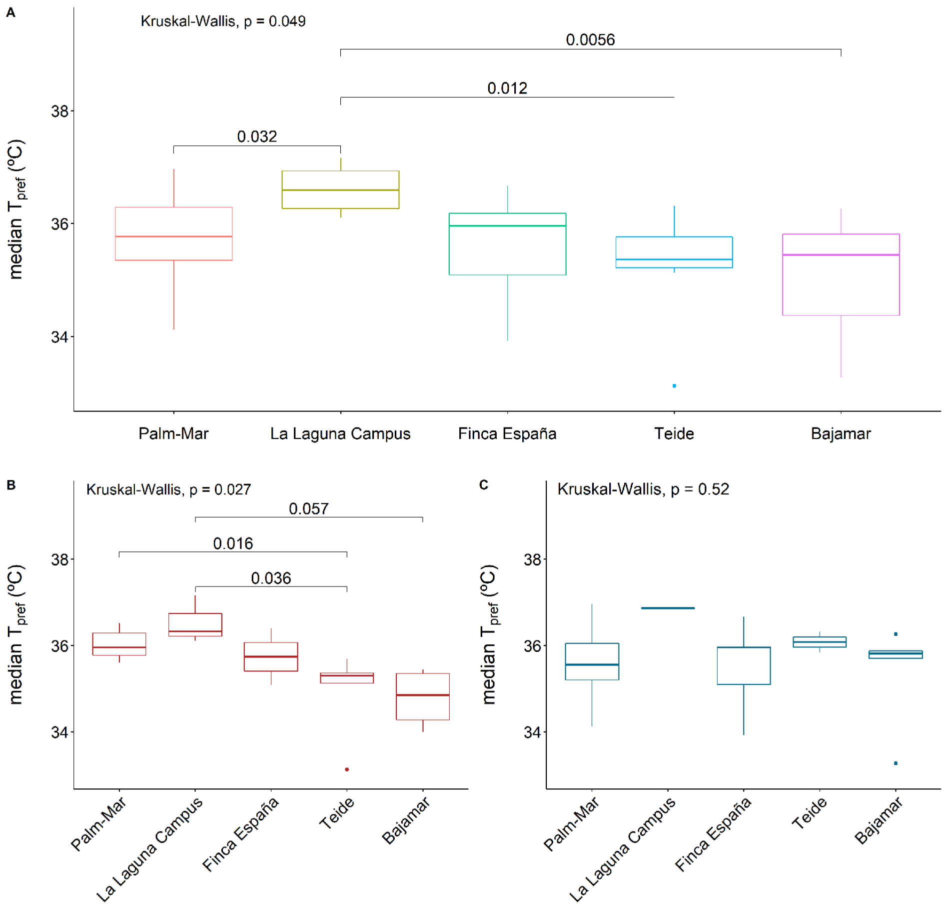

Figure 2. Wilcoxon sum-rank boxplots of median preferred temperature (T_{pref}) for the different populations of *Gallotia galloti*. Kruskal-Wallis rank sum test values for the entire population (A), males (B), and females (C) are shown, as are statistically significant pairwise comparisons.

Our data set includes two paired comparisons of *Gallotia* populations belonging to the same subspecies (with similar genetic backgrounds), occurring at high and low elevations. On the one hand, the populations at Palm-Mar and near the Pico del Teide summit can both be assigned to the subspecies *G. g. galloti* and span an enormous elevational difference from near sea level to about 3500 m. They tolerate substantial differences in rainfall and temperature patterns between the two sites (Fig. 4). On the other hand, the populations from Bajamar and La Laguna belong to the subspecies *G. g. eisentrauti*, with a lesser elevational range of about 800 m. If we assume that lizards adjust their physiology – either through adaptation or acclimation – to the long-term environmental conditions they experience, we can predict differences in T_{pref} and IWL characterizing each of these population pairs. The possibility of such a thermophysiological adaptation is supported by the general correlation of T_{pref} with environmental temperature at the level of lacertid species (Garcia-Porta et al., 2020). This suggests that lizards in hotter environments have higher preferred temperatures, although such a pattern was not found at a population level in several case studies (e.g., Belasen et al., 2016). On the other hand, it can be expected that in higher-humidity habitats, selective pressures to reduce water loss are relaxed and the IWL of lizards in such habitats might be higher as a consequence. Such a pattern has been found at both species level (Carneiro et al., 2015, 2017; Garcia-Porta et al., 2020) and population level (Belasen et al., 2016) in lacertids as well as other lizards (e.g., Dml'el et al., 1997).

Focusing primarily on the thermophysiology results of males for the reasons outlined above, our results

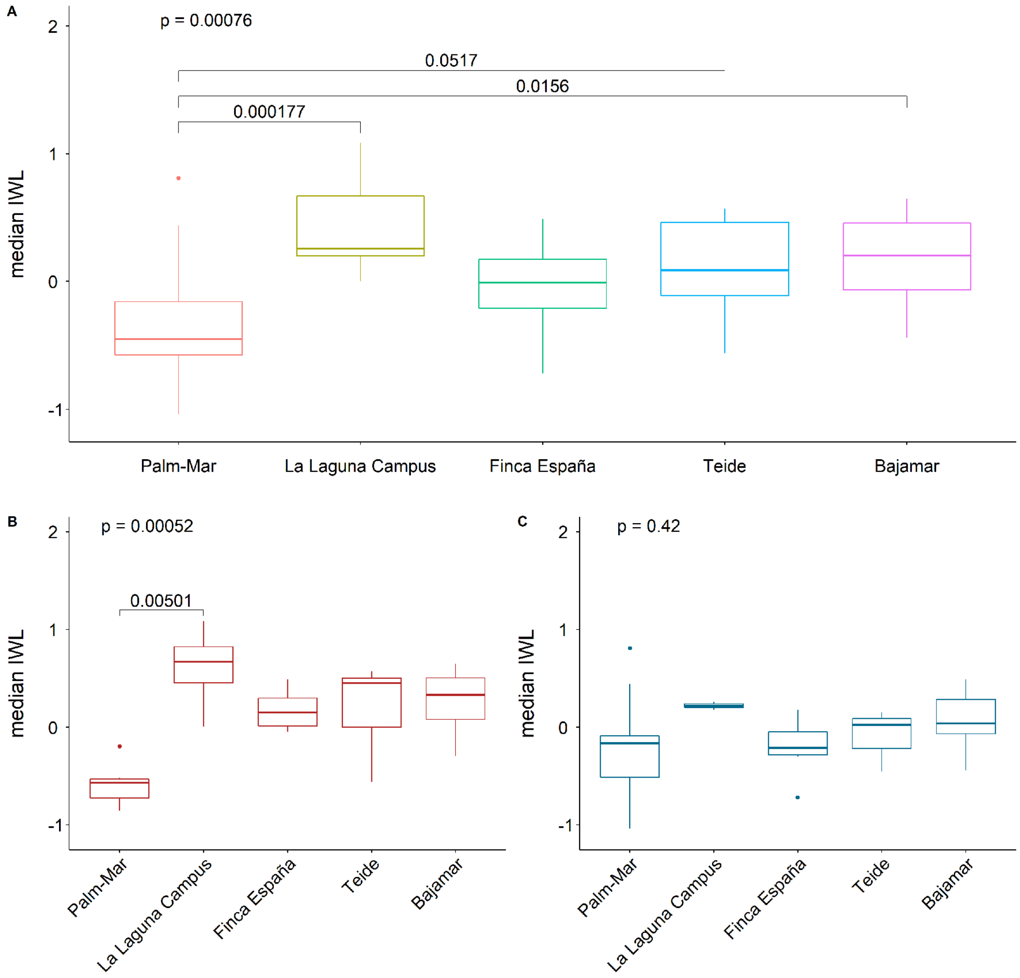

Figure 3. Tukey boxplots of the median instant evaporative water loss (IWL) for the different populations of *Gallotia galloti.* Results from two-way ANOVA test values for the entire population (A), males (B), and females (C) are shown, as are statistically significant pairwise comparisons.

partly conform to the predictions. In the Palm-Mar population, males had significantly higher T_{pref} values than at the Pico del Teide site. At such a high elevation, with an annual mean temperature of only 10.9ºC, lizards withstand extended periods of cold temperatures, often below freezing, during which they may not be able to reach higher body temperatures via behavioural thermoregulation. We hypothesize that a preference for lower temperatures may be advantageous for this lizard population, so as to maintain their activity over a sufficiently long period for successful reproduction. For our second elevational comparison, between Bajamar and La Laguna, no significant differences in T_{pref} were found, indicating that perhaps the environmental conditions at the higher-elevation site (La Laguna) are not extreme enough to trigger modifications of the lizards' thermophysiological preferences.

For water loss, we again observed distinct differences between Palm-Mar and Pico del Teide. These were not significant when analysing data from males alone, but we suspect this was due to low sample sizes. In fact, a graphical inspection of the results (Fig. 3B) shows that male lizards from Palm-Mar had distinctly lower IWL values not only in comparison to those from Pico del Teide, but also when compared to all other populations. Palm-Mar is the most arid site sampled and it is highly plausible that lizards in this population are under strong pressure to reduce their water loss to a minimum. At first glance, Pico del Teide is also an extremely arid environment of bare lava rocks, almost

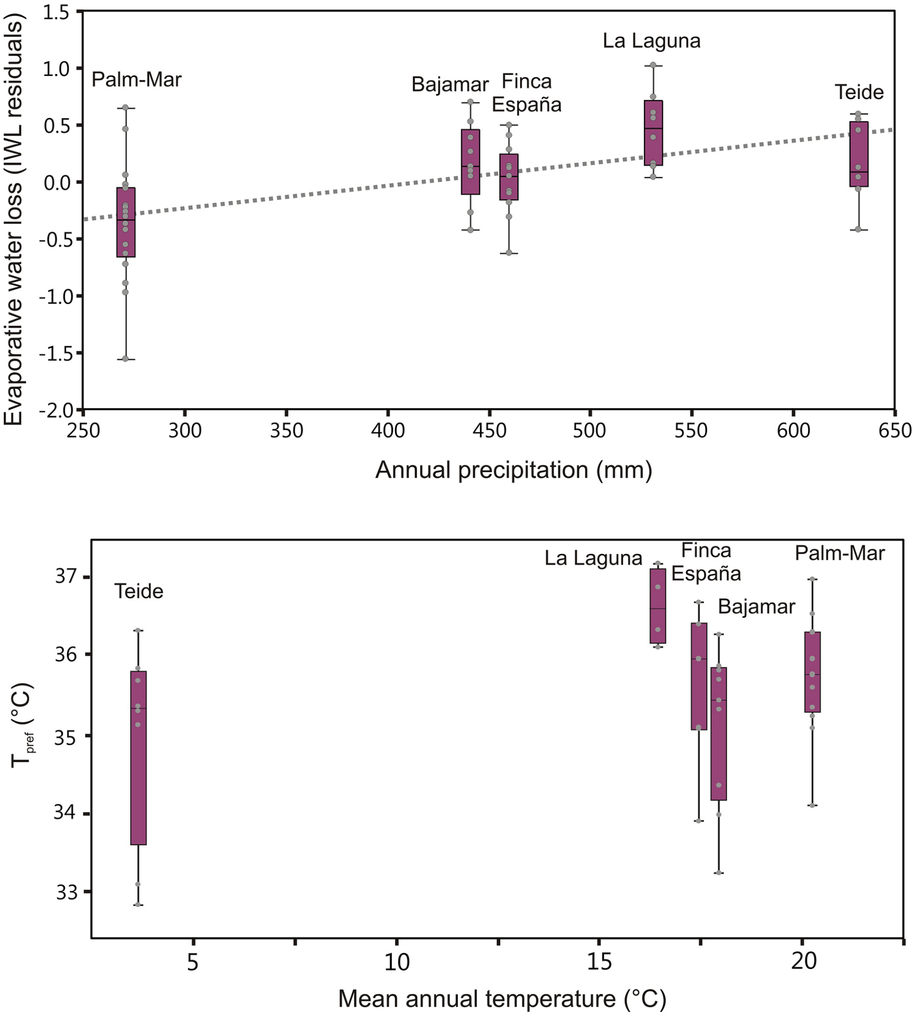

Figure 4. Relation of instant evaporative water loss (IWL) and preferred temperature (T_{pref}) relative to two bioclimatic variables. The boxplots show median, quartiles, minimum, and maximum median IWL and T_{pref} of all individuals studied per site. Single values are shown as grey dots. Localities are arranged according to annual precipitation (bioclim12) and annual mean temperature (bioclim1). The upper panel trend line shows a possible correlation of evaporative water loss (IWL) with precipitation, which is significant if including individuals as data points. No correlation with any bioclimatic variable was observed for T_{pref}.

without vegetation. However, the bioclimatic data reveal that the mountain receives distinctly higher annual precipitation than Palm-Mar, indicating that the pressure to reduce water loss at this site (as in all the other more mesic sites) would be reduced compared to Palm-Mar. Our second environmental comparison between Bajamar and La Laguna revealed no IWL differences, probably reflecting the fact that these are both relatively mesic sites. In fact, over all sites, our data suggest that precipitation could be positively correlated with lizard evaporative water loss (Fig. 4).

When interpreting our results, it is essential to consider that our approach of correlating values at the level of individuals involves the risk of pseudoreplication, so we stress that our analysis mainly serves to develop hypotheses that later require thorough testing against larger datasets with more extensive sampling, where populations can be used as data points to exclude pseudoreplication entirely. Furthermore, our experimental setup does not allow us to determine whether the observed ecophysiological differences between *G. galloti* populations are due to adaptation or acclimation. Specimens were tested 1–2 days after collection, which is insufficient to ensure full acclimation to common conditions at the experimentation site. We speculate, however, that especially the most clearly detectable differences of the Palm-Mar population from the remaining populations may be influenced by an adaptive component, considering the aridity of this site compared to many other environments in Tenerife and the indications of environmental adaptation in *G. galloti* found in a genomic screening by Brown et al. (2016).

It remains a striking ecological feature that *G. galloti* has been able to populate as diverse a range of environmental and elevational conditions, including locations at elevations > 3500 m. In contrast, other lacertid lizards occurring at such high elevations are usually montane specialists. This pattern may be grounded in a particular adaptability or phenotypic plasticity of *G. galloti*, but another critical factor may be the absence of competing species on Tenerife, allowing these lizards to persist in suboptimal habitats. The only other lacertid currently occurring there, *G. intermedia,* is now restricted to a few coastal cliffs and is characterized by different body size and behaviour, which likely limit competition with *G. galloti*. The same was almost certainly also true for the extinct giant species, *G. goliath* (see Maca-Meyers et al., 2003 for a taxonomic analysis of Tenerife *Gallotia* species).

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