



Geographic patterns of stress in insular lizards reveal anthropogenic and climatic signatures

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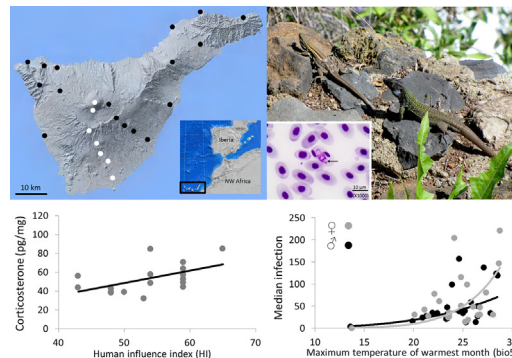
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HIGHLIGHTS

- The impact of anthropization on insular lizards is scarcely known.
- Three health/stress indicators were analysed along an environmental gradient.
- Corticosterone and hematic parasites co-vary with human development and climate.
- Environmental impacts are different for males and females.
- Monitoring lizard populations in islands may allow anticipating cascading effects.

GRAPHICAL ABSTRACT



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ABSTRACT

Anthropization of insular ecosystems may have negative impacts on native populations of lizards, which provide core ecosystem services on islands. We aimed to identify environmental factors to explain the interlocal variation in faecal glucocorticoids, parasite intensity, and body condition in populations of insular lizards. A cross-sectional design during the summer of 2017 and 2018 was used to sample 611 adult lizards, *Gallotia galloti*. Interlocal variation of three stress indicators was analysed in response to environmental variables across a wide environmental gradient in Tenerife (Canary Islands): (i) concentration of faecal glucocorticoids, (ii) intensities of infection by hematic parasites, and (iii) body condition. The data, with low spatial autocorrelation, were analysed using multimodel inference and model cross-validation. Bioclimatic variables associated with the extreme hot and dry climate of summer were the most informative predictors. Interlocal variation in faecal corticosterone in males was best fitted to a model that included the maximum temperature of the warmest month, although the best predictor was habitat anthropization. The thermal annual range, associated with extreme thermal events, was positively related to faecal corticosterone in females. Extreme hot temperatures were positively related to the median parasite intensities in both sexes, while the highest mean intensities of infection were found in females from the most xeric coastal localities. None of the predictors tested, including faecal glucocorticoids, explained individual or interlocal variation in body condition. Effects of human pressure and climate change on insular populations of lizards can be additive. However, the uncoupled relationship found between body condition and the faecal glucocorticoid content suggests that current negative effects may be aggravated during

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drought periods in summer. Given the impact of climate change on islands, our results may be of application to other archipelagos, where lizards also play key ecological roles.

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1. Introduction

Islands worldwide are suffering from increasing anthropogenic pressure, but information on the responses of insular endemics in this context is scarce. Anthropogenic impacts on insular endemics include both direct and indirect effects of human activities on viability and extinction of insular populations (Wood et al., 2017; Crowley et al., 2019). Main stressors on islands are human infrastructure development (buildings, roads, intensive agriculture and their associated pollutants), and human-driven introduction of exotic predators (Rodda and Savidge, 2007; Medina and Nogales, 2009; Chi et al., 2020). In addition, and as a scarcely studied concern, anthropogenic change in climate may as well impact insular biotas (Bellard et al., 2014; Mairal et al., 2018).

Conspicuous anthropogenic actions can quickly decrease population sizes (Bootton et al., 2017; Josserand et al., 2017), but they are not the only ones affecting wildlife. Other stressors could also hinder effects on wildlife survival (Dupoué et al., 2017). These may activate different physiological mechanisms at the individual level that were evolved in vertebrates to restore homeostasis. The most important of which is likely the activation of the hypothalamic-pituitary-adrenal (HPA) axis that activates the secretion of glucocorticoids in adrenal glands in response to acute bouts of environmental stress (Harvey et al., 1984). These adrenal hormones increase fat catabolism and elevate the metabolic rate (Dunlap, 1995 and references therein). Such mobilisation of fat reserves, if not compensated by food intake, is expected to decrease body condition, while derivation of energy to self-maintenance happens in detriment of other important activities, such as immune response to fight diseases (Raffel et al., 2006; Rollins-Smith, 2017). Thus, if the bout of stress is short-term, the activation of the HPA axis is an adaptive strategy with positive feedback in the survival of individuals, as long as individuals had full access to food (Cote et al., 2006). On the contrary, if the environmental stressors persist and encompass the reproductive period, dramatic long-term effects on individuals and populations are expected, which might eventually lead to extinction (e.g., Sinervo et al., 2010; Riddell et al., 2019).

The reproductive status of individuals, their health, fat reserves, and intra- and inter-specific interactions may also influence the response of populations to stress (Oppliger et al., 1998; French and Moore, 2008). In this sense, parasites have been used as reliable indicators of environmental perturbation (reviewed in Vidal-Martínez et al., 2010). However, environmental correlation with parasites can be interpreted in two opposite directions. On one hand, Marcogliese (2005) concluded that 'healthy environments have healthy parasites', although this specifically applies to parasites with heteroxenous life cycles that need different hosts to complete their reproduction and transmission. In this case, any environmental perturbation that reduces the abundance of vectors would eventually reduce the parasite abundance and its persistence in the ecosystem (Martínez and Merino, 2011; Padilla et al., 2017). On the other hand, parasites have also been used as bio-indicators of environmental perturbation on the host's immune competence to fight infections (Sures, 2004; Vidal-Martínez et al., 2010). Two experimental studies that support this showed that lizards of the family Lacertidae reared under conditions of (i) high sustained temperatures, and (ii) high density of conspecifics, increased their intensity of hematic parasites (Oppliger et al., 1996, 1998). These experiments support that local intensities of hematic parasites reflect the impact of environmental stressors on the immune competence. In addition, a third recent experiment demonstrated that lacertids exposed to sustained increased temperatures suffered a reduction of white blood cell

counts and expression of M-type immunoglobulins, giving support to the immunosuppressive effects of environmental warming on lizards (Han et al., 2020).

The main objective of this study was to evaluate the anthropogenic impact on insular populations of lizards. Populations of an endemic lizard, *Gallotia galloti* (Squamata: Lacertidae) were investigated across various climates and habitats in Tenerife (Canary Islands) (Thorpe and Brown, 1989). The present study was performed during the warmest period of the year because one of its main aims was to investigate concomitant effects of sustained warm temperatures and drought on the lizard populations under natural conditions. The phenotypic parameters of lizards analysed were (i) the concentration of faecal glucocorticoids, as a proxy to the basal level of activation of the HPA axis in response to environmental stress (Dunlap and Wingfield, 1995; Josserand et al., 2017), (ii) intensities of infection by hematic parasites, as a proxy of immune competence to fight parasites (Rollins-Smith, 2017), and (iii) body condition, using a scaled index that reflects the extension of fat reserves in small vertebrates (i.e., Peig and Green, 2009). These stress indicators were analysed separately by sex because *G. galloti* (i) is a largely dimorphic species (Molina-Borja et al., 1997), with males having longer and more robust bodies than females, and hence, with potentially dimorphic capabilities to cushion environmental perturbations, and (ii) gonadal and fat storage cycles are asynchronous in lacertids (Carretero, 2006), with likely differing seasonal constraints between the sexes; for example post-gravid females are recovering after laying during this period of the year (e.g., Megía-Palma et al., 2020), hence, this is an opportunity to analyse how additional stressing factors affect them. Expected outcomes include higher parasite intensities, higher faecal corticosterone, and lower body condition in localities with higher environmental stress.

2. Materials and methods

2.1. System of study

Tenerife (Canary Islands) is located in the Northern Atlantic subtropical region (28.44228, -16.97465). It covers an area of 2034.38 km² and an increasing human population of 904,713 inhabitants (ISTAC, 2018). With the Teide volcano in the centre of the island, Tenerife reaches an elevation of 3718 masl. This geography promotes strong heterogeneity in climate regimes and habitats (del Arco et al., 2006). There is evidence supporting sustained climate change on the island with a mean raise of 0.09 °C per decade in Tenerife over the last 70 years (Martín et al., 2012).

2.2. Model species

Adults of *G. galloti* (Fig. S1a) are mainly herbivorous (Roca et al., 2005) and are important fruit dispersers in xeric habitats of the island (Valido and Nogales, 1994). Relatively to other species *G. galloti* is a long-lived species (>9 years) as inferred from skeletochronological analyses (Castanet and Baez, 1991). Two subspecies, *Gallotia galloti galloti* and *Gallotia galloti eisentrauti*, are used as operational units based on overall external morphology and coloration (Molina-Borja et al., 1997; Huyghe et al., 2005). However, diverging traits between subspecies might result from a combination of ancient isolation in the NE part of the island with recent gene flow (Brown et al., 2016) and local adaptation to xeric/mesic conditions (Thorpe and Brown, 1989). Thus, xeric habitats at low, mid, and high elevations, representing 2/3rds of Tenerife, are typically inhabited by *G. g. galloti*, while *G. g. eisentrauti* is restricted to humid habitats at low and mid elevations in the North. *G.*

galloti is parasitized by hematic parasites of the genus *Karyolysus* (Coccidia: Adeleorina: Karyolysidae) (Fig. S1b; Tomé et al., 2018) and hematophagous mites of the genus *Ophionyssus* (Acari: Mesostigmata: Macronyssidae) (Fain and Bannert, 2000). These mites are the most likely vectors of *Karyolysus* (Bannert et al., 1995). The parasitic hematic stage undergoes asexual reproduction (merogony) inside lizards' red cells (Bannert et al., 1995) and in other lacertids they have been demonstrated to reduce the host's fitness in terms of aerobic capacity, running performance, and even tail regeneration (Oppliger et al., 1996; Oppliger and Clobert, 1997; Garrido and Pérez-Mellado, 2014).

2.3. Sampling

In July of 2017 and 2018, adult lizards were sampled in 24 localities that encompassed a wide range of environmental conditions across Tenerife (Fig. 1). The subspecies *eisentrauti*, of the North, had a smaller representation in the sample with 7 localities sampled versus 17 localities sampled for the subspecies *galloti*. This is not statistically balanced, but as explained, it has biogeographic justification (representing ~1/3 of the sample ~ same distribution proportion of subspecies in Tenerife). If sampling in the North would have been more dense (closer points) we had incurred in high risk of spatial autocorrelation. The elevation (masl) and the coordinates for each sampling site were registered with a GPS device (GPSMAP 64s, Garmin, Kansas, USA). Sampling was carried out using pitfall traps (N = 15–30) baited with tomato that were placed in the study area ~10 m apart one from another and checked for lizards every 15–20 min (Megía-Palma et al., 2016a). Only adult individuals were sampled for this study; according to a minimum snout to vent length (SVL) of 100 mm for males, and 80 mm for females (Salvador, 2015). The gravidity status of females was assessed by palpation.

2.4. Indicators of physiological stress

2.4.1. Faecal glucocorticoid metabolites (CORT)

Lizards were transported to the lab in individual cotton bags and faecal samples were gently obtained within the next 6 h by massaging their

belly (Megía-Palma et al., 2016a). Faecal samples were immediately stored at -20°C and then transported and stored at -80°C until their processing. To extract the content of faecal glucocorticoid metabolites, faecal samples were dried at 50°C overnight, and then approx. 63 mg of dry sample was placed in an assay tube with $400\ \mu\text{l}$ of 90% methanol and minced. Tubes were vortexed at high speed in a multi-tube vortex for 30 min. Subsequently, samples were centrifuged at 1000 G for 10 min. Finally, $100\ \mu\text{l}$ of supernatant was diluted in $200\ \mu\text{l}$ of steroid free serum (DRG Instruments GmbH, Marburg, Germany) and stored at -20°C until being analysed. A commercial corticosterone enzyme immunoassay kit (EIA, DRG Instruments GmbH) was used for quantification according to the manufacturer's instructions. Samples were analysed in duplicate. Linearity was tested with serial dilutions of a faecal extracted pool and proved to be parallel to the expected line. The analytical sensitivity was calculated by subtracting 2 SD from the mean of 20 replicate analyses of the blank (zero binding) according to the manufacturer's instructions and was found to be $<1.63\ \text{nmol/l}$. The recovery of faecal glucocorticoid metabolites was $118.3\% \pm 3.10$ (N = 2). The between-assay and within-assay coefficients of variation were 15.6% and 11.13%, respectively. Log_{10} -transformed values of CORT_{ind} of 348 faecal samples (179 males and 169 females) were calculated in a subsample of lizards from 17 of the localities.

2.4.2. Intensity of hematic parasites (PI and PM)

Lizards were bled at the base of the tail with sterilized needles following the protocol described in Megía-Palma et al. (2016b). Blood ($\sim 10\ \mu\text{l}$) was taken with heparinized capillaries and a drop was smeared in a slide and later stained with Giemsa (Megía-Palma et al., 2016a). Hematic parasites were quantified in a total of 5000 blood cells (Megía-Palma et al., 2016b). Both the median (PI) and the mean (PM) intensity of parasites were calculated (sensu Rózsa et al., 2000).

2.4.3. Body condition (SMi)

Lizards were measured using a ruler to the nearest of 1 mm and weighed to the nearest of 0.01 g with a digital scale. Body condition of the adult lizards was calculated using the scaled body-mass index

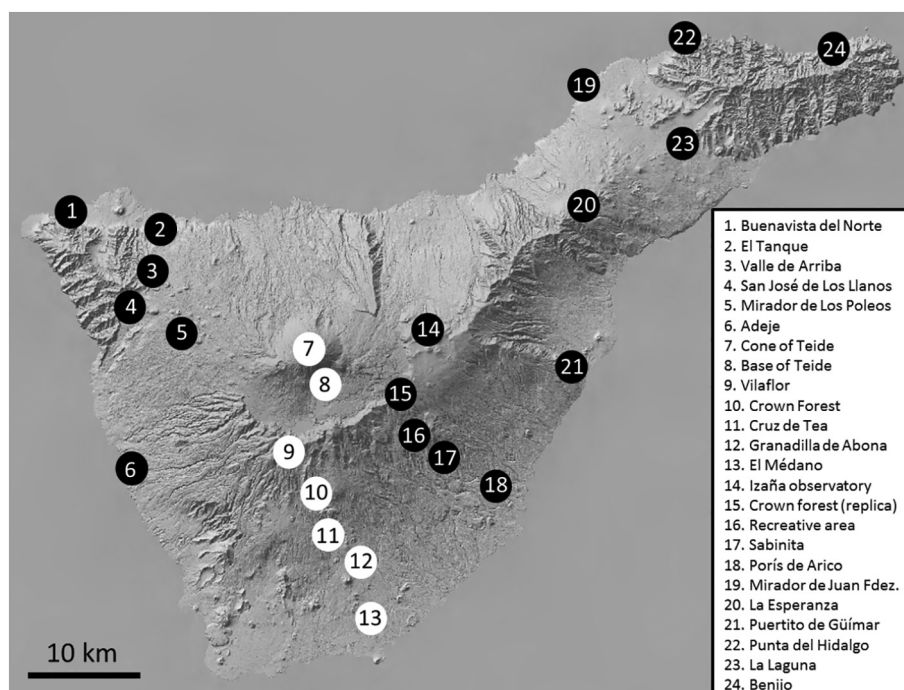


Fig. 1. Map of 24 sites where lizards (*G. galloti*) were sampled in Tenerife (2017 and 2018). Black dots indicate localities where data on body condition, blood parasites, and glucocorticoid metabolites were obtained. White dots indicate localities where only data on body condition and blood parasites were collected.

(SMi). The reduced major-axis (Li, 2012) of the mass on body length was calculated using the rma.v1.21 software (Bohonak, 2004). SMi was calculated separately for males and females because, regardless fat storage, both sexes intrinsically differ in body shape and robustness (Molina-Borja et al., 1997). Moreover, the cycles of fat bodies depletion are well-known to differ during the year between sexes in lacertids (reviewed in Carretero, 2006) and the SMi best reflects this variation. SMi has also been significantly associated with the body content in fat and has been presented as a reliable indicator of environmental stress (e.g., pollutants and parasites) in wild populations of small vertebrates (Peig and Green, 2009, 2010; Maceda-Veiga et al., 2014).

2.5. Environmental predictors of stress

2.5.1. Relative lizard abundance (RLA)

Lizard counts were always performed within a similar temperature range (24–28 °C) in sunny warm days and between 11:00 and 13:30 that is the daily peak of activity (Bohórquez-Alonso et al., 2011). The time invested per locality was very similar (~1 h) with few exceptions that required a longer effort (Cone of Teide, La Esperanza, and Valle de Arriba). RLA was estimated per site using an adapted protocol described by Mesquita et al. (2007). RLA was calculated by dividing the number of lizards trapped during the first hour by the number of traps used.

2.5.2. Mite intensities (MI)

Mites were counted on the body of the lizards using a 10× magnifying glass (e.g., Álvarez-Ruiz et al., 2018). The median local intensities of mite infestation were used as a biotic predictor for local intensities of hematic parasites.

2.5.3. Bio-climatic variables

Information was downloaded on 19 bio-climatic modelled variables (including temperature and precipitation between 1950 and 2000) from the WorldClim-Global Climate Data 1.4 dataset, at 30 arc sec (~1 km²) (Hijmans et al., 2005). The representativeness of these bio-climatic modelled variables was tested at a local scale by comparing the obtained averaged data from 50-year averaged data with the current mean temperatures and humidity conditions during the summer of 2018. Between the 7th and the 16th of July 2018, one data-logger (ibutton model: DS1923 Hygrochron) per locality was synchronically set in a randomly selected subsample of 18 localities. Data-loggers were placed in sunny areas under small stones of approximately 30 cm³ and recorded temperature and relative humidity every 65 s. Individual Spearman correlations and sequential-Bonferroni-adjusted significance coefficients were used to compare the mean temperature and relative humidity extracted from each data-logger with their corresponding 19 bio-climatic variables.

2.5.4. Normalized difference vegetation index (NDVI)

The normalized difference vegetation index (NDVI) was extracted from satellite images taken during the first week of July of 2017 and 2018 (eMODIS v6.0, NASA) where NDVI values are positively correlated with vegetation cover and primary production (Jenkinson et al., 2010).

2.5.5. Human development index (HI)

The human development index, normalized by area and biome is a global dataset of 1-kilometer covering human population pressure (population density), human land use and infrastructure (built-up areas, night time lights, land use/land cover), and human access (roads) (Sanderson et al., 2002; WCS and CIESIN, 2005). Higher HI values indicate higher human development.

2.6. Statistical analyses

2.6.1. Individual and intralocal variation in CORT, PI, and SMi

Sexual and individual variation of the three response variables associated with environmental stress was first explored (SMi_{ind}, CORT_{ind}, and PI_{ind}). For this particular aim, Gaussian linear models for SMi_{ind} and log-transformed CORT_{ind}, and a negative binomial model for PI_{ind} (Pennyquick, 1971) were fitted. Sex, locality, and their interaction were set as predictors for CORT_{ind} and PI_{ind}. SMi_{ind} was tested separately for males and females and CORT_{ind} was added as predictor for SMi_{ind}. Based on an information criterion (AICc), the interaction term was removed when it was not significant (Burnham et al., 2011). Locality was not included as a random factor, because interlocal differences were one of the questions investigated.

2.6.2. Interlocal variation and spatial autocorrelation

Median values of CORT and SMi were used, separated per sex, as single values per locality. In addition, both median (PI) and mean values of local intensities of hematic parasites were calculated because they provide different biological information about the distribution of parasites in the sample (Rózsa et al., 2000). Prior to model building, whether values of CORT, PI, and SMi showed spatial autocorrelation (SAC) was tested using Moran's I matrix, where the null hypothesis equals the spatial independency of the data (Legendre and Legendre, 1998). The data of PI_{females} showed significant SAC (sd = 0.047, P = .024). However, all the remaining response variables showed spatial independency: CORT_{males} (sd = 0.065, P = .23) and CORT_{females} (sd = 0.066, P = .86); PI_{males} (sd = 0.049, P = .098), Mean intensity_{males} (sd = 0.048, P = .12), and Mean intensity_{females} (sd = 0.046, P = .79); SMi_{males} (sd = 0.050, P = .24) and SMi_{females} (sd = 0.047, P = .77). Therefore, an inverse distance-weighted function of neighbouring response (covariate) was calculated to correct for SAC only the model of PI_{females} (Dormann et al., 2007).

2.6.3. Model building

Statistical analyses were run in R version 3.4.3 (R Core Team, 2017). AICc criterion was used to fit appropriate distributions to the residuals of all the models. All these candidate models were weight-corrected by the corresponding number of samples per locality. Models for CORT, log₁₀-transformed values of both PI and mean intensities, and SMi were fitted to Gaussian linear distributions. Sampling year (2017 or 2018) and the corresponding subspecies (*G. g. galloti* or *G. g. eisentrauti*) were set as factor predictors. In addition, relative lizard abundance (RLA), PI, MI, the human development index (HI), elevation (mamsI), SMi, and the normalized difference vegetation index (NDVI) were set as continuous predictors. Water may be spatially and/or seasonally restricted in Tenerife (e.g., Sedlacek et al., 2012). This, in turn, may influence the biological responses of lizards by decreasing food availability (Kearney et al., 2013), constraining thermoregulation (Sannolo and Carretero, 2019) and limiting reproduction (Dupoué et al., 2020). Thus, water points in 1 km² for all sampled localities were also set as a predictor, which were counted from maps (<https://www.ign.es/>). The eight bio-climatic predictors that were significantly correlated with our data of mean temperature and humidity sampled in the field (see Results) were also included in the models. Since they showed a high mean pairwise collinearity (>0.70), separated models named "candidate models" that included one of these eight bio-climatic variables were built and their AICc coefficients compared to assess the most informative one (= with the lowest AICc; Table 1). The parametric distribution of all the candidate model residuals was confirmed and their multicollinearity checked by examination of their VIF coefficients (Schroeder et al., 1990). When multicollinearity between elevation and the bio-climatic variable was too high the effect of elevation was removed.

Table 1

AICc coefficients of the models built with each of the eight bio-climatic variables (WorldClim) chosen for analysis. In bold are marked the candidate models with the lowest AICc coefficient (= the most informative ones) and the percentage of the variance explained. These ones were used to build the final models by applying the multimodel inference analysis.

	CORT _{males}	%	CORT _{females}	%	PI _{males}	%	PI _{females}	%	PMean _{males}	%	PMean _{females}	%	SMI _{males}	%	SMI _{females}	%
Temp seasonality (bio4)	230	–	239	–	80.7	–	104.6	–	102.3	–	307	–	194	–	170	24.4
Max temp warmest month (bio5)	224	66.5	244	–	76.1	68.2	99.2	43.4	–29.6	72.5	266	–	197	–	171	–
Min temp coldest month (bio6)	230	–	239	–	80.0	–	103.9	–	94.0	–	304	–	194	–	170	24.1
Temp annual range (bio7)	229	–	234	68.2	89.2	–	105.3	–	189.2	–	320	–	193	38.3	170	25.8
Mean temp driest quarter (bio9)	226	–	243	–	78.1	–	101.5	–	31.6	–	289	–	196	–	171	–
Mean temp warmest quarter (bio10)	226	–	243	–	77.6	–	101.5	–	27.9	–	287	–	196	–	170	23.2
Precip driest month (bio14)	230	–	275	–	87.1	–	108.5	–	5.1	–	270	–	202	–	178	–
Precip driest quarter (bio17)	230	–	281	–	86.4	–	106.3	–	–20.6	–	239	45.1	203	–	178	–

2.6.4. Multimodel inference and cross-validation

Multimodel inference was applied to the candidate models (Bartoń, 2018). For this, the models were considered sufficiently informative when their $\Delta AICc \leq 4$ (Burnham and Anderson, 2004) (Tables S2–S9 in Supplementary material, Appendix A). Model averaging was used to get a final model and calculate the relative importance of each predictor. For this, only the models that included the effect (i.e., conditional average) were considered to calculate the significance ($\alpha < 0.05$) of the predictors, their z-standardized β coefficient, and their standard error. The resulting final models were cross-validated using a k-fold split of 3 in the R-package 'DAAG' (Mairdonald et al., 2015). Finally, the percentage of the variance explained by each significant predictor was calculated by means of their sum of squares.

3. Results

3.1. Validation of bio-climatic models for Tenerife

Results indicated that the averaged bio-climatic variables modelled for 1950–2000 (WorldClim) fairly reflect current climatic conditions of July in Tenerife during the sampling period. Specifically, temperatures registered in the field in 2018 using data-loggers were significantly correlated, after correction by sequential Bonferroni, with five of the bio-climatic variables extracted from WorldClim: i.e., the maximum temperature of the warmest month (bio5) ($\rho = 0.67$, $P = .002$), the mean temperature of the driest quarter (bio9) ($\rho = 0.69$, $P = .001$), the mean temperature of the warmest quarter (bio10) ($\rho = 0.67$, $P = .002$), the precipitation of the driest month (bio14) ($\rho = -0.68$, $P = .001$), and the precipitation of the driest quarter (bio17) ($\rho = -0.73$, $P = .0005$).

In addition, the averaged field data of relative humidity were significantly correlated with three of the bio-climatic variables: i.e., the seasonality of temperature (bio4) ($\rho = -0.81$, $P < .0001$), the minimum temperature of the coldest month (bio6) ($\rho = 0.66$, $P = .002$), and the annual range of temperatures (bio7) ($\rho = -0.80$, $P < .0001$). Based on this validation, these bio-climatic variables were considered representative for further analyses.

3.2. Faecal glucocorticoid metabolites

A decoupled relationship between the secretion of corticosterone, the body condition, and the parasitaemia was found; all of them showing independent responses to different environmental stressors. There were significant differences among localities in CORT_{ind} ($F_{16, 314} = 2.48$, $P = .001$; Fig. 2). However, sexual differences were not significant ($F_{1, 314} = 0.62$, $P = .43$), and this trend was similar among localities (sex:locality; $F_{16, 314} = 1.15$, $P = .31$).

For CORT_{males}, the model that included the maximum temperature of the warmest month (bio5) was the most informative and explained

66.5% of the observed variance (Table 1). However, the multimodel inference produced 16 likely models and suggested that the human development index ($z = 2.10$, $P = .036$) was the most informative predictor. This was confirmed by cross-validation, and it explains 28.6% of the observed variance in CORT_{males} (Table 2).

For CORT_{females}, the candidate model that included temperature annual range (bio7) was the most informative and explained 68.2% of the observed variance (Table 1). The multimodel inference approach applied to this candidate model produced 13 likely models. The model averaging protocol suggested that bio7 and HI were the most important predictors for CORT_{females}, although they were not significant (bio7: $z = 1.78$, $P = .075$; HI: $z = 1.70$, $P = .090$). The cross-validation approach applied to a final model that included these two predictors dropped HI, but erected bio7 as a significant predictor for CORT_{females} (Table 2).

3.3. Hematic parasites

An overall 92.4% (565/611) prevalence of infection by intraerythrocytic parasites of the genus *Karyolysus* (Tomé et al., 2018) was found. There were significant differences of PI_{ind} between localities ($F_{23, 527} = 6.62$, $P < .0001$; Fig. S2). The one-way model was more informative ($\Delta AICc = -22$) than the model that included the interaction locality*sex. When the effect of the interaction was removed from the model, there were also significant sexual differences ($F_{1, 527} = 6.41$, $P = .012$). Females, with a mean \pm SE infection of 134.25 ± 18.80 blood parasites (min = 0, max = 3900), were significantly more

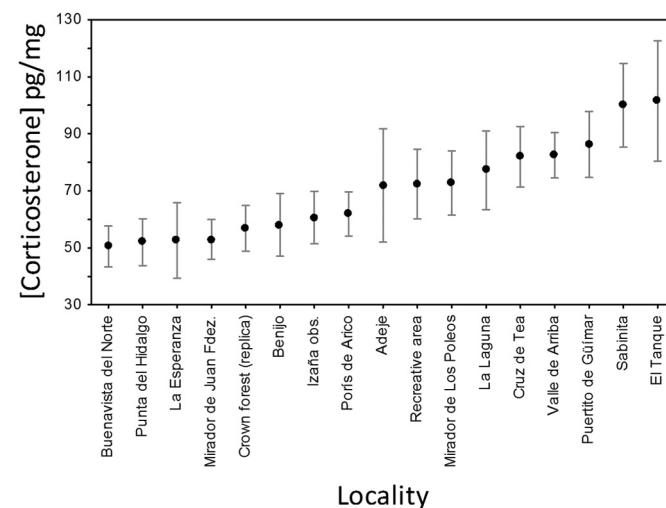


Fig. 2. Interlocal variation (pg/mg) in mean \pm se concentration of excreted corticosterone metabolites by *Gallotia galloti* in Tenerife shown in increasing order.

Table 2
Final models estimated by multimodel inference and model averaging from the candidate models (see Table 1). Generalized model were built as follows: response ~ year + lineage + RLA + SMi + NDVI + HI + PI + MI + Elevation + bio + water. Column 'Importance' shows the average weights in the final models. Column 'β' shows the z-standardize estimated coefficients. On the right, it is shown the results of the final models, where significant predictors confirmed by cross-validation were marked in bold. Column 'SS' shows the partial sum of squares.

	Importance	β	df	F-value	P-value	SS	% explained
CORT_{males}							
Human influence index (HI)	0.69	1.31	1	6.01	0.027	1101	28.6
Residuals			15			2748	71.4
CORT_{females}							
Temperature annual range (bio7)	0.53	4.47	1	5.17	0.039	1563	24.7
Human influence index (HI)	0.47	1.60	1	1.78	0.20	537	8.5
Residuals			14			4236	66.8
log₁₀-PI_{males}							
Maximum temperature of warmest month (bio5)	1.00	0.18	1	23.08	0.0001	7.37	44.4
Subspecies	0.73	-0.29	1	7.34	0.013	2.34	14.1
Residuals			20			6.90	38.5
log₁₀-PI_{females}							
Maximum temperature of warmest month (bio5)	0.90	0.20	1	24.2	<0.001	24.53	50.6
Subspecies	0.63	-0.37	1	2.7	0.12	2.73	5.6
Residuals			21			21.25	43.8
log₁₀-Mean intensity_{males}							
Maximum temperature of warmest month (bio5)	1.00	0.06	1	20.40	<0.001	1.44	40.7
Subspecies	1.00	-0.10	1	6.14	0.023	0.43	12.3
Body condition (SMi)	1.00	-0.01	1	5.37	0.032	0.38	10.7
Normalized Difference Vegetation Index (NDVI)	1.00	0.44	1	0.08	0.77	0.006	0.1
Relative lizard abundance (RLA)	1.00	0.11	1	0.06	0.81	0.004	0.1
Residuals			18			1.27	36.1
log₁₀-Mean intensity_{females}							
Precipitation of driest quarter (bio17)	1.00	-0.07	1	25.9	<0.001	3.23	54.1
Residuals			22			2.74	45.9
SMi_{males}							
Temperature annual range (bio7)	0.58	-0.02	1	3.93	0.060	126	15.1
Residuals			22			706	84.9
SMi_{females}							
-			-	-	-	-	-
Residuals			23			-	100

infected than males that had 86.04 ± 9.43 (min = 0, max = 1300) (Fig. 3a).

For PI_{males} and $PI_{females}$ (i.e., median intensities), candidate models that included the maximum temperature of the warmest month (bio5) was the most informative and explained 68.2% and 43.4% of variance respectively in male and female hosts (Table 1). The multimodel inference approach applied to this candidate models produced 16 and 11 likely models, respectively. The model averaging protocol suggested that bio5 (males: $z = 4.07, P < .0001$; females: $z = 2.48, P = .013$), and the subspecies (males: $z = 2.10, P = .036$; females: $z = 1.92, P = .054$) were the most informative predictors. The cross-validation of the final models confirmed the significance of bio5 that explained 44.4% of the observed variation in PI_{males} and 50.6% of $PI_{females}$, and the subspecies in the model of PI_{males} that explained 14.1% of the variance (Table 2).

Median and mean intensities of infection were correlated, but the correlation in males ($r^2 = 0.81$) was stronger than in females ($r^2 = 0.60$) (Fig. 3b). Therefore, similar results were found for mean infections in males (i.e., PM_{males}); 4 likely models were produced by model averaging and suggested that body condition significantly contributed ($z = 2.06, P = .040$), altogether with bio5 and subspecies, to explain 10.7% more of the observed variance (Tables 1 and 2). For $PM_{females}$, the candidate model that included precipitation of the driest quarter (bio17) was the most informative and explained 45.1% of the observed variance (Table 1). The multimodel inference approach produced 5 likely models for $PM_{females}$. Bio17 was the most important predictor ($z = 3.24, P = .001$), which was confirmed by cross-validation. It explained 54.1% of the observed variance (Table 2).

3.4. Body condition

Body condition (SMi_{ind}) significantly varied between localities in both sexes (SMi_{males} : $F_{16, 152} = 14.76, P < .001$; $SMi_{females}$: $F_{16, 145} = 4.91, P < .001$). However, no significant effect of $CORT_{ind}$ was detected on the individual variation in SMi in either of the sexes (males: $F_{1, 152} = 0.36, P = .55$; females: $F_{1, 145} = 0.19, P = .67$).

The alternative candidate models that included the temperature annual range (bio7) and the temperature seasonality (bio4) were the most informative for SMi_{males} and $SMi_{females}$, respectively (Table 1). The multimodel inference produced 31 likely models for SMi_{males} and 19 for $SMi_{females}$. Bio7 was the most important predictor for SMi_{males} , but its effect was only marginally significant (z -value = 1.77, $P = .077$), and remained as such after cross-validation (Table 2). For $SMi_{females}$, none of the predictors studied here were informative enough based on the multimodel inference criterion.

4. Discussion

Insular lizards respond to environmental stress in a complex manner. The human development index best explained the interlocal variation in faecal corticosterone concentration in the males of *G. galloti*. However, the most informative candidate model also included the maximum temperature of the warmest month, suggesting that the effects of human perturbation and climatic extremes are additive and together magnify their negative impact (Jokinen et al., 2011). Several factors associated with human activities may explain this result. The historical

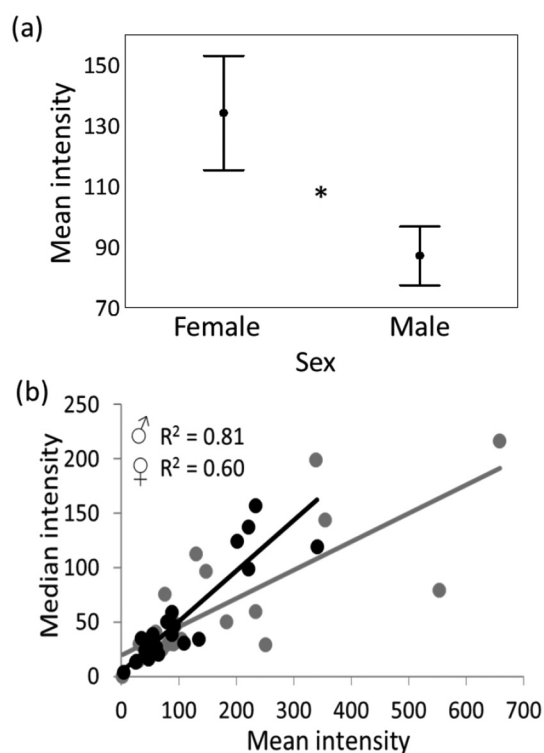


Fig. 3. (a) Sexual differences in mean \pm SE intensity of hematic parasites. (b) Relationship between mean and median intensities of parasites in males (black) and females (grey).

introduction of invasive predators, with especial emphasis on cats and rats, which mainly remain associated to human settlements, is one of the main causes of extinction of insular vertebrates in the world, including the Canary Islands (Traveset et al., 2009; Medina et al., 2011). Thus, the proximity to towns and crop lands might as well increase the abundance of rodents and feral cats and, hence, the pressure on lizard populations. The anthropization index included land use, however, the proximity to crops itself, despite the intensive use of pesticides in Tenerife (e.g., Sánchez-Hernández, 2001; Villa et al., 2003), is unlikely to have had a strong influence in our data because, given the size of the home range area described for the species (see Molina-Borja, 1985), 87% of our sampling localities were not close enough to crop fields, and the vegetation index used (also applied to agricultural studies) had a relatively low importance in the models. Nonetheless, while the effects of some common organophosphorus phytochemicals at their current concentration used in agriculture seems innocuous to *G. galloti* (i.e., Fossi et al., 1995), others interfere with their hepatic metabolism at different dosages (Sánchez et al., 1997) and might have additive effects on stress. In females, faecal glucocorticoid concentration was best explained by the temperature annual range that was calculated as the difference between maximum and minimum yearly temperatures (see Hijmans et al., 2005) and, as commented, positively correlated with elevation in Tenerife. This suggested that there is sexual difference in the sensitivity to environmental stress with females being more directly affected by annual fluctuation of temperatures, while males are more directly affected by human activity and extreme hot temperatures (Fig. 4a and b). Nonetheless, the models that included the temperature annual range and temperature seasonality (standard deviation of temperatures $\times 100$) were the most informative explaining the observed variation in body condition of both males and females, supporting that *G. galloti* is affected by yearly oscillation of temperatures, which is intensified with elevation. This is congruent with the high conservatism in the thermal niche preferred by *G. galloti* in the laboratory despite the lizards tested in thermal gradients came from different elevations in Tenerife (Carretero et al., unpublished data).

Interlocal variation in parasite intensities, an indicator of stress in lizards (Oppliger et al., 1998), was best predicted by the warm and dry climate of summer. Although the subspecies and the body condition of the lizards contributed to explain interlocal differences in parasitaemia, its effect was smaller. Thus, our results posit local intensities of infection by *Karyolysus* as a bio-marker of climatic stress in endemic populations of free-ranging lizards in Tenerife. Median intensities of hematic parasites were higher in warmer localities, in line with previous studies that revealed the immunosuppressive effect of sustained high temperatures on lacertid hosts (i.e., Han et al., 2020) and its effect on the number of hematic parasites (Oppliger et al., 1996). The negative effect of high temperatures may be behaviourally buffered by thermoregulation in free-ranging lizards (Kearney et al., 2009). However, the positive relationship between the maximum temperature of the warmest month and median intensities of parasites suggested that environmental temperatures in July along the day, and in most habitats, approach the upper limit of the preferred thermal range of *G. galloti* (Vickers et al., 2011). This may lead lizards to have periods of inactivity especially during the warmest hours (Dupoué et al., 2018). Altogether with scarcity of food resources in the most xeric localities of Tenerife (Rodríguez et al., 2008), this may constrain the allocation of energy into immune defence in detriment of self-maintenance (French and Moore, 2008; Dupoué et al., 2020).

In males, both mean and median infections were higher in localities with higher extreme temperatures of summer. In females, median infections were also higher in the hottest localities. However, mean values of infection in females were higher in localities with the lowest summer precipitation (Fig. 4c–f). Remarkably, discrepancy of the results for means and medians in females, the former influenced by extreme values of infection rates (Rózsa et al., 2000), suggests that some females in the most xeric localities pay a higher immunological toll from dehydration than others (Dupoué et al., 2020). Additive effects of heat waves and dehydration increase the oxidative damage in gravid lizards (Dupoué et al., 2020; Han et al., 2020), which may undermine their immune defences (Tobler et al., 2015; Han et al., 2020).

In most cases, water taken with food is enough to correct water balance in lizards (but see Wright et al., 2013). Therefore, if lizards can find sufficient succulent plants or fruits they can compensate it. However, (gravid) females will always be at a disadvantage at the end of the reproductive season due to water being in high demand by developing eggs (e.g., Bruschi et al., 2018). This may be a key consideration to interpret the observed patterns because most of the captured females during July were recovering after egg laying and 20% of them were still gravid. Therefore, in some of the females, immunological costs may unbalance the trade-off between allocation of lipids into fat bodies and deviation of energy to mount an anti-parasitic response (e.g., French et al., 2007). In support of this hypothesis, females exhibited parasite intensities 54% higher than males, reaching 78% of the examined erythrocytes in the most arid localities. This suggests that low precipitation and the scarcity of fleshy plants and fruits in these localities may increase the vulnerability of females to extreme summer temperatures (Wang et al., 2016). Thus, despite both sexes had similar levels of faecal glucocorticoid metabolites, females may suffer higher costs as suggested by the sex-reversed pattern of infection found, since, in general, male hosts are often found to have higher infection rates (Álvarez-Ruiz et al., 2018).

Padilla et al. (2017) reported a similar distributional pattern for the genus *Plasmodium* in Tenerife which was investigated in 12 bird species; being its highest prevalence in bird hosts occurring at xeric coastal localities. This common pattern between *Plasmodium* (birds) and *Karyolysus* (lizards) suggests that (i) coastal localities of Tenerife may gather ecological characteristics that favour transmission, and/or (ii) the hosts are more susceptible to infections in the warmest localities by causes proposed here or other.

Glucocorticoid secretion, in the mid-term, is expected to have cascading effects that increased lipid catabolism and reduced the energy

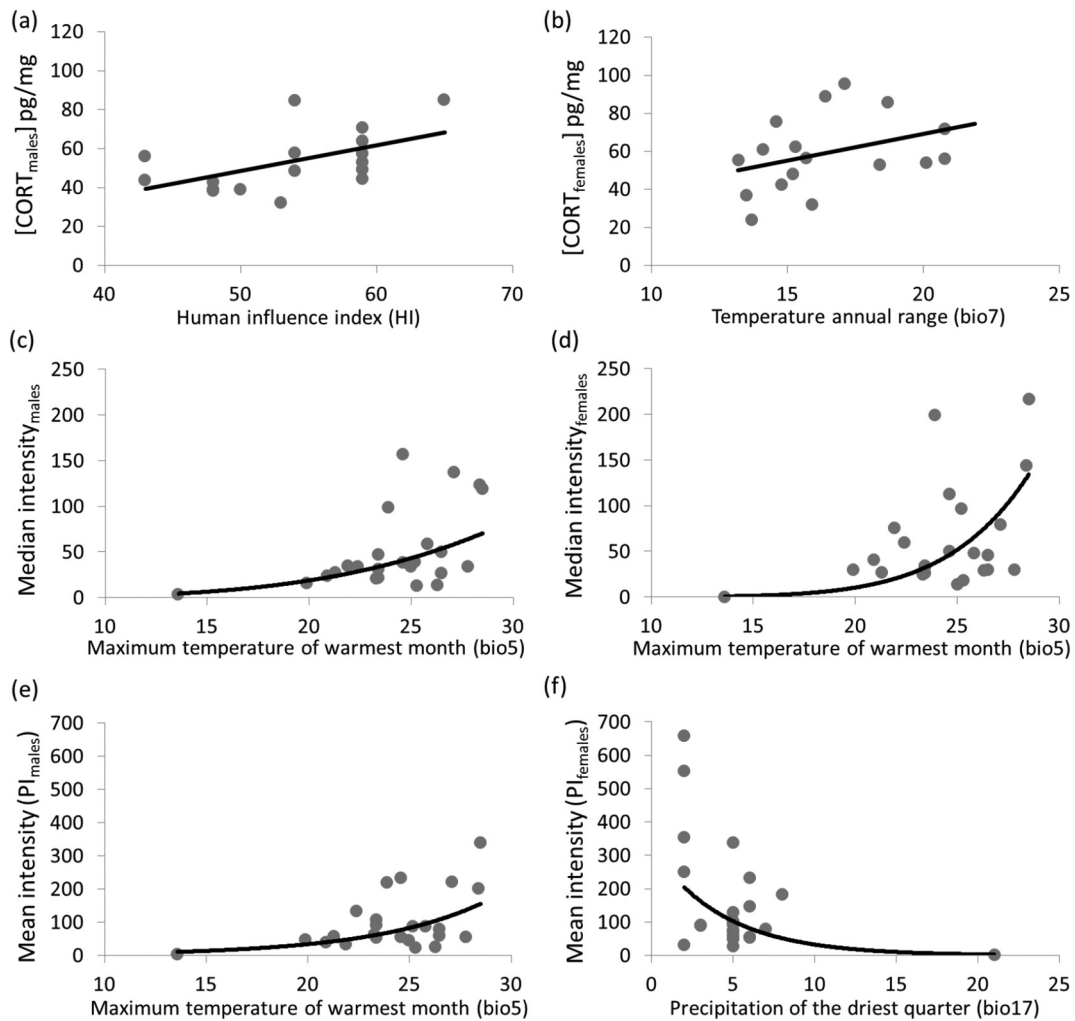


Fig. 4. Relationship between median glucocorticoid concentration and (a) human influence in males ($n = 17$), and (b) temperature annual range in females ($n = 17$). The maximum temperature of the warmest month was the best predictor for (c) the median intensity of hematic parasites in males ($n = 24$) and (d) females ($n = 24$), and (e) the mean intensity of males ($n = 24$). (f) The mean intensity of hematic parasites in female lizards was negatively correlated to precipitation of the driest quarter ($n = 24$). Note that females had more hematic parasites in localities with lower precipitation.

allocated to the immune function in lizards, especially under food-restricted environments (Raffel et al., 2006; Rollins-Smith, 2017). Therefore, if environmental constraints for lizards in Tenerife were sustained over time, a negative effect of environmental stressors on the body condition of the lizards was expected (Dunlap, 1995; Romero and Wikelski, 2001). As opposed to this, (i) a not significant relationship between faecal corticosterone concentration and body condition at the individual level, and (ii) a decoupled relationship between the secretion of corticosterone, the body condition, and the parasitaemia were found; all of them showing independent responses to different environmental stressors. Such results suggest that the relationships observed reflect acute responses to stress associated with the extreme xeric conditions of summer. Interestingly, water deprivation, in combination with heat waves, has been associated with reduced secretion of glucocorticoids and cessation of activity in lizards, suggesting that this may happen when environmental restrictions exceed their limits of physiological response (Crowley, 1987; Ryan et al., 2016; Dupoué et al., 2018). As opposed to this, lizards in Tenerife remain active during summer and show coupled responses (corticosterone secretion and parasite intensities) with stressors of human and climatic origins. Therefore, the current environmental perturbations may still fall within the physiological limits of response to stress of *G. galloti*. However, climatic trends in the last decades showed a sustained increase of temperature in Tenerife (Martín et al., 2012) and projections

of human development predict an intensification of anthropogenic pressure on insular ecosystems (Chi et al., 2020).

5. Conclusions

Island ecosystems worldwide are suffering the strong impacts of climate change (e.g., Pockley, 2001; Bellard et al., 2014; Mairal et al., 2018), and given the unique biodiversity treasured by islands and the fragile nature of their ecosystems this represents a major conservation concern. However, the impact of anthropization and climate change on the health of insular endemics is still far from being understood. As part of an island phenomenon many insular species of lizards in the world evolve frugivorous habits (Olesen and Valido, 2003). This confers insular lizards a key role as seed dispersers and, hence, habitat engineers (e.g., Valido and Olesen, 2007; de Miranda, 2017). However, answering the question as to whether anthropic perturbation can provoke cascading effects in insular ecosystems by affecting the health of ecological actors and, hence, disturbing ecological networks, goes beyond the scope of this study and will require further research. By applying a cross-sectional sampling approach during summer, environmental stressors that negatively affect different physiological responses of *G. galloti* in Tenerife were identified. Importantly, the relationships indicated the impact of anthropization and the extreme climatic conditions of summer on the endemic populations of lizards in Tenerife, while ecological

differences between subspecies contributed to explain the interlocal variation in parasitization. Furthermore, given the phenological asymmetry in reproductive effort between the sexes, our results particularly emphasise the relevance of analysing environmental impacts separately per sex. The intensities of infection by hematic parasites may be a practical tool for the long-term monitoring of endemic populations of lizards aimed to anticipate the impacts of insular anthropization and climate change on the ecosystem services that lizards provide in islands.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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CRedit authorship contribution statement

Rodrigo Megía-Palma: Conceptualization, Methodology, Investigation, Formal Analysis, Validation, Writing-Original draft preparation. **Isaac Pozo:** Methodology. **Lucía Arregui:** Investigation. **Anamarija Žagar:** Investigation. **Nina Serén:** Investigation, Writing – Review Editing. **Miguel Ángel Carretero:** Conceptualization, Investigation, Supervision, Writing – Review Editing. **Santiago Merino:** Conceptualization, Resources, Project administration, Writing – Review Editing.

Data availability statement

Data will be available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.141655>.

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