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Thermoregulation strategies and microhabitat structure as determinants of susceptibility to heat waves in two sympatric Mediterranean lizards

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Abstract

Heat waves are becoming common climatic phenomena in the western Mediterranean. Ectotherms are sensitive to rapid climatic shifts owing to the intrinsic dependence of their physiology on environmental temperature and humidity. Assessing microclimatic trends in behaviour, physiology, immunology, and susceptibility to infestations in lizard species with dissimilar thermal preferences can contribute to understanding differences in susceptibility to heat waves of these ectotherms. We investigated *Acanthodactylus erythrurus* and *Psammodromus algirus*. Two active thermoregulator lizards, with the former species sustaining a warmer body temperature. We investigated their response at multiple levels in two habitat plots differing in microclimatic environments and predicted that the more thermophilic species would better tolerate heat waves. We sampled 420 lizards during most of their annual activity period in two consecutive years with heat waves. The hydric environment appeared to be a major determinant explaining behavioural, cellular, and endocrinological responses in both lizard species. Maximum relative humidity (rain events) was associated in both species with a reduction in thermoregulatory effort and total white blood cells (an important component of the immune system). Faecal glucocorticoid metabolites concentration was lower in both species upon environments of high relative humidity stochasticity. The high temperature associated with heat waves also explained some of the responses. The rise of nocturnal temperatures increased mite loads in both species and was associated with a significant decrease in total white cells only in *P. algirus*, the less thermophilic species. Moreover, the increase of maximum diurnal temperatures and thermal stochasticity explained a significant increase of ectoparasitic mites only for *P. algirus*, a species with an overall higher mite prevalence and load. The results suggested that heat waves can incur higher costs on less thermophilic lizard species in terms of a higher exposure to ectoparasites and a reduction in circulating white blood cells.

Keywords *Acanthodactylus erythrurus* · Behavioural response · Climatic stress · Faecal corticosterone · Cellular response · *Psammodromus algirus* · Thermal microhabitat impoverishment

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1 Introduction

Climate change projections predict a rapid increase in the intensity, frequency, and duration of heat waves (i.e., sustained periods of abnormally high temperatures relative to the typical conditions for that time of year that occur over several consecutive days) in the western Mediterranean (Giorgi and Lionello 2008; Pereira et al. 2021).This geographic region harbours one of the highest diversities of reptile species in the Palearctic (Pascual et al. 2011; Tarjuelo and Aragón 2023). Although the region may have undergone several climate change periods since the Pleistocene, it is a concerning situation because reptile species can be particularly vulnerable to heat waves (Dupoué et al. 2022; Lemaître et al. 2022). These climatic phenomena can periodically produce environmental temperatures that exceed the upper thresholds of lizard's heat tolerance (Zhang et al. 2023), a situation that is aggravated by drought (Dupoué et al. 2018; Sannolo and Carretero 2019; Herrando-Pérez et al. 2020).

Active thermoregulators (different from thermoconformers) can compensate warm environmental conditions by downregulating their body temperature via an effective selection of thermal microhabitats that enable cooling down their body temperatures (Díaz et al. os2022). Therefore, we expect that Mediterranean lizards respond to eventual heat waves by adjusting their thermoregulatory behaviour to preclude fatal overheating (Vickers et al. 2011; Díaz et al. 2022; Megía-Palma et al. 2022). Although a significant reduction of lizard metabolic activity and eventual dormancy periods are possible responses to heat waves in lizards (e.g., Dupoué et al. 2018), some other behavioural adjustments are also possible (e.g., a shuttling rate increase); the latter can imply some costs because the more the shuttles between thermal microhabitats to effectively thermoregulate the higher the exposure to ectoparasites (Megía-Palma et al. 2022).

Extreme temperatures pose a threat to lizard physiological performance and survival (e.g., Dupoué et al. 2018; Han et al. 2020; Lemaître et al. 2022). However, temperate lizards are plastic species with rapid physiological responses to microclimatic shifts (Megía-Palma et al. 2020; Giacometti et al. 2024). For example, they can elevate the levels of glucocorticoids (GC) in peripheral blood in response to stress stimuli, which can elicit mobilization of fat bodies and increase foraging activity (Cote et al. 2010; but see; De-Almeida-Prado et al. 2024). This physiological response can be adaptive in contexts of abundant food availability (Millspaugh and Washburn 2004; Cote et al. 2010; Racic et al. 2020). Otherwise, sources of stress such as microclimatic instability and sustained drought can have significant negative effects on the body condition of lizards (Cote et al. 2010; Schlesinger et al. 2010). This said, and although GC upregulation in the blood might be an important component of lizards' response to heat waves, this coping response may be contingent on heat waves' duration and intensity (Telemeco and Addis 2014; Dupoué et al. 2018). For example, lizards experimentally exposed for five months to a heat treatment with mean +6 °C as compared to control lizards suffered a reduction in circulating white cell counts and immunoglobulin type M expression (Han et al. 2020). It suggests that infection susceptibility can increase in lizards subjected to sustained climate warming (e.g., Megía-Palma et al. 2020; Rutschmann et al. 2021; Mediavilla et al. in press).

We analysed behavioural and physiological parameters as well as mite loads in free-ranging lizards of two species, *Acanthodactylus erythrurus* (Lacertidae: Lacertinae) and *Psammodromus algirus* (Lacertidae: Gallotinae), in two sampling plots that may offer dissimilar thermoregulation opportunities due to previously identified differences in vegetation structure (Sears et al. 2016; Megía-Palma et al. 2022). This was done across most of their annual activity period during two consecutive years with different heat waves regimes. This included 2021 and 2022, the latter year summed the longest daily series of consecutive nights over 23 °C (termed tropical night) in the Mediterranean basin since 1950 and the hottest summer on record in Europe (Ballester et al. 2023; Yavaşlı and Erlat 2024). *A. erythrurus* has a 2.9 °C higher (i.e., 46.0 vs. 43.1 ºC) average critical thermal maximum (i.e., upper body temperature at which lizards lost their righting response; *sensu* Huey and Stevenson 1979) (Herrando-Pérez et al. 2020). Moreover, the top sprinting performance occurs at 5 °C higher in *A. erythrurus* (Bauwens et al. 1995). Our hypothesis is that lizards will adjust their behaviour and physiology in response to warming and, more specifically, that *A. erythrurus* will be more heat-tolerant than *P. algirus* due to their physiological differences. The main objective of the study was to investigate whether these responses are species-specific and how they relate to the microclimatic environment.

2 Material and methods

2.1 Model species

We investigated two mid-sized lizard species of the family Lacertidae: *P. algirus* and *A. erythrurus.* The mean ± SE adult snout-vent length of *P. algirus* in the sample was 70.44 ± 0.31 mm (range = 58–80 mm; *n* = 282) and for *A. erythrurus* it was 71.73 ± 0.46 mm (range = 58–86 mm; *n* = 138). The first species has a Mediterranean origin in the Iberian Peninsula and is considered a habitat generalist across its distribution range in this area, Mediterranean France, and northern Africa (Carrascal et al. 1989; Carranza et al. 2006; Llanos-Garrido et al. 2021). On the contrary, *A. erythrurus* is the only representant of the tribe Eremiadini in Iberia because the genus has an African origin (Tamar et al. 2016). This species is distributed in the Mediterranean region of the Iberian Peninsula where it shows preference for open habitats, with disperse vegetation soft reliefs, and loose soils (Belliure 2015).

2.2 Field sampling

We captured lizards using a *lasso* in a heterogeneous matrix of evergreen forest dominated by holm-oak trees (*Quercus ilex*) and gum rockrose bushes (*Cistus ladanifer*) in the centre of the Iberian Peninsula (Madrid, Spain; 40.50°N, 3.76°W; ~ 680 m above sea level). This forest has a sandy substrate that resulted from the erosion of granite rock. Fieldwork was performed in 2021 and 2022 and covered most of the period in which lizards are active annually, namely from April to September. We followed our previous sampling design and captured lizards in two habitat plots that differ in their distance to a road with moderate traffic flow (9,054 vehicles/day) (Barrientos and Megía-Palma 2021). One of the sampling plots, placed at the bottom of a valley, was an area of 6.6 ha ranging in distance between 0 and 150 m from the mentioned road. Thus, this sampling plot has a lower cover of ground level vegetation, gramineous plants, and bushes (Megía-Palma et al. 2022) (hereafter, plot with worse vegetation structure —WVS). The second area (hereafter, plot with better vegetation structure —BVS), placed on the surrounding hills of the same side of the road, was 7.9 ha and ranged between 350 and 550 m from it (Barrientos and Megía-Palma 2021). This design left a 200-m band between both sampling plots. We note that the size of the smallest of our sampling plots exceeded by approximately 75 times the maximum home range of 0.09 ha described for *P. algirus* (Díaz, 1993). We only sampled adult lizards and for 2–3 days in the second week of each month from 10:00 am to 17:00 pm, employing a constant sampling effort of two experienced researchers. We marked the lizards with xylene-free white paint to avoid recapturing them during the same month. We estimated 5% of recaptures between consecutive months as the white paint lasts for several weeks (Megía-Palma et al. 2022).

2.3 Microclimate

Data on temperature (ºC) and relative humidity (%) were obtained on one hour-basis with data-loggers (ibutton model: DS1923 Hygrochron) that were deployed on the ground, four in each of the two sampling plots (eight in total), from April to September in 2021 and 2022. We recovered all the dataloggers initially deployed, downloaded and assigned the microclimatic data to the lizards attending to their month of capture and sampling plot. Using the recordings of the data loggers, we calculated 30 microclimatic variables (Table S7) and summarized them using a principal component analysis after varimax factor rotation. We considered those factors with eigenvalue > 1. We performed full factorial ANOVAs testing the three-way interaction between year, month, and sampling plot on the microclimatic PCs as well as their principal effects, and every combination of two-way interactions between them.

2.4 Lizard capturability, thermoregulatory behaviour, and exposure to ectoparasites

We calculated an index of lizard capturability (as a proxy of field lizard activity) for each capture day, namely the number of lizards captured per minute a first approach in this population to estimate the resilience of the lizards during heatwaves. Within the first 1–2 seconds after we captured a lizard, and avoiding handling it, we measured the body temperature (T_b). We also measured air temperature 1 m above the ground at the point of capture (T_air). Despite the caveats described against infrared thermometer for thermal studies with lizards (Carretero 2012), we used an instant touchless one (0.1 °C precision in ~0.5 s; ThermoFlash®, LX-26 Evolution, NEXMED Technology Co. Ltd., NY, USA) following its previous validation Megía-Palma et al. (2022). Active thermoregulators may exert more effort to maintain their body temperature within their preferred temperature as the difference between air and ground temperatures decreases (e.g., Besson and Cree 2010; Megía-Palma et al. 2022). We calculated an index of thermoregulatory effort (TE) as $|M_{ST} - T_b| / |M_{ST} - T_{air}|$. We used for this index the temperatures of the ground and air temperature registered at the exact location of each lizard as a proxy of thermal microhabitats occupied by the lizards in the field. M_{ST} in this formula is the median of the temperatures selected by the species in an artificial thermal gradient (i.e., an environment independent of the ecological costs and constraints that can influence temperature regulation in the field) (Hertz et al. 1993). We used from the literature 37.15 °C as M_{ST} for *A. erythrurus* and 35.40 °C for *P. algirus* (Bauwens et al. 1995). The use of absolute values in the formula avoids the issue of mixing positive and negative relationships by considering the absolute deviation from M_{ST}. Thus, in this thermal index, the closer to zero the higher the TE of the lizard. We quantified the ectoparasites (mites) on the lizards using a magnifying glass (10×) in the field as a proxy of their exposure to ectoparasites (Barrientos and Megía-Palma 2021).

2.5 Body condition

We used a transparent ruler (accuracy = 1 mm) to measure the body length of the lizards from the tip of the snout to the cloaca (hereafter, SVL) and the tail length from the cloaca to the tip of the tail. We used a digital scale (accuracy = 0.02 g) to weigh the lizards. We calculated a body condition index as the residuals of the regression of $\log_{10}$-transformed scores of body mass on the $\log_{10}$-transformed scores of body length and we included tail length as covariate (Barrientos and Megía-Palma 2021). This was calculated separately per species and sex because the annual cycle of fat body depletion differs between sexes in lacertids (Carretero 2006), and to control the possibly confounding phylogenetic effects. Lizards were released on the point of capture immediately after collecting the data which was accomplished within 5 min.

2.6 Leukocyte profiles

We collected a blood sample (~2 µl) from the ventral area of the tail of the lizards using sterile needles (25 G, BD Microlance) within 1–2 minutes after capture (Megía-Palma et al. 2022). A rapid blood acquisition may favour obtaining haematic basal parameters (Davis et al. 2008). We smeared the blood samples on microscope slides that were air-dried and fixed with methanol. Smears were stained using Diff-Quick (*Panóptico rápido*, Casa Álvarez, Madrid, Spain), a stain that allows the chromatic discrimination of white blood cell lines (Megía-Palma et al. 2023). A single researcher (SBC) used a light optic microscope (BA410, Motic, Kowloon, Hong Kong) to differentially count white blood cells in 50 microscope fields at × 1,000 magnification and with a homogeneous distribution of erythrocytes. We discriminated heterophils, eosinophils, basophils, lymphocytes, monocytes, and azurophils. We also calculated a ratio between heterophils and lymphocytes (H:L ratio) as a measure of cellular stress because circulating heterophils increase in peripheral blood in proportion to lymphocytes that enter internal organs following stress challenges (Woodley and Moore 2002; Davis et al. 2008; Han et al. 2020; Megía-Palma et al. 2023). Since we aimed to have an offset term (i.e., a measure of sampling effort in the blood smears) in the models of total white blood cells (TWBC) and H:L ratios, we counted the number of erythrocytes in two random microscope fields in every blood smear (mean ± standard error erythrocytes/field in *A. erythrurus* = 127.10 ± 0.88; in *P. algirus* = 130.90 ± 0.54). The offset term was calculated by multiplying the average of these erythrocyte counts by 50 as an estimate of the total number of erythrocytes counted (Megía-Palma et al. 2023).

2.7 Concentration of faecal glucocorticoid metabolites (FGM)

Blood GC quantification requires sampling a considerable blood volume that can be harmful for small ectotherms that have a smaller volume of total blood than endotherms (Yokota et al. 1985). A less invasive alternative for lizards is the quantification of GC metabolites in faecal samples (Annaïs et al. 2024). Therefore, we gently massaged the belly of the lizards to obtain the faecal samples (Megía-Palma et al., 2016), which was avoided in gravid females, or when individuals did not produce faeces after few tries. Thus, we obtained fresh faecal samples from 78.38% of the lizards. This was done in the field within a maximum of 5 minutes after capture. Faeces were directly collected in vials of 1.5 ml and deposited in a cooler with ice until they were stored at −20 °C until analysis. To extract the glucocorticoid metabolites in faeces we followed the methods described in Megía-Palma et al. (2022). The samples collected from both species were randomly distributed in the assays and the recovery of FGM was 109.4%. The between-assay and within-assay coefficients of variation were 5.2% and 7.1%, respectively. The results were expressed as nanograms per gram of dry faecal matter.

2.8 Statistical analyses

The T_b scores were not normally distributed and so we compared T_bs of the two species using a non-parametric Mann-Whitney U. We used a model averaging approach in R version 4.4.1 (R Core Team 2024) to model as response variables TE, body condition, ectoparasites, TWBC, H:L ratio, and FGM. The model for capturability index included species, year, month, sampling plot, and every two-way interaction between them. In addition, we also included the mean faecal glucocorticoid metabolites calculated per month, species, and sampling plot (FGM_{mean}), and its interaction with species upon the hypothesis that FGM may correlate with lizard activity (Megía-Palma et al. 2022). A weighing term was included in the model to account for the sample size per species, month, and sampling plot. All remaining models included as predictors species, year, sampling plot, sex, and the two-way interactions between species and the microclimatic principal components, between species and year, year and sampling plot, year and sex, sex and sampling plot, and a three-way interaction between species, year, and sampling plot. We added to the models of TWBC counts and heterophile to lymphocyte ratio (H:L) the offset term ‘number of estimated erythrocytes in 50 microscope fields’ that stands for the sampling effort performed per blood smear. Model averaging is specially recommended in evolutionary ecology to retain degrees of freedom when sample size is relatively small in relation with the number of terms tested (Hegyi and Garamszegi 2011). In addition, we used the Akaike’s information criterion corrected for small sample size (AICc) (Bedrick and Tsai 1994). We considered equally likely all the selected models with ΔAICc ≤ 2 in relation to the best model (i.e., the one with the lowest AICc) (Burnham and Anderson 2004). After model selection, we obtained a final average model using the ‘dredge’ function in the R package ‘MuMIn’ (Barton 2018). We also calculated the sum of AICc weights of all the models where each of the predictors appeared (i.e., conditional average) to calculate the relative importance of each predictor in the final average model. Using this procedure, we calculated the estimated significance ($\alpha < 0.05$) of the effects and their z-standardised *ß* coefficient ± adjusted standard error, which enables comparing their magnitude. If a two-way interaction was retained in the final model, we calculated the significance and correlation score (R^2) of the continuous predictor for each level in the interaction. When just a single model complied with the criterion of difAICc ≤ 2 (this occurred in two of the response variables), an ANCOVA based on type 3 Fisher’s test was performed on the full model to evaluate the significance of the effects. In addition, for the variation in H:L ratio, we used the dataset with the FGM data ($n = 330$) under the hypothesis that FGM and H:L ratios are expected to correlate because both can reflect recent stressors undergone by the lizards (Megía-Palma et al. 2022, 2023). We checked the residual distributions and the autocorrelation of the models based on a variance inflation factor (maximum VIF score in the six models = 3.49) using the vif() function of the 'car' package (Fox and Weisberg 2019).

3 Results

We collected data of a total of 420 adult lizards (*A. erythrurus* 2021 = 27 females, 25 males; *P. algirus* 2021 = 59 females, 75 males; *A. erythrurus* 2022 = 41 females, 45 males; *P. algirus* 2022 = 73 females, 75 males). However, as commented, we could not get faecal samples in the field from 21% of them and the sample size for the analysis of FGM was 330.

3.1 Microclimate

In 2021, heat waves took place between the 6th and 23rd of July and between the 7th and 17th of August (Dirección General de Salud Pública 2022). In 2022, they took place between the 12th and 18th of June, the 9th and 26th of July, and between the 30th of July and 15th of August (de Meteorología 2022) (Fig. 1a). A top maximum temperature of 82.29 °C and a median diurnal relative humidity of 14.83% was recorded in July 2022 in the BVS sampling plot (77.86 °C and 26.10% in July 2021) (Tables S1 and S2). Other details about the microclimatic data (e.g., nocturnal temperatures and relative humidity per month and sampling plot) can be consulted in the supplementary tables S1–S6. There were five principal components with eigenvalue > 1 that together explained 94.8% of the observed variance in the microclimatic data (for interpretation of PCs see Table S7). The microclimatic environment was significantly different in the two sampling plots. PC1 scores were higher both years in the BVS plot (Fig. 1b; Table S8). This indicates that maximum diurnal and monthly temperatures, as well as the diurnal and monthly variation (standard deviation) of temperatures were overall higher away from the road. The interaction between year and month was significant, indicating significant differences in PC1 scores between the same months in different years, but an overall temporal trend was not evident (Figure S1). PC2 had significantly higher scores in 2022, with no significant differences between sampling plots (Fig. 1b; Table S8). Therefore, in our study area, 2022 had higher diurnal, nocturnal, and monthly maximum scores of relative humidity. The interaction between year and month was significant, with evident lower PC2 scores only for August of 2021 (Figure S1). PC3 scores were significantly higher in 2022 (Table S8) and near the road (WVS). Thus, 2022 and the WVS plot had higher median and minimum monthly temperatures, minimum diurnal temperatures, and mean, median, minimum, and maximum nocturnal temperatures. The interaction between month and year was significant; relatively higher PC3 scores were recorded in April, May, June, and July of 2022 (Figure S1). PC4 significantly varied across sampling plots and years, with a lower variation (standard deviation) in monthly and diurnal humidity scores in the BVS plot in 2022 (Fig. 1). In addition, the interaction between year and month was also significant (Table S8); relatively higher humidity variation scores were registered in April, May, and June of 2021 and with a similar variation in the following months (Figure S1). The three-way interaction between year, month, and sampling plot significantly explained PC5 (Figure S2), indicating different patterns of the minimum diurnal and monthly humid-

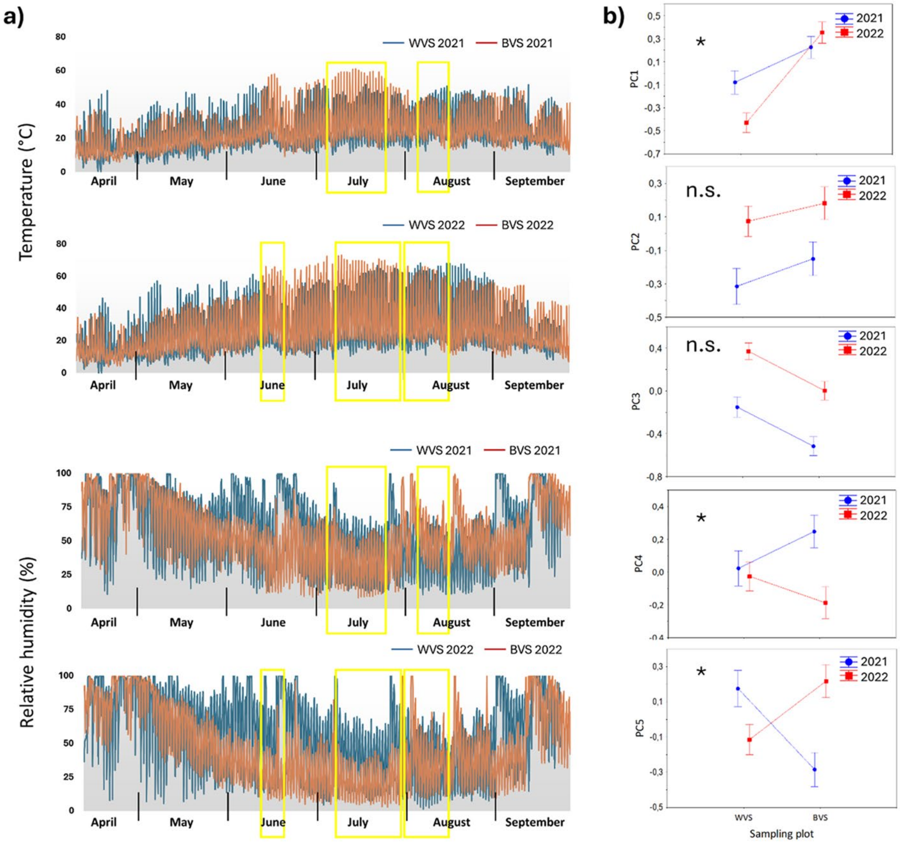

Fig. 1 (**a**) Temperature (upper plot) and relative humidity profiles of 2021 (blue) and 2022 averaged from data collected using eight dataloggers deployed in the field (WVS = worse vegetation structure; BVS = better vegetation structure; Megía-Palma et al. 2022). Yellow squares depict heat wave periods. (**b**) Effects graphs of the two-way interaction between year and sampling plot on the five microclimatic PCs showing that the two sampling plots posed contrasting microclimatic environments (for PCA interpretation see Table S7). Symbols and error bars represent the means ± standard error, respectively. Asterisks in the plots indicate significant effect of year × sampling plot ($p < 0.05$); n.S. = not significant (see Table S8)

ity scores between sampling plots across years and months. For example, differences in PC5 scores between 2021 and 2022 were relatively higher in April and May of 2022 for the BVS sampling plot than in the WVS sampling plot and periods (Figure S2).

3.2 Lizard capturability, thermoregulatory behaviour, and exposure to ectoparasites

Using activity indices based on random field observations are methodologically problematic. Thus, any conclusion derived from the analysis of the capturability index here calculated should be taken with caution. The capturability index was best fitted by a generalized linear model with a Gamma residual distribution after $\log_{10}$-transforming 2 + capturability scores. A single model complied with the assumption of AICc ≤ 2 (hence, no model averaging performed). An ANCOVA indicated that there were significant effects of the interaction between month and species, with a higher capturability score for *P. algirus* in May (Table S9; Fig. 2). Interestingly, there was a significant and negative effect of FGM_{mean}, with no significant effect of the interaction with species (Table S9). Thus, when mean faecal glucocorticoids were the highest, the capturability index was the lowest for both lizard species.

The mean ± standard error (SE) T_b of *A. erythrurus* was 37.90 ± 0.25 °C and significantly higher than T_b of *P. algirus* (34.47 ± 0.20 ºC) (Mann-Whitney $U = 7653.0$, $p < 0.001$). The TE scores were best fitted by a generalized linear model with a Gamma residual distribution and a log link function after $\log_{10}$-transforming 1 + TE scores. Fourteen models had AICc ≤ 2 (Tables S10a and b). There was an important effect of the three-way interaction between species, year, and sampling plot (Table 1). *Acanthodactylus erythrurus* performed significantly lower thermoregulatory effort (higher TE scores) in the WVS plot in 2022 as compared to *P. algirus* in the same plot and year and as compared to all lizard groups in 2021 (Table S11; Fig. 3a). There was also an important effect of the interaction between species and PC4 on lizards' TE scores. The TE behaviour of *P. algirus* was significantly lower (higher TE scores) upon high monthly and diurnal humidity stochasticity (Fig. 3b), whereas the opposite was observed for *A. erythrurus*. PC5 was an important negative predictor for TE scores in the two species. Thus, lizards increased their TE behaviour when monthly and diurnal minimum humidity scores were the highest (Figure S3).

Mite prevalence for *A. erythrurus* was 47.8% (females = 48.5%, males = 47.1%), whereas for *P. algirus* was 87.2% (females = 84.1%, males = 90.0%). Lizards' mite load was best fitted by a general (Gaussian) linear model after $\log_{10}$-tranforming 1 + mite count scores. Fifteen models had AICc ≤ 2 (Table S12). There were independent important effects of species, but not of year or sex, on mite intensity (Table 2). *Acanthodactylus erythrurus* (7.72 ± 2.14 mites) had lower mite intensities than *P. algirus* (14.94 ± 1.35 mites). PC2, PC3 and PC5 were positive predictors of mite load for both lizard species (Figure S4). Thus, mites were more abundant when humidity and temperature were higher. There were important effects of the interactions between species and PC1 and PC4 (Table 2). Upon microclimatic contexts of both higher stochasticity and maximum monthly and diurnal temperatures, mite load was significantly higher in *P. algirus* and significantly lower in *A. erythrurus* (Fig. 4a). In contrast, mite load was significantly lower in *P. algirus* upon high stochasticity of monthly and daily humidities, a microclimatic scenario that showed null trend with mite load in *A. erythrurus* (Fig. 4b).

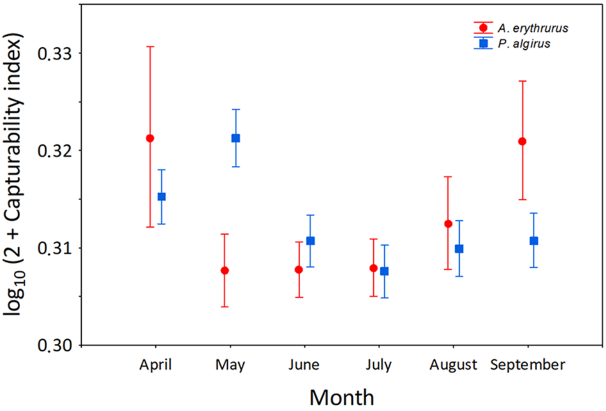

Fig. 2 Predicted means ± standard error of the capturability index (lizards captured per minute) represented per month and species

Table 1 Results of model averaging for thermoregulatory effort (TE) scores of *A. erythrurus* (AE) and *P. algirus* ($N = 420$). WVS = worse vegetation structure near a road. Adj SE = adjusted standard error. For the interpretation of PC1–PC5 see Table S7

	Importance	Estimate	Adj SE	z-value	*P*-value
(Intercept)		−0.919	0.017	55.238	<0.001
Year (2021)	**1.00**	**−0.040**	**0.019**	**2.102**	**0.036**
Sampling plot (WVS)	1.00	0.015	0.020	0.746	0.456
Year (2021) : Sampling plot (WVS)	1.00	−0.019	0.019	1.005	0.315
Species (AE)	1.00	0.030	0.017	1.795	0.073
Sex (Female)	0.62	0.018	0.015	1.194	0.233
Sex (Female) : Year (2021)	0.04	−0.006	0.015	0.409	0.683
Species (AE) : Year (2021)	1.00	−0.018	0.019	0.953	0.341
Sex (Female) : Sampling plot (WVS)	0.18	−0.013	0.015	0.916	0.360
Species (AE) : Sampling plot (WVS)	1.00	0.029	0.019	1.514	0.130
Species (AE) : Year (2021) : Sampling plot (WVS)	**1.00**	**−0.047**	**0.018**	**2.579**	**0.010**
PC1	0.56	0.014	0.021	0.669	0.504
PC1 : Species (AE)	0.09	−0.021	0.024	0.893	0.372
PC2	**1.00**	**0.032**	**0.016**	**1.990**	**0.047**
PC2 : Species (AE)	0.00	0.005	0.018	0.252	0.801
PC3	0.00	0.001	0.018	0.069	0.945
PC3 : Species (AE)	0.00	0.012	0.021	0.567	0.571
PC4	1.00	0.005	0.019	0.273	0.785
PC4 : Species (AE)	**1.00**	**−0.089**	**0.019**	**4.726**	**<0.001**
PC5	**1.00**	**−0.035**	**0.017**	**2.017**	**0.044**
PC5 : Species (AE)	0.30	0.014	0.019	0.698	0.485

3.3 Body condition

Body condition was best fitted by a general (Gaussian) linear model. Twenty-nine models had AICc ≤ 2 (Table S13). There were important effects of the year and the two-way interaction between sex and sampling plot (Table 3). Thus, both species of lizards had higher body condition scores in 2021, and females had better body condition in the WVS plot than in the BVS plot (Table S14).

3.4 Leukocyte profiles

Lymphocytes were the most abundant white blood cell, followed by azurophils in *P. algirus* and heterophils in *A. erythrurus* (more details on cell counts per species in Table S15). TWBC was best fitted by a generalized linear model with a negative binomial residual distribution and a log link function. A single model complied with the assumption of AICc ≤ 2 (hence, no model averaging performed). There were significant effects of the year and the interaction between species and year (Table S16); *A. erythrurus* had lower TWBC than *P. algirus* in 2022 (mean ± standard error for *A. erythrurus* = 75.30 ± 6.10, $n = 86$; mean ± standard error for *P. algirus* = 86.43 ± 4.93, $n = 148$), whereas TWBC were similarly higher in both species in 2021 (*A. erythrurus* = 95.73 ± 6.85, $n = 52$; *P. algirus* = 95.31 ± 5.29, $n = 134$). The principal effects of PC1 on TWBC was significantly positive (Table S16); TWBC increased in both species upon microclimatic contexts of high temperature stochasticity and maximum monthly and diurnal temperatures (Figure S5a). The principal effects of PC2 and

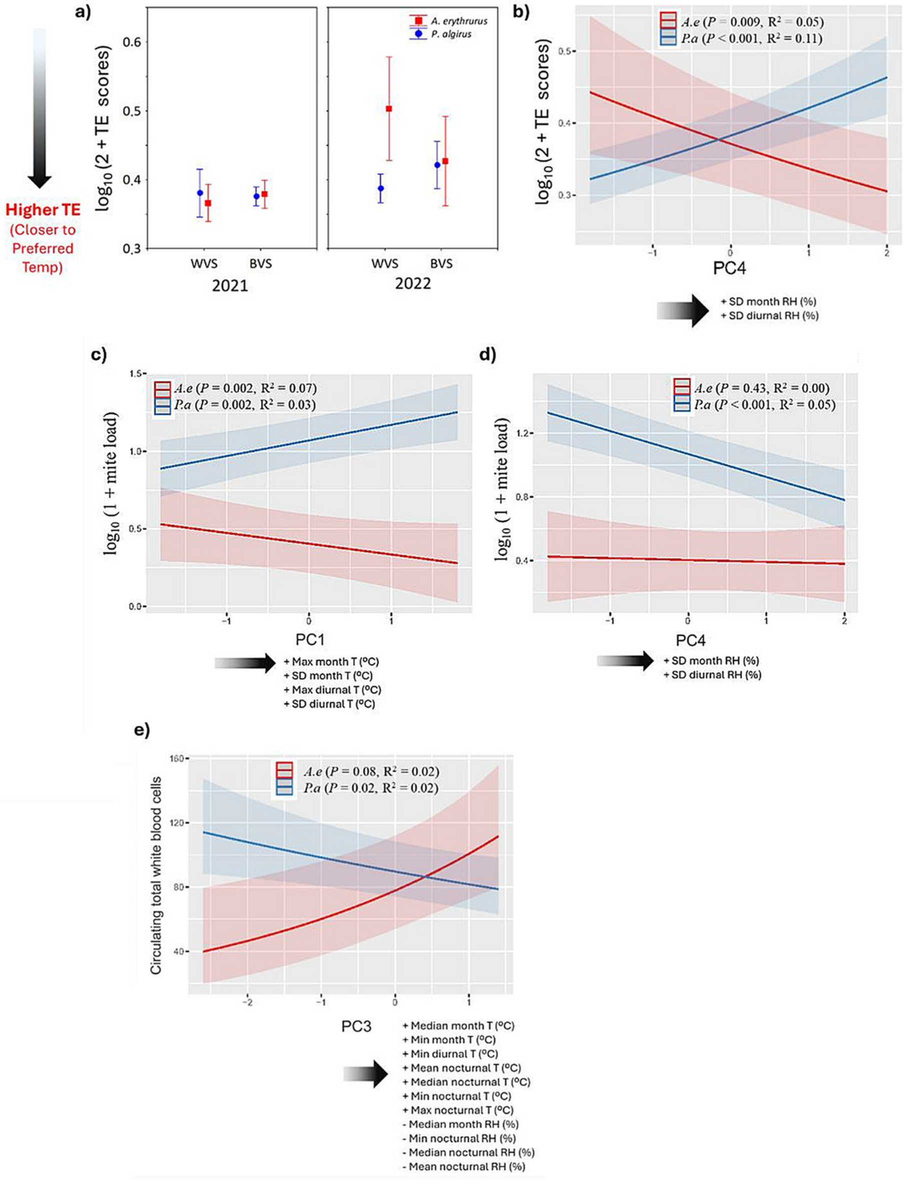

Fig. 3 (**a**) Three-way interaction plot showing the mean ± standard error of the lizards' TE scores across levels of sampling plot and year. See Bonferroni's post-hoc test in Table S11 for interpretation of pairwise significant differences. (**b**) Relationship between thermoregulatory effort (TE) scores and PC4 in *A. erythrurus* (*A.E*) and *P. algirus* (*P.A*). (**c** and **d**) Relationships between the log-transformed mite load and PC1 and PC4 in *A. erythrurus* (*A.E*) and *P. algirus* (*P.A*). (**e**) Relationship between total blood cell counts (TWBC) and PC3 in *A. erythrurus* (*A.E*) and *P. algirus* (*P.A*). Shaded areas represent the standard deviation

Table 2 Results of model averaging for mite load of *A. erythrurus* (AE) and *P. algirus* ($N=420$). WVS = worse vegetation structure near a road. Adj SE = adjusted standard error. For the interpretation of PC1–PC5 see Table S7

	Importance	Estimate	Adj SE	z-value	*P*-value
(Intercept)		0.655	0.027	24.510	<0.001
Year (2021)	0.63	0.025	0.032	0.779	0.436
Sampling plot (WVS)	1.00	0.085	0.046	1.834	0.067
Year (2021) : Sampling plot (WVS)	0.24	−0.034	0.027	1.258	0.208
Species (AE)	**1.00**	**−0.275**	**0.027**	**10.312**	**<0.001**
Sex (Female)	0.00	0.003	0.024	0.126	0.900
Sex (Female) : Year (2021)	0.00	0.019	0.024	0.775	0.438
Species (AE) : Year (2021)	0.29	−0.042	0.033	1.282	0.200
Sex (Female) : Sampling plot (WVS)	0.00	0.015	0.024	0.641	0.521
Species (AE) : Sampling plot (WVS)	0.10	0.055	0.053	1.033	0.302
Species (AE) : Year (2021) : Sampling plot (WVS)	0.00	0.001	0.033	0.026	0.979
PC1	1.00	0.022	0.039	0.562	0.574
PC1 : Species (AE)	**1.00**	**−0.085**	**0.032**	**2.636**	**0.008**
PC2	**1.00**	**0.136**	**0.026**	**5.213**	**<0.001**
PC2 : Species (AE)	0.05	−0.015	0.029	0.509	0.611
PC3	**1.00**	**0.119**	**0.037**	**3.232**	**0.001**
PC3 : Species (AE)	0.37	−0.053	0.037	1.415	0.157
PC4	**1.00**	**−0.086**	**0.029**	**2.929**	**0.003**
PC4 : Species (AE)	**1.00**	**0.062**	**0.028**	**2.204**	**0.028**
PC5	**1.00**	**0.053**	**0.026**	**2.022**	**0.043**
PC5 : Species (AE)	0.16	0.023	0.027	0.822	0.411

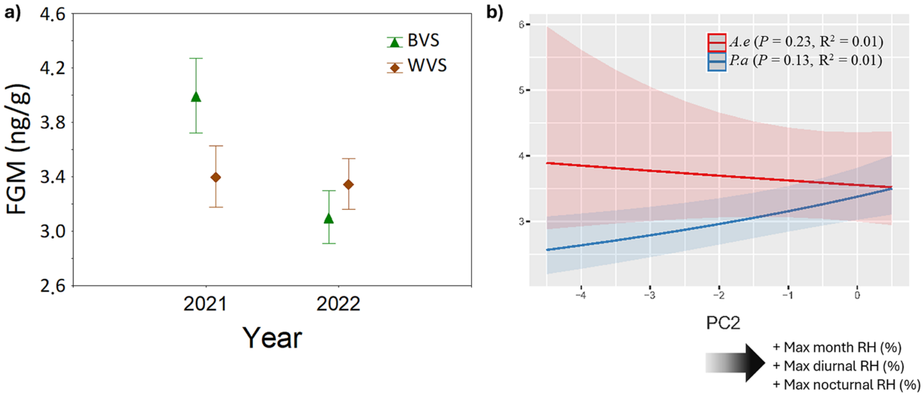

Fig. 4 (**a**) Interaction plot showing the variation in the faecal glucocorticoid concentration (FGM) of the lizards in the two sampling plots (WVS = worse vegetation structure; BVS = better vegetation structure). The plot depicts the mean ± SE. A bonferroni post-hoc test indicated significant differences only for BVS in 2021 (Table S19). (**b**) Relationship between FGM and PC2 in *A. erythrurus* (*A.E*) and *P. algirus* (*P.A*). Shaded areas represent the standard deviation

Table 3 Results of model averaging for the body condition of *A. erythrurus* (AE) and *P. algirus* (N=420). WVS = worse vegetation structure near a road. Adj SE = adjusted standard error. For the interpretation of PC1–PC5 see Table S7

	Importance	Estimate	Adj SE	z-value	*P*-value
(Intercept)		0.000	0.002	0.172	0.864
Year (2021)	**1.00**	**0.005**	**0.002**	**2.298**	**0.022**
Sampling plot (WVS)	1.00	0.003	0.003	1.186	0.235
Year (2021) : Sampling plot (WVS)	0.09	−0.002	0.002	0.887	0.375
Species (AE)	0.80	0.000	0.002	0.081	0.935
Sex (Female)	0.50	0.000	0.002	0.001	0.999
Sex (Female) : Year (2021)	0.03	−0.001	0.002	0.804	0.422
Species (AE) : Year (2021)	0.71	−0.003	0.002	1.62	0.105
Sex (Female) : Sampling plot (WVS)	**0.50**	**0.004**	**0.002**	**1.99**	**0.047**
Species (AE) : Sampling plot (WVS)	0.80	−0.005	0.003	1.722	0.085
Species (AE) : Year (2021) : Sampling plot (WVS)	0.00	−0.002	0.002	0.946	0.344
PC1	0.41	0.000	0.003	0.017	0.987
PC1 : Species (AE)	0.38	−0.004	0.003	1.544	0.123
PC2	0.00	0.001	0.002	0.319	0.750
PC2 : Species (AE)	0.00	0.003	0.002	1.371	0.170
PC3	0.28	−0.003	0.002	1.221	0.222
PC3 : Species (AE)	0.00	−0.002	0.003	0.779	0.436
PC4	0.36	−0.002	0.002	0.957	0.339
PC4 : Species (AE)	0.09	0.002	0.002	0.982	0.326
PC5	0.00	0.001	0.002	0.511	0.610
PC5 : Species (AE)	0.00	0.001	0.002	0.625	0.532

PC5 were significantly negative (Figure S5b and S5c); TWBC decreased in both species upon microclimatic contexts of maximum relative humidity, likely during long precipitation events. The effect of the two-way interactions between species and PC3 was significant (Table S16). The observed decrease of circulating TWBC in response to the general increase in temperatures and reduction of relative humidity (see Table S7 for details) was significant for *P. algirus* (Fig. 3e), although with a rather low correlation coefficient (R^2 = 0.02).

The heterophil to lymphocyte ratio (H:L) was best fitted by a generalized linear model with Gamma residual distribution and a log link function after $\log_{10}$-transforming 2 + H:L scores. A single model complied with the assumption of AICc ≤ 2 (hence, no model averaging performed). Thus, the analysis of the covariance (ANCOVA) performed on the full model indicated a significant effect of sex; the H:L ratio was significantly higher in females (0.141 ± 0.012 H:L; males = 0.098 ± 0.008 H:L) (Table S17). The relationship between FGM and H:L ratio was not significant (Figure S6).

3.5 Concentration of faecal glucocorticoid metabolites (FGM)

In total we analysed FGM of 60 females (27.67 ± 8.83 ng/g) and 52 males (21.98 ± 5.19 ng/g) of *A. erythrurus*, and 93 females (27.92 ± 8.15 ng/g) and 125 males (30.95 ± 8.25 ng/g) of *P. algirus*. FGM scores were best fitted by a generalized linear model with Gamma residual distribution and an inverse link function after we $\log_{10}$-transformed them. Thirty-two models had AICc ≤ 2 (Table S18). There were important effects of the year and the interaction between sampling plot and year (Table 4); the lizards in 2021 had significantly

Table 4 Results of model averaging for faecal glucocorticoid metabolites (FGM) of *A. erythrurus* (AE) and *P. algirus* (n = 330). WVS = worse vegetation structure near a road. Adj SE = adjusted standard error. For the interpretation of PC1–PC5 see Table S7

	Importance	Estimate	Adj SE	z-value	*P*-value
(Intercept)		0.293	0.005	59.022	< 0.001
Year (2021)	**1.00**	**−0.021**	**0.007**	**3.081**	**0.002**
Sampling plot (WVS)	1.00	0.013	0.009	1.383	0.167
Year (2021) : Sampling plot (WVS)	**1.00**	**0.016**	**0.006**	**2.643**	**0.008**
Species	0.68	−0.004	0.005	0.822	0.411
Sex (Female)	0.18	−0.002	0.005	0.497	0.619
Sex (Female) : Year (2021)	0.16	−0.008	0.005	1.621	0.105
Species (AE) : Year (2021)	0.04	0.004	0.006	0.599	0.549
Sex (Female) : Sampling plot (WVS)	0.00	−0.001	0.005	0.119	0.906
Species (AE) : Sampling plot (WVS)	0.27	−0.007	0.006	1.243	0.214
Species (AE) : Year (2021) : Sampling plot (WVS)	0.00	−0.002	0.005	0.465	0.642
PC1	0.72	0.014	0.008	1.650	0.099
PC1 : Species (AE)	0.02	−0.002	0.007	0.239	0.811
PC2	1.00	−0.010	0.006	1.502	0.133
PC2 : Species (AE)	**0.61**	**0.011**	**0.006**	**1.995**	**0.046**
PC3	0.29	−0.007	0.006	1.080	0.280
PC3 : Species (AE)	0.00	−0.002	0.006	0.290	0.772
PC4	**1.00**	**0.018**	**0.006**	**2.868**	**0.004**
PC4 : Species (AE)	0.00	−0.003	0.006	0.488	0.626
PC5	0.36	−0.007	0.006	1.238	0.216
PC5 : Species (AE)	0.00	−0.003	0.005	0.688	0.491

higher mean ± standard error FGM scores in the BVS plot as compared to any other combination of sampling plot and year (Table S19 and Fig. 3c). Moreover, they generally had higher mean ± standard error FGM scores in 2021 (31.05 ± 6.44 ng/g, n_{2021} = 143) than in 2022 (25.82 ± 5.70 ng/g, n_{2022} = 187). PC4 had a positive effect on FGM of both species (no effect of the interaction between PC4 and species). Thus, FGM was higher in both lizard species upon microclimatic contexts of high monthly and diurnal stochasticity in humidity

(Figure S7). There was also an important effect of the interaction between species and PC2 (Table S18); however, the partial correlations between FGM and PC2 were not significant for any of the species (Fig. 3d).

4 Discussion

The two sampling plots investigated underwent significantly different microclimatic environments during the lizards' activity periods of 2021 and 2022. However, this was not mirrored in significant differences of capturability index (a proxy for lizards' activity) because monthly variation accounted for most of its variance; a general reduction of capturability for both species was observed during the summer, the warmest period. Interestingly, $\mathrm{FGM}_{\mathrm{mean}}$ negatively correlated with the capturability index. This suggests that sustained high metabolic activity (i.e., high FGM) is costly for these populations of lizards and is followed by rest periods. Faecal glucocorticoid metabolites were lower in the warmer year. Taken together with the negative relationship between $\mathrm{FGM}_{\mathrm{mean}}$ and the capturability index, this lower FGM suggests that lizards' activity was higher in the warmer year, likely associated with a more intense thermoregulation activity (Megía-Palma et al. 2022). In this sense, our results supported that the active thermoregulatory behaviour of *A. erythrurus* and *P. algirus* compensated the significant differences found in the microclimatic environments experienced near and away from the road. This might be facilitated by the seasonal shift in thermal preferences of the lizards (Díaz et al. 2006; Giacometti et al. 2024), a phenomenon not considered by our thermoregulation index and that we acknowledge as a limitation. Nonetheless, our results suggest that the variation in lizards' thermoregulatory effort correlated with microclimatic oscillations in stochasticity and maximum scores of relative humidity. The latter positively correlated with an increase in thermoregulatory effort in both lizard species that, in line with previous studies on this system, implies costs in terms of increased exposure to haematophagous mites (Megía-Palma et al. 2022). In support of our results, a recent study shows that *P. algirus* significantly increased thermoregulatory effectiveness during heat waves of May 2022 (Díaz and Llanos-Garrido 2025). We interpret that such behaviour implies more shuttling and a higher exposure to mites because mite load increases in *P. algirus* in correlation with the distance travelled (Barrientos and Megía-Palma, 2021). Mite load was higher in *P. algirus*, but lower in *A. erythrurus*, upon microclimatic contexts of both higher stochasticity and maximum monthly and diurnal temperatures. It was also lower in *P. algirus* upon high stochasticity in monthly and daily relative humidity. This translates in higher mite loads in June and July, and a significant decrease in August, when substrate dryness is high (Megía-Palma et al. 2025). These species-specific differences in microclimatic trends of mite loads suggest a differential effect of temperature and humidity on the host-parasite encounter rates. The trend observed for *P. algirus* conforms to a higher exposure to hematophagous mites as the thermoregulatory activity of this species increases to compensate thermally restrictive environments of high thermal stochasticity and temperature. Interestingly, the opposite pattern observed in *A. erythrurus* suggests that this species reduces its travelled distance upon the same microclimatic conditions. To explain such opposed patterns, we evoke species differences in thermal strategies with a higher thermal preference in *A. erythrurus* (3.43 °C higher mean T_b) as well as its preferential selection for drier microhabitats (expected lower mite abundance) where this species performs few and short displacements (Belliure et al. 1996). This is expected to reduce mite-lizard encounters (Barrientos and Megía-Palma 2021). In addition, the spatial distribution, and the microhabitat selection of the two lizard species may also contribute to explain the higher mite prevalence and infestation intensity of *P. algirus*. This species was more abundantly found in humid microhabitats of the forest matrix with leaf litter where mites may also be abundant (Wu et al. 2019; BeVier et al. 2022). However, although *A. erythrurus* was also found in the forest matrix, it was more abundant in the sandier and drier forest clearings with high solar radiation (authors, pers. obs.) where mites may be less abundant due to the lower soil humidity. Thus, the microhabitat preference of *A. erythrurus* and the short displacements performed by this species (Belliure et al. 1996) could favour lower mite-lizard encounter rates than in *P. algirus*. Both species similarly increased their mite load as the environmental humidity and temperature rose, which can simply mirror a seasonal increase of mite abundances in the environment (Klukowski 2004; Megía-Palma et al. 2025).

The lizards body condition was unaffected by microclimatic oscillations, with females of both species showing higher body condition in the plot with worse vegetation structure. This contradicts previous studies of a negative effect of degraded habitats on the body condition of females of *P. algirus* (Amo et al. 2007). The similar activity patterns and observed abundance of lizards in the two plots suggests that despite the differences in vegetation structure, food items may be sufficiently available in both plots. We can only speculate that the higher body condition near the road might be explained by a higher detectability of arthropods in an open and degraded habitat.

Psammodromus algirus had low circulating TWBC upon increasing temperatures and low humidity, whereas *A. erythrurus* had the lowest TWBC scores in the hottest and driest year despite the consistency of its higher field body temperatures, suggesting that heat waves can hamper in similar fashion the immunocompetence of these two lizard species (Han et al. 2020).

Heterophiles to lymphocytes ratios were not significantly correlated with FGM scores, indicating a discrepancy between these two widely used biomarkers of physiological stress. Nonetheless, FGM does not necessarily reflect physiological stress, but rather the metabolic activity of the lizards during the previous days (MacDougall-Shackleton et al. 2019; Megía-Palma et al. 2022). The heterophiles to lymphocytes ratio is indeed widely accepted as a cellular index of physiological stress (Davis et al. 2008). In our study, it was higher in females of both species, suggesting that they were consistently subjected to higher physiological stress than males across months, years, and sampling plots. This result conforms to a higher responsiveness of females to stress stimuli (Langkilde and Shine, 2006; Dupoué et al. 2020; Megía-Palma et al. 2020). However, the analyses were unable to discriminate environmental from intrinsic effects. Interestingly, the fact that females consistently showed higher H:L ratios and higher body condition conforms to a sustained status of stress (Kyrou et al. 2006; Patterson and Abizaid 2013) that will require further investigation.

The higher FGM scores found closer to the road in 2021 might reflect a lower activity of the lizards in the significantly colder environment of this sampling plot and year. Either a partial inactivation of the lizards during the activity period, and/or a low availability of potential prey (i.e., active arthropods) due to a colder microclimatic environment, may increase the activation of the hypothalamus-pituitary axis that enables the mobilization of fat reserves to keep energetic demands of vital organs during periods of putative low prey item availability (Cote et al. 2010). In support of this interpretation, we found a nearly significant effect of the two-way interaction between year and sampling plot on capturability index that mirrors this pattern (Table S9).

5 Conclusions

The reaction norms in response to microclimatic oscillations differed in five out of the 30 species-by-microclimate interaction tests performed. These interactions partially explained the observed variance at behavioural (thermoregulatory effort), endocrinological (FGM), cellular levels (TWBC), and associated costs (mite load). In nine of these tests, the principal effect of the microclimatic components explained the observed variation in the response, while the species-by-microclimate interaction failed to do so, supporting a similar response for both species. The hydric environment appeared to be a major determinant explaining behavioural, cellular, and endocrinological responses in both lizard species. However, the high temperature associated with heat waves also explained some of the responses. The fact that lizards remained active during events of extreme heat as well as the observed microclimatic trends in behavioural, physiological, and cellular responses suggest that physiological upper threshold of heat tolerance of *A. erythrurus* and *P. algirus* falls well within the thermal/hydric proximal environment posed by heat waves with some behavioural and/or physiological signs of acclimation in this anthropized environment. Nonetheless, heat waves may incur higher costs on less thermophilic lizard species in terms of a higher exposure to ectoparasites and a reduction in circulating white blood cells.

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Author contributions Conceptualization: RMP; Methodology: RMP, IB, SBC; Data acquisition: all authors; Formal analysis and investigation: SBC, RMP; Writing - original draft preparation: SBC, RMP; Writing - review and editing: all authors; Funding acquisition for hormonal analysis: IB; Resources: IB, RB, RMP; Supervision: RMP.

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Data availability All data generated are available—upon acceptance of the manuscript—at Mendeley Data Repository (Reserved DOI: http://10.17632/zf95hn5rw4.1).

Declarations

Conflict of interest The authors declare no conflict of interest.

References

Amo L, Lopez P, Martín J (2007) Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammodromus algirus* lizards. Can J Zool 85:743–751

Annaïs C, Paula SC, Sergi OM, Manel LB (2024) Non-invasive measurement of glucocorticoids: the reptile perspective. J Zool 323:87–96

Ballester J, Quijal-Zamorano M, Méndez Turrubiates RF, Pegenaute F, Herrmann FR, Robine JM, Basagaña X, Tonne C, Antó JM, Achebak H (2023) Heat-related mortality in Europe during the summer of 2022. Nat Med 29:1857–1866

Barrientos R, Megía-Palma R (2021) Associated costs of mitigation-driven translocation in small lizards. Amphibia-Reptilia 42:275–282

Barton K (2018) MuMIn: multi-model inference. R package version 1.40.4. https://CRAN.R-project.org/package=MuMIn

Bauwens D, Garland T, Castilla AM, Van Damme R (1995) Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. Evolution 49:848–863

Bedrick EJ, Tsai CL (1994) Model selection for multivariate regression in small samples. Biometrics 50:226–231

Belliure J (2015) Lagartija colirroja *Acanthodactylus erythrurus*. In: Carrascal LM, Salvador AEDS,. *Enciclopedia Virtual de los Vertebrados Españoles*. Museo Nacional de Ciencias Naturales. Madrid. http://www.vertebradosibericos.org. Last accessed:April 2025

Belliure J, Carrascal LM, Diaz JA (1996) Covariation of thermal biology and foraging mode in two Mediterranean lacertid lizards. Ecology 77:1163–1173

Besson AA, Cree A (2010) A cold-adapted reptile becomes a more effective thermoregulator in a thermally challenging environment. Oecologia 163:571–581

BeVier GT, Ayton C, Brock KM (2022) It ain't easy being orange: lizard colour morphs occupying highly vegetated microhabitats suffer greater ectoparasitism. Amphibia-Reptilia 43:287–297

Burnham KP, Anderson DR (2004) Multimodel inference, understanding AIC and BIC in model selection. Sociol Met Res 33:261–304

Carranza S, Harris DJ, Arnold EN, Batista V, González De La Vega JP (2006) Phylogeography of the lacertid lizard, *Psammodromus algirus*, in Iberia and across the Strait of Gibraltar. J Biogeogr 33:1279–1288

Carrascal LM, Diaz JA, Cano C (1989) Habitat selection in Iberian *Psammodromus* species along a Mediterranean successional gradient. Amphibia-Reptilia 10:231–242

Carretero MA (2006) Reproductive cycles in Mediterranean lacertids: plasticity and constraints. In: Corti C, Cascio PLO, Biaggini M (eds) Mainland and insular lizards. A Mediterranean perspective. Firenze University Press, Florence, pp 33–54

Carretero MA (2012) Measuring body temperatures in small lacertids: infrared vs. contact thermometers. Basic Appl Herpetol 26:99–105

Cote J, Clobert J, Poloni LM, Haussy C, Meylan S (2010) Food deprivation modifies corticosterone-dependent behavioural shifts in the common lizard. Gen Comp Endocrinol 166:142–151

Davis AK, Maney DL, Maerz JC (2008) The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. Funct Ecol 22:760–772

de Meteorología AE (2022) Resumen estacional climatológico. Área de Climatología y Aplicaciones Operativas. http://hdl.handle.net/20.500.11765/13966. Last accessed:March 2025

De-Almeida-Prado DM, de Figueiredo AC, Lima AS, Gomes FR, Madelaire CB (2024) Corticosterone treatment results in fat deposition and body mass maintenance without effects on feeding behaviour or immunity in female lizards (*tropidurus catalanensis*). Comp Bioc Phy Part Mol Int Phy 297:111712

Díaz JA, Iraeta P, Monasterio C (2006) Seasonality provokes a shift of thermal preferences in a temperate lizard, but altitude does not. J Therm Biol 31:237–242

Díaz JA, Izquierdo-Santiago R, Llanos-Garrido A (2022) Lizard thermoregulation revisited after two decades of global warming. Funct Ecol 36:3022–3035

Díaz JA, Llanos-Garrido A (2025) When spring becomes summer: global warming modifies seasonal patterns of thermoregulatory behaviour in a heliothermic lizard. J Therm Biol 133:104243

Dirección General de Salud Pública (2022) Vigilancia y control de los efectos de las olas de calor 2022. Plan de respuesta ante los riesgos. Consejería de Sanidad. Comunidad de Madrid. https://www.comunidad.madrid/sites/default/files/doc/sanidad/calo/20220614_plan_vigilancia_olas_de_calor_2022.pdf [Last accessed:XX

Dupoué A, Blaimont P, Angelier F, Ribout C, Rozen-Rechels D, Richard M, Miles D, de Villemereuil P, Rutschmann A, Badiane A, Aubret F, Lourdais O, Meylan S, Cote J, Clobert J, Le Galliard JF (2022) Lizards from warm and declining populations are born with extremely short telomeres. Proc Natl Acad Sci 119:e2201371119

Dupoué A, Blaimont P, Rozen-Rechels D, Richard M, Meylan S, Clobert J, Miles DB, Martin R, Decencière B, Agostini S, Le Galliard JF (2020) Water availability and temperature induce changes in oxidative status during pregnancy in a viviparous lizard. Funct Ecol 34:475–485

Dupoué A, Rutschmann A, Le Galliard JF, Clobert J, Blaimont P, Sinervo B, Miles DB, Haussy C, Meylan S (2018) Reduction in baseline corticosterone secretion correlates with climate warming and drying across wild lizard populations. J Anim Ecol 87:1331–1341

Fox J, Weisberg S (2019) An R Companion to Applied regression. Sage, Thousand Oaks CA

Giacometti D, Palaoro AV, Leal LC, de Barros FC (2024) How seasonality influences the thermal biology of lizards with different thermoregulatory strategies: a meta-analysis. Bio Rev 99:409–429

Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. Glob PlanChan 63:90–104

Han X, Hao X, Wang Y, Wang X, Teng L, Liu Z, Zhang F, Zhang Q (2020) Experimental warming induces oxidative stress and immunosuppression in a viviparous lizard, *Eremias multiocellata*. J Therm Biol 90:102595

Hegyi G, Garamszegi LZ (2011) Using information theory as a substitute for stepwise regression in ecology and behavior. Behav Ecol Sociobiol 65:69–76

Herrando-Pérez S, Belliure J, Ferri-Yáñez F, Van den Burg MP, Beukema W, Araújo MB, Terblanche JS, Vieites DR (2020) Water deprivation drives intraspecific variability in lizard heat tolerance. Basic Appl Ecol 48:37–51

Herrando-Pérez S, Monasterio C, Beukema W, Gomes V, Ferri-Yáñez F, Vieites DR, Buckley LB, Araújo MB (2020) Heat tolerance is more variable than cold tolerance across species of Iberian lizards after controlling for intraspecific variation. Funct Ecol 34:631–645

Hertz PE, Huey RB, Stevenson RD (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am Nat 142:796–818

Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am Zool 19:357–366

Klukowski M (2004) Seasonal changes in abundance of host-seeking chiggers (Acari: trombiculidae) and infestations on fence lizards, *sceloporus undulatus*. J Herpetol 38:141–144

Kyrou I, Chrousos GP, Tsigos C (2006) Stress, visceral obesity, and metabolic complications. Annals New York Aca Sci 1083:77–110

Langkilde T, Shine R (2006) How much stress do researchers inflict on their study animals? A case study using a scincid lizard, Eulamprus heatwolei. J. Exp. Biol 209(6):1035–1043

Lemaître JF, Gaillard JM, Gilson E (2022) Telomeres as a sentinel of population decline in the context of global warming. Proc Natl Acad Sci 119:e2211349119

Llanos-Garrido A, Briega-Álvarez A, Pérez-Tris J, Díaz JA (2021) Environmental association modelling with loci under divergent selection predicts the distribution range of a lizard. Mol Ecol 30:3856–3868

MacDougall-Shackleton SA, Bonier F, Romero LM, Moore IT (2019) Glucocorticoids and “stress” are not synonymous. Integr Org Biol 1:1–8

Mediavilla C, Fandos G, Blázquez-Castro S, Reguera S, Barrientos R, Megía-Palma R (in press) Spatial, temporal, and host-specificity patterns of three genera of blood coccidian parasites in two syntopic Mediterranean lizards. Integr Zool 1–10. https://doi.org/10.1111/1749-4877.70008

Megía-Palma R, Arregui L, Pozo I, Žagar A, Serén N, Carretero MA, Merino S (2020) Geographic patterns of stress in insular lizards reveal anthropogenic and climatic signatures. Sci Total Environ 749:141655

Megía-Palma R, Barja I, Barrientos R (2022) Fecal glucocorticoid metabolites and ectoparasites as biomarkers of heat stress close to roads in a Mediterranean lizard. Sci Total Environ 802:149919

Megía-Palma R, Jiménez-Robles O, Hernández-Agüero JA, De la Riva I (2020) Plasticity of haemoglobin concentration and thermoregulation in a mountain lizard. J Therm Biol 92:102656

Megía-Palma R, Mediavilla C, Reguera S, Barrientos R (2025) Fenología de la reproducción y exposición a ácaros hematófagos en dos lacértidos mediterráneos. Ecosistemas 34:2773–2773

Megía-Palma R, Merino S, Barrientos R (2022) Longitudinal effects of habitat quality, body condition, and parasites on colour patches of a multiornamented lizard. Behav Ecol Sociobiol 76:73

Megía-Palma R, Redondo L, Blázquez-Castro S, Barrientos R (2023) Differential recovery ability from infections by two blood parasite genera in males of a Mediterranean lacertid lizard after an experimental translocation. JExp Zool Part A: Ecol Int Phys 339:816–824

Millspaugh JJ, Washburn BE (2004) Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. Gen Comp Endocrinol 138:189–199

Pascual LL, Luigi M, Alessandra F, Emilio B, Luigi B (2011) Hotspots of species richness, threat and endemism for terrestrial vertebrates in SW Europe. Acta Oecol 37:399–412

Patterson ZR, Abizaid A (2013) Stress induced obesity: lessons from rodent models of stress. Front Neurosci 7:130

Pereira SC, Carvalho D, Rocha A (2021) Temperature and precipitation extremes over the Iberian Peninsula under climate change scenarios: a review. Climate 9:139

R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing: https://www.R-project.org/

Racic A, Tylan C, Langkilde T (2020) Effects of temperature on plasma corticosterone in a native lizard. Sci Rep 10:16315

Rutschmann A, Dupoué A, Miles DB, Megía-Palma R, Lauden C, Richard M, Badiane A, Rozen-Rechels D, Brevet M, Blaimont P, Meylan S, Clobert J, Le Galliard JF (2021) Intense nocturnal warming alters growth strategies, colouration and parasite load in a diurnal lizard. J Anim Ecol 90:1864–1877

Sannolo M, Carretero MA (2019) Dehydration constrains thermoregulation and space use in lizards. PLoS One 14:e0220384

Schlesinger CA, Christian KA, James CD, Morton SR (2010) Seven lizard species and a blind snake: activity, body condition and growth of desert herpetofauna in relation to rainfall. Aust J Zool 58:273–283

Sears MW, Angilletta MJ Jr, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA (2016) Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. In Proceedings of the National Academy of Sciences, vol 113. pp 10595–10600

Tamar K, Carranza S, Sindaco R, Moravec J, Trape JF, Meiri S (2016) Out of Africa: phylogeny and biogeography of the widespread genus *Acanthodactylus* (Reptilia: lacertidae). Mol Phylogenet Evol 103:6–18

Tarjuelo R, Aragón P (2023) Assessing vulnerability of reptile hotspots through temporal trends of global change factors in the Iberian Peninsula. Sci Total Environ 871:161917

Telemeco RS, Addis EA (2014) Temperature has species-specific effects on corticosterone in alligator lizards. Gen Comp Endocrinol 206:184–192

Vickers M, Manicom C, Schwarzkopf L (2011) Extending the cost-benefit model of thermoregulation: high temperature environments. Am Nat 117:452–461

Woodley SK, Moore MC (2002) Plasma corticosterone response to an acute stressor varies according to reproductive condition in female tree lizards (*urosaurus ornatus*). Gen Comp Endocrinol 128:143–148

Wu Q, Richard M, Rutschmann A, Miles DB, Clobert J (2019) Environmental variation mediates the prevalence and co-occurrence of parasites in the common lizard, *zootoca vivipara*. BMC Ecol 19:1–11

Yavaşlı DD, Erlat E (2024) Tropical nights in the Mediterranean: a spatiotemporal analysis of trends from 1950 to 2022. Int J Climatol 44:1472–1488

Yokota SD, Benyajati S, Dantzler WH (1985) Comparative aspects of glomerular filtration in vertebrates. Kidney Blood Press Res 8:193–221

Zhang Q, Han XZ, Burraco P, Wang XF, Teng LW, Liu ZS, Du WG (2023) Oxidative stress mediates the impact of heatwaves on survival, growth and immune status in a lizard. In Proceedings of the Royal Society B, vol 290. pp 20231768

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