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Living on the edge: thermoregulation at the niche margin in the Bedriaga's rock lizard

Pierluigi Bombi[1],*, Fabrizio Calò[2], Daniele Salvi[3]

1 - Institute of Research on Terrestrial Ecosystems, National Research Council, via Salaria km 29.300, 00015 Monterotondo, Rome, Italy
2 - Department of Biology, University of Rome 'Tor Vergata', via della Ricerca Scientifica 1, 00133 Rome, Italy
3 - Department of Health, Life & Environmental Sciences, University of L'Aquila, Via Vetoio snc, 67100 L'Aquila-Coppito, Italy
*Corresponding author; e-mail: pierluigi.bombi@cnr.it
ORCID iDs: Bombi: 0000-0002-7322-5724; Calò: 0009-0002-9430-8243; Salvi: 0000-0002-3804-2690

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Abstract. Thermoregulation is essential for ectotherms but its relative cost, especially under ongoing climate change, depends on the thermal quality of habitats. Populations at the warm margin of a thermal niche could be negatively affected by environmental temperatures that approach the limits of a species' thermoregulation capacity. This study aims to define the thermal niche of the Bedriaga's rock lizard, *Archaeolacerta bedriagae*, a rock-dwelling species endemic to the Corsica and Sardinia islands (western Mediterranean Sea), and to investigate its thermoregulation effectiveness at the warm edge of its niche. We collected data on climate, body temperature, and microhabitat temperature throughout the species' range to characterize its thermal niche. We found that *A. bedriagae* does not occupy the entire climatic space available across its distribution range; rather, it selects temperate climates. Remarkably, thermoregulation effort increases when the habitat thermal quality decreases towards warmer sites. Populations at the warm edge of the thermal niche show the best thermoregulation effectiveness, but they are also more sensitive to the effects of climate change as they may already be at (or beyond) the species' maximum thermal capacity under the current conditions. We observed such a pattern at the extreme hot side of the thermal niche. This study provides key information on the thermoregulatory response of *A. bedriagae* to ongoing climate change that can be useful to identify populations facing a higher extinction risk either currently or in the near future.

Keywords: *Archaeolacerta bedriagae*, climate change, Corsica, Sardinia, thermal niche.

Introduction

Environmental temperatures are among the most important conditions regulating the presence of animals. It is a characteristic of the habitat and part of a species' ecological niche (Magnuson, Crowder and Medvick, 1979). Thermal niche is the range of temperature needed for a species to live and reproduce and it directly influences fitness (Magnuson, Crowder and Medvick, 1979; Kearneya, Shine and Porter, 2009; Taylor et al., 2021). Maintaining an optimal thermal range is especially important for ectotherms such as reptiles. Thermoregulation is the process that allows animals to maintain body temperature within their thermal range, suitable for metabolism. In ectotherms, thermoregulation includes behavioural mechanisms, such as moving between sun and shade, changing time of activity, exploring microenvironments with suitable thermal conditions (Hertz, Huey and Stevenson, 1993; Blouin-Demers and Nadeau, 2005; Artacho et al.,

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2017). However, not all reptiles thermoregulate in the same way; some species or populations are mainly thermoconformers (Hertz, Huey and Stevenson, 1993) while others are good thermoregulators. The cost of thermoregulation includes energetic costs for behavioural adjustments (Huey and Slatkin, 1976; Hertz, Huey and Stevenson, 1993) and diverts time away from other activities like foraging or mating. This, however, strongly depends on the thermal quality of the habitat (Huey and Slatkin, 1976; Hertz, Huey and Stevenson, 1993).

Several studies have demonstrated that many species are effective thermoregulators especially in habitats with low thermal quality where thermoregulation is costly (Blouin-Demers and Weatherhead, 2001; Blouin-Demers and Nadeau, 2005; Row and Blouin-Demers, 2006). This suggests that in extreme climatic conditions the disadvantages of being thermoconformers (e.g., reduced physiological efficiency, increased risk of predation, reduced foraging success) outweigh the costs of thermoregulation. Thus, when thermal quality is reduced, thermoregulation effort increases (Vickers, Manicom and Schwarzkopf, 2011). Since the thermal quality of the habitat can change over time, the species' thermoregulation strategy become essential for success in a changing environment.

Defining the thermal niche of species, their efficiency of thermoregulation, and clarifying relationships with climatic variables is essential to understand how species will respond to ongoing climate change (Huey et al., 2009; Frishkoff, Hadly and Daily, 2015; Piantoni, Navas and Ibargüengoytía, 2016; Kirchhof et al., 2017; Li et al., 2017). In this respect, populations that live at the warm margin of a species' thermal niche are usually more vulnerable to ongoing climate changes because they exist in conditions close to their upper limit of tolerance (Huey et al., 2009; Sunday et al., 2014; Bombi et al., 2017) and therefore face a higher risk of local extinction (Araújo et al., 2013; Artacho et al., 2017; Kirchhof et al., 2017). Overall, climate change is negatively affecting reptiles worldwide, with negative impacts on growth, reproduction, population size, and distribution (Huey et al., 2009; Walters, Blanckenhorn and Berger, 2012; Buckley, Ehrenberger and Angilletta, 2015; Walker, Stuart-Fox and Kearney, 2015). Investigating the thermoregulation capacities of populations in the light of climate change is important to understand the extent to which they can cope with such changes and to develop effective long-term conservation strategies.

In this study, we focused on the Bedriaga's rock lizard, *Archaeolacerta bedriagae*, endemic to Corsica and Sardinia, two large islands in the Mediterranean Sea. This species has a high biogeographical and conservation importance, representing a relict lineage within the Lacertini radiation (Mendes et al., 2016) and being classified as Near Threatened, with a decreasing population trend, in the International Union for the Conservation of Nature red list (IUCN, 2008). The typical habitat of the species is represented by large rocky outcrops from sea level, with hot Mediterranean climate, up to 2710 m a.s.l, with cold mountain conditions (Bombi and Vignoli, 2004; Bombi et al., 2009a, b; Sindaco et al., 2010; Salvi, Bombi and Sindaco, 2016). This wide range of environmental conditions faced by *A. bedriagae* make it particularly suitable to study the thermoregulation strategy and capacity of populations. The main aims of this paper are to define the thermal niche of the species and to clarify the effects of high temperatures on populations at the warm margin of its thermal niche. First, we described the thermal niche of the species at two different scales: (1) at the species range scale and (2) at the microhabitat scale. Second, to assess the thermoregulation effectiveness at each sampling site, and its variation across the thermal niche gradient, we measured the relationship between lizards' body temperature and environmental temperature at the capture point. This approach allowed us to test the hypothesis that site thermal quality influences the thermoregulation effectiveness of the *A. bedriagae* populations across its distribution range and provides insights on the extinction risk of marginal populations under climate change.

Materials and methods

Data collection

To characterize the thermal niche of *A. bedriagae* and to estimate the thermoregulation effectiveness of each studied population we used climate data of known sites of presence and field-sampled temperature data. Known sites of presence of *A. bedriagae* were organized through a critical review of the available literature (e.g., Delaugerre and Cheylan, 1992; Bombi and Vignoli, 2004; Bombi et al., 2009a, b; Salvi et al., 2009a, b; Salvi and Bombi, 2010; Salvi et al., 2010; Bombi, Salvi and Bologna, 2012). Climate data were obtained from the WorldClim high spatial resolution databank (version 2.1; Fick and Hijmans, 2017). We used 11 bioclimatic variables (i.e., WorldClim Bio1 – Bio11) referring to the period 1970-2000 at a resolution of 30 arc-seconds that corresponds to a resolution of about 700 meters at the latitude of the study area (i.e., Corsica and Sardinia islands). We collected field-sampled temperature data in eight sites throughout the range of *A. bedriagae* between May 2003 and September 2004, during the period of highest activity of the species (see fig. 1 and supplementary table S1). Sites were represented by large rocky outcrops, of variable size (from 100 m^2 to 14 000 m^2), emerging from mediterranean vegetation, which we thoroughly explored during each sampling session, searching for surface active lizards both exposed to sun or in shadowed spots at different times of day. Overall, we captured 58 lizards, measured their body temperature immediately after capture, and released them at the capture point. At the same time, we measured the temperature of the rock at the exact position where the lizard was firstly detected and the temperature of the air 20 cm above the same position. We used a Delta Ohm HD9218 thermocouple to measure all the temperature data.

Thermal niche

To define the thermal niche of *A. bedriagae* at the species-range scale we extracted climate data from the WorldClim climatic surfaces for (1) the entire study area (about 32 800 km^2), (2) all the known sites of presence of *A. bedriagae*, and (3) the eight population sampling sites. We described the thermal niche at the whole range scale using two approaches. One based on the first two principal components calculated by a PCA (see supplementary table S2) on all the bioclimatic variables related to the environmental temperature. The other approach focused on the two variables that mostly determine lizards' activity period and may be critical for thermoregulation: Max Temperature of Warmest Month (Bio5) and Mean Temperature of Warmest Quarter (Bio10). We chose these two variables because they bring information about seasons when lizards' activity is the highest and because they may have the greater influence on the species thermoregulation effectiveness (see below for details). In both cases, we used binomial GLMs to assess the climatic variable effects on the presence/absence of the species (see supplementary table S3 for details). This

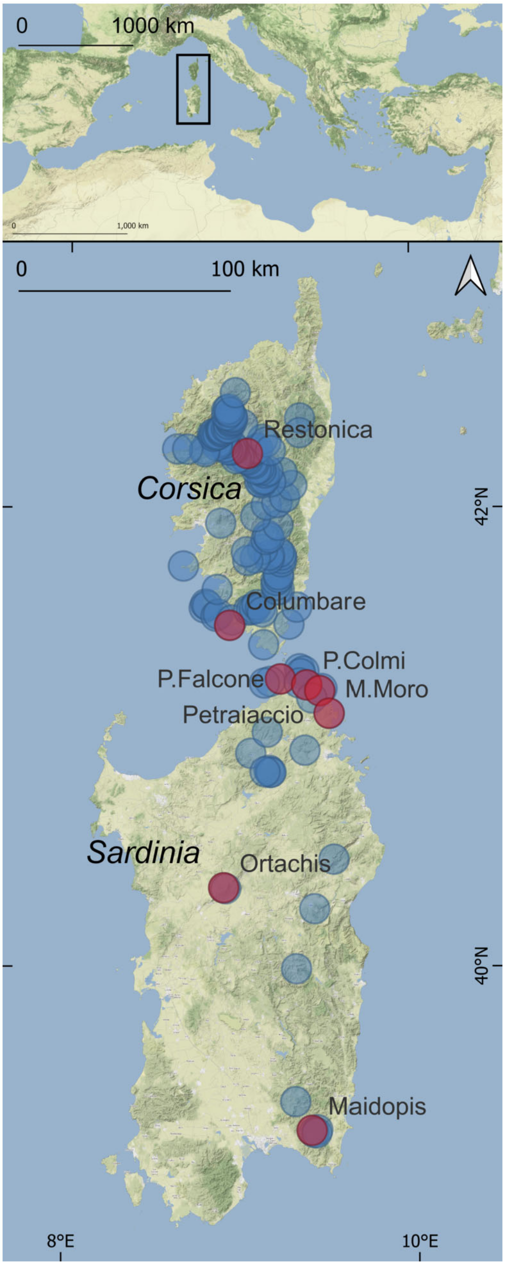

Figure 1. Studied populations of *Archaeolacerta bedriagae* (red dots) and known sites of presence of the species in Corsica and Sardinia (blue dots). Map tiles by Stamen Design, under CC BY 3.0.

allowed clarifying how *A. bedriagae* selects sites within a wider range of available conditions.

In order to assess the species thermal niche at the microhabitat scale, we analysed field-sampled temperature data. Body, air, and rock temperatures were compared through binomial GLMs using the measured temperature as independent variable and the categories body/air, body/rock, and air/rock as responses (see supplementary table S3 for details). The relationship between lizards' body temperature and environmental temperatures (air and rock temperatures) was analysed by gaussian GLMs, using body temperature as dependent and air and rock temperatures as predictors (see supplementary table S3 for details). This analysis provides information on how *A. bedriagae* selects microhabitat temperature to control its body temperature.

Thermoregulation effectiveness

Thermoregulation effectiveness in each sampling site was calculated as the coefficient of the gaussian GLM with lizards' body temperatures as response and environmental temperatures as predictor variables (see supplementary table S3 for details). We explored how both air and rock temperature influence lizards' body temperature. We used the coefficient value as a proxy of thermoregulation effectiveness (Van Damme et al., 1990; Hailey and Coulson, 1996; Ortega, Mencía and Pérez-Mellado, 2016; Díaz, Izquierdo-Santiago and Llanos-Garrido, 2022). High values of the coefficient indicate low effectiveness because imply that body temperature strictly follows the environmental temperature. Low values indicate high effectiveness because imply that lizard body temperature does not follow rock or air temperature variations. The maximum effectiveness corresponds to a coefficient equal to zero. In such case, changes of environmental temperature, due to different time of the day, exposure, microsite selection, or other interacting factors, do not modify lizard body temperature.

Finally, we explored the effect of the site climatic conditions on the population thermoregulation effectiveness by analysing the relationships between the effectiveness and relevant climate variables. To do this, we fitted gaussian GLMs with the thermoregulation effectiveness in the sites (coefficients of body temperature with respect to rock and air temperature) as response variable and the relative climatic conditions, using both the 'Mean Temperature of Warmest Quarter' and the 'Max Temperature of Warmest Month' as predictors (see supplementary table S3 for details). In order to exclude an effect of the sampling period on this relationship, we also fitted the same GLMs including the sampling period as a covariate. In addition, to further test the reliability of the site coefficients (thermoregulation effectiveness) we used an approach based on null models (Gotelli and Graves, 1996). Site coefficients were calculated 1000 times randomizing the temperature data and the relative relation between climate and thermoregulation effectiveness was recalculated with the new coefficients. The proportion of times that the simulated p-value (derived from permutations) was lower than the observed p-value (from original, non-permutated data) was calculated and used as an aggregate p-value, indicating the probability that the final pattern derives by chance from random data. All the data management and the analyses were made in R (R Core Team, 2022) using the packages: geodata (Hijmans, Ghosh and Mandel, 2022), and rgdal (Bivand, Keitt and Rowlingson, 2023), the map of *A. bedriagae* distribution and sampling site locations was made in QGIS 3.24 (QGIS.org, 2022).

Results

The analysis of the thermal niche of *A. bedriagae* at the range scale showed that this species does not occupy the entire climatic space available throughout Corsica and Sardinia. This is evident both in the climatic space defined by the PCA based on 11 climatic variables and on Bio5 and Bio10 (fig. 2A, B). Most of the climatic variance in the study area is explained by the first axis of the PCA (92%), while PC2 explains a smaller portion of variance (7%). PC1 is mostly associated with Temperature Seasonality (variable loading = 0.99) and PC2 with Isothermality (−0.44), Max Temperature of Warmest Month (−0.39), and Mean Temperature of Wettest Quarter (−0.37). The results of the binomial GLMs showed a highly significant effect of climatic conditions on the occupation of sites for the variables PC1 and PC2 (McFadden's $R^2 = 0.18$, $p < 0.001$ for both variables; see supplementary table S3) as well as for Mean Temperature of Warmest Quarter and Max Temperature of Warmest Month (McFadden's $R^2 = 0.19$, $p < 0.001$ for both variables) (see table 1 for temperature data). This indicates that *A. bedriagae* mostly occurs in relatively cold and mild climates with low seasonal temperature variation whereas this species occupies few sites with high temperature and large seasonal variation.

At the microhabitat scale, the thermal niche of *A. bedriagae* is linked to the microenvironmental conditions, as lizard body temperature is related to both air and rock temperatures (McFadden's $R^2 = 0.22$, $p < 0.001$ and McFadden's $R^2 = 0.097$, $p < 0.05$ respectively) (fig. 3B). However, the species has a relatively high and constant body temperature

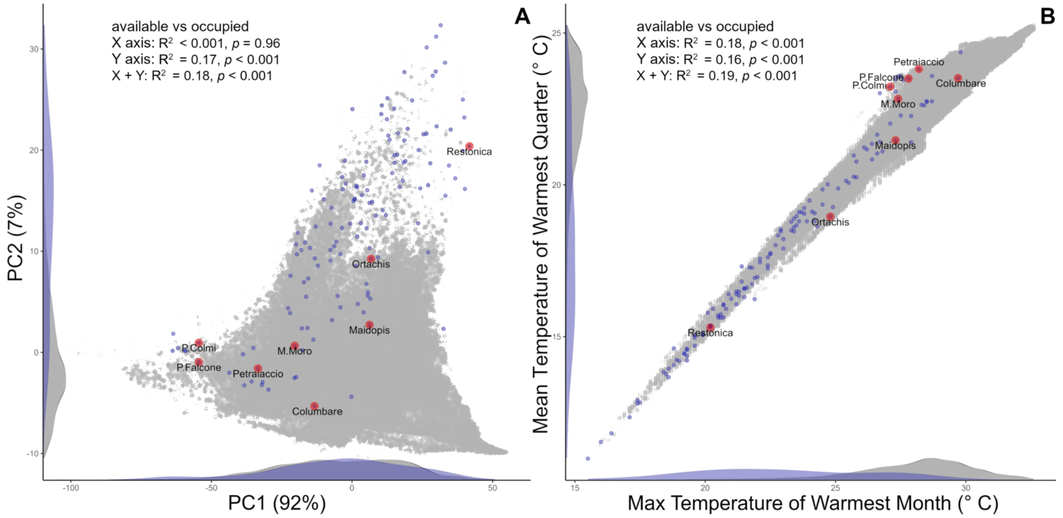

Figure 2. Thermal niche of *Archaeolacerta bedriagae* at the species range scale. Synthesis of the thermal niche through PCA of eleven bioclimatic variables based on temperature data (A) and detail of the niche described by two specific thermal variables (Max Temperature of Warmest Month – Bio 5 and Mean Temperature of Warmest Quarter – Bio 10) (B). PC1 is mostly associated with Temperature Seasonality (0.99) and PC2 to Isothermality (−0.44), Max Temperature of Warmest Month (−0.39), and Mean Temperature of Wettest Quarter (−0.37). In both plots, grey dots represent thermic availability in the study area, blue dots represent thermic conditions in all the known sites of *A. bedriagae* presence, and red dots represent thermic conditions in the population sampling sites. Polygons on the axes represent the frequency distribution of the values of thermic availability in the study area (grey polygons) and the frequency distribution of temperature variable values at the presence sites (blue polygons). On the top left of each plot are reported the results of the GLMs comparing climatic conditions at available and occupied sites on the *X* and *Y* axes.

Table 1. Descriptive statistics of Mean Temperature of Warmest Quarter (°C) and Max Temperature of Warmest Month (°C) in available and occupied sites, measured body temperature (°C), measured air temperature (°C), and measured rock temperature (°C).

		Minimum	Maximum	Mean	Standard deviation
Mean Temperature of Warmest Quarter	Available sites	10.98	25.25	22.07	1.99
	Occupied sites	10.98	24.37	18.12	3.18
Max Temperature of Warmest Month	Available sites	15.50	32.60	27.91	2.45
	Occupied sites	15.50	29.80	23.01	3.33
Body temperature		28.20	36.50	32.56	1.84
Air temperature		12.00	31.20	22.82	4.10
Rock temperature		20.1	41.10	29.31	4.78

(see table 1 for values), which is usually warmer than air and rock temperatures (McFadden's $R^2 = 0.84$, $p < 0.001$ and McFadden's $R^2 = 0.14$, $p < 0.001$ respectively) (fig. 3A). At the studied sites, rock temperature (see table 1 for values) is generally higher (McFadden's $R^2 = 0.32$, $p < 0.001$) than air temperature (see table 1 for values) but these two variables are related (McFadden's $R^2 = 0.18$, $p < 0.01$).

Thermoregulation effectiveness, measured as the coefficients of regressions between lizard body temperature and rock and air temperatures, changed from site to site. The coefficients of the linear regressions between body temperatures and rock temperatures range from −0.03 in P. Colmi and Petraiaccio to 0.25 in Restonica (fig. 4A and supplementary table S1). The regression coefficients between lizard body temperature and air temperatures range from −0.11 in Petraiaccio to 0.59 in Restonica (fig. 4B and supplementary table S1). Significant, or almost significant differences among

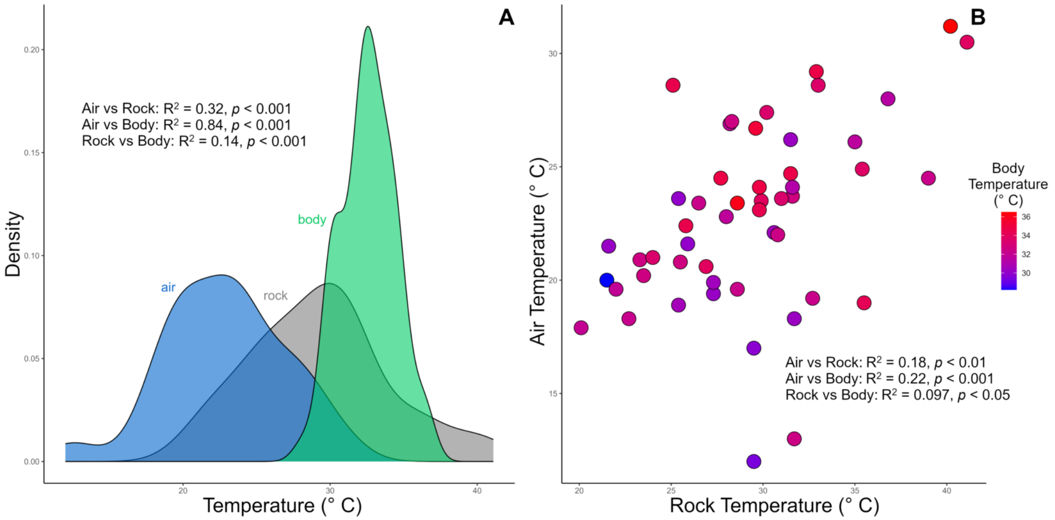

Figure 3. Thermal niche of *Archaeolacerta bedriagae* at the microhabitat scale. Distribution of lizard body temperature values and environmental temperature values (rock temperature and air temperature) (A) and relationship between rock and air temperature values at the population sampling sites (B). In the first plot, blue polygon represents the distribution of air temperature data, grey polygon represents rock temperature data, and green polygon represents lizard body temperatures. In the second plot, dots are coloured according to the corresponding lizard body temperature. The embedded text indicates the GLMs results used for comparing air, rock, and lizard body temperatures and to assess their association.

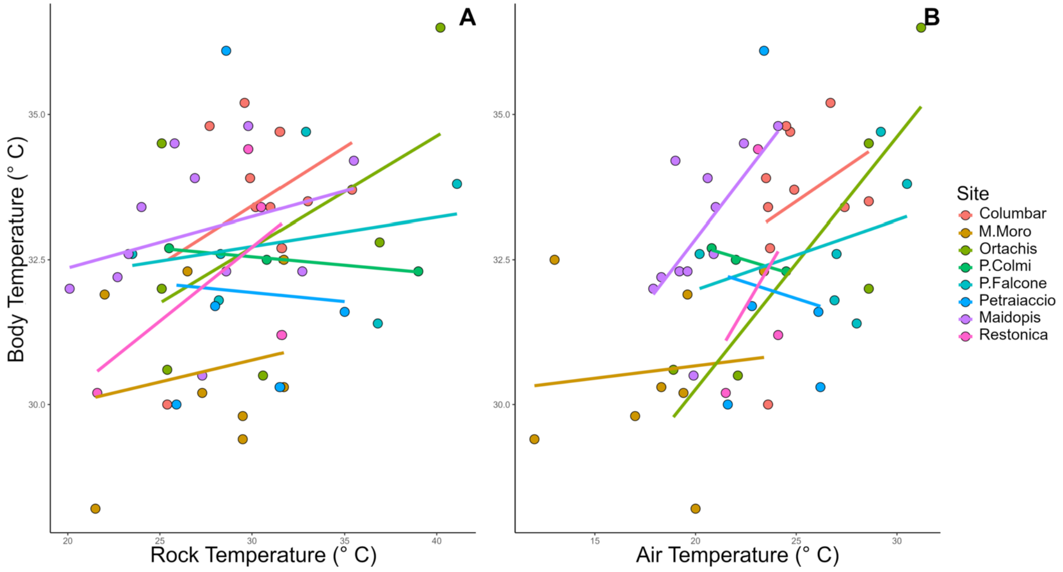

Figure 4. Thermoregulation effectiveness of the studied populations of *Archaeolacerta bedriagae*. Relationships between lizard body temperature and rock temperature (A) and air temperature (B) at each population sampling site. Dots and regression lines are coloured according to the sampling site. The coefficients of the regression lines indicate the thermoregulation effectiveness in each site.

sites were found for body and air temperatures (Anova $F_{\mathrm{body}} = 2.02$, $p_{\mathrm{body}} = 0.07$ and Anova $F_{\mathrm{air}} = 8.20$, $p_{\mathrm{air}} < 0.001$ respectively), whereas rock temperatures were not significantly different among sites (Anova $F_{\mathrm{rock}} = 1.08$, $p_{\mathrm{rock}} = 0.38$). Nevertheless, the thermoregulation effectiveness is not related to population differences in mean body temperatures ($r_s = 0.45$, $p = 0.27$), air temperatures ($r_s = 0.07$, $p = 0.88$), and rock temperatures ($r_s = -0.29$, $p = 0.50$). In addition, when we included the sampling period as a covariate in the GLMs, it was not significant in any case (see Table S3 for details), meaning that thermoregulation effectiveness of each population is not dependent on the sampling period.

Thermoregulation effectiveness increases approaching the warm niche margin. The warmest sites (i.e., Petraiaccio, P. Colmi, M. Moro, and P. Falcone) are close to the warm edge of the species thermal niche, and these populations showed low coefficients, while at the coldest sites (i.e., Restonica and Ortachis) populations have high coefficients (fig. 5). One site, Columbare, located at the warmest extreme of the thermal niche (highest 'Max Temperature of Warmest Month' and one of the highest 'Mean Temperature of Warmest Quarter'), does not follow this pattern and showed low and intermediate thermoregulation effectiveness. Linear models fitted on a dataset excluding this anomalous population showed increased significance (see values in fig. 5 and supplementary table S3 for detailed results). This pattern is confirmed by the null-model "aggregate" test, which indicated significant trends for both the two climate variables ($p = 0.026$ for the Max Temperature of Warmest Month and 0.003 for the Mean Temperature of Warmest Quarter).

Discussion

Thermal niche of Archaeolacerta bedriagae

The distribution range of the Bedriaga's rock lizard encompasses sites along the northern Sardinian and southern Corsican coasts, from sea level up to the highest mountains both in Sardinia (1783 m asl in the Gennargentu mountains; Salvi et al., 2010) and Corsica (2710 m a.s.l. in M. Cinto; Delaugerre and Cheylan, 1992). Such an eurizonal distribution indicates that this lizard is able to cope with a wide range of climatic conditions across its range and might suggest that climate is not limiting for the presence of the species. However, our results indicate that this is not true for warmer conditions. Indeed, we found that, while the number of populations of *A. bedriagae* is higher in the cold tail of the thermal availability, presence sites become rare in warmer conditions. Since the cold edge of the realized niche (sensu Hutchinson, 1957; Moore et al., 2023) corresponds to the coldest available conditions, we suppose that the cold margin of the realised niche is limited by climatic availability, but the fundamental niche (sensu Hutchinson, 1957; Moore et al., 2023) could be larger in this direction. On the contrary, the absence of the lizard from the warmest areas of Corsica and Sardinia, as well as its rarity and range fragmentation in relatively warm conditions that are abundantly available across these islands, would suggest that the warm edge of the realized niche is very close to the limit of the fundamental one. This is in close agreement with results from Bombi et al. (2009b) that showed a negative effect of high summer temperature conditions ("Maximum Temperature of Warmest Month" variable) on the distribution of *A. bedriagae* in Sardinia.

The body temperature of ectotherms depends on the environmental temperature but also on body biophysical and morphological features and on behavioural and physiological mechanisms (Blais et al., 2023). This allows lizards

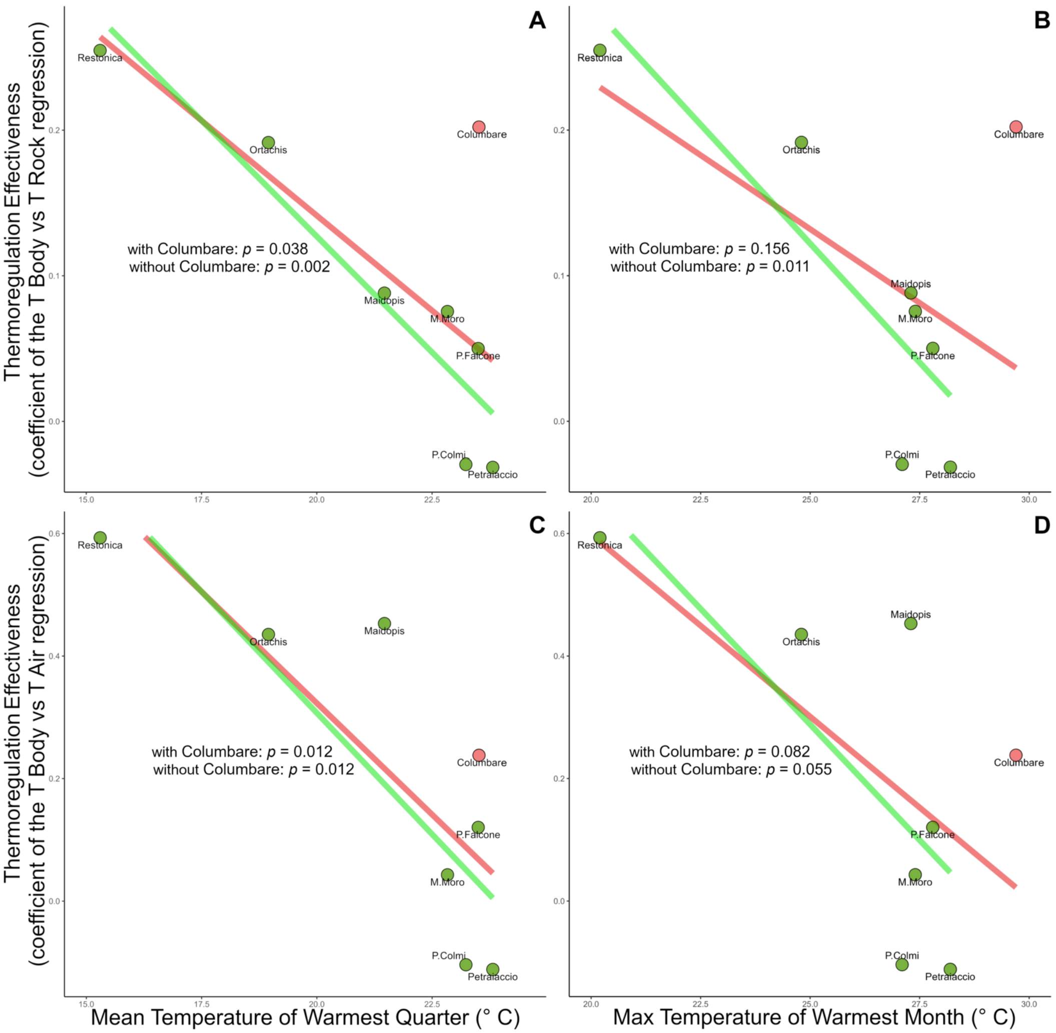

Figure 5. Relationship between lizard thermoregulation effectiveness and environmental temperatures. Top-left and top-right plots represent the relationships between the 'thermoregulation effectiveness with respect to rock temperature' and the two climatic variables, Mean Temperature of Warmest Quarter (A) and Maximum Temperature of the Warmest Month (B). Bottom-left and bottom-right plots represent the relationships between the 'thermoregulation effectiveness respect to air temperature' and the two climatic variables (C and D). The red lines are the regression lines of the relation between the thermoregulation effectiveness and the climate variable considering all the sites and the green lines are the regression lines of the same relation excluding the outlier site (Columbare) indicated by the red point.

to control, at some degree, the body temperature that is related to but different from air and ground temperatures. Bauwens et al. (1990) measured body temperatures of a high-elevation population of *A. bedriagae* and recorded values that were comparable with our measured values and similar to those registered for other sympatric lacertid lizards (Van Damme et al., 1990). The tight curve of the frequency distribution of lizard body temperatures indicates that *A. bedriagae* is able to maintain, through thermoregulatory mechanisms, a relatively constant temperature in a diverse array of environmental microclimates. Biophysical traits of *A. bedriagae* (such as shape, colour, size) could further contribute to maintain a body temperature higher than the microenvironment. When air and/or rock are too cold or too hot, thermoregulation mechanisms can be insufficient for maintaining the body temperature within the activity range and lizards take shelter in rock crevices.

Thermoregulation and Niche Margin Effect

Several studies demonstrated that the thermoregulation effort in reptiles depends on the thermal quality of the habitat (e.g., Huey and Slatkin, 1976; Row and Blouin-Demers, 2006; Sagonas et al., 2017). Based on this, one can expect that the effort in thermoregulation, and thus the effectiveness of the mechanism, changes with air and/or rock temperatures. We found changes in the thermoregulation effectiveness across sites as well as differences in air and body temperatures. This, together with the stronger relationship between body and air temperatures than between body and rock temperatures, suggests that air temperature is a main driver of body temperature in these lizards. Nevertheless, our results indicate that the thermoregulation effectiveness is not related to the microenvironmental temperatures.

Under extreme and challenging climatic conditions, the thermoregulatory effort increases when thermal quality of the habitat decreases (e.g., Blouin-Demers and Nadeau, 2005; Vickers, Manicom and Schwarzkopf, 2011; Artacho et al., 2017). Our study focuses on the warm side of the thermal niche of *A. bedriagae*; thus, in our case, the habitat thermal quality decreases when the climate at the site is warmer. In this light, the observed increase of thermoregulation effectiveness (reduction of the coefficients) from colder to warmer sites is coherent with the expected pattern and indicates that the thermoregulation effort is related to macroclimatic gradients. We call such relationship “Niche Margin Effect”. The Niche Margin Effect could be used to detect the niche edge, identify the most extreme sites, and forecast potential impacts of climatic alterations.

The sites located on the niche edge can sometimes experience conditions that are beyond the thermoregulation capacity of the species (Moore et al., 2023). In these circumstances, a higher thermoregulation effort might not correspond to an increased thermoregulation effectiveness. This could be the case of the site Columbare, which does not follow the trend showed by the other populations of increased thermoregulation effectiveness in warmer sites and seems to respond differently to the Niche Margin Effect. If the experienced temperatures are too far beyond the species thermoregulation capacities (or beyond them for too long), a negative impact and ultimately local extinction of the population could be expected.

In view of current global warming, thermoregulation processes have deep consequences for the long-term conservation of ectothermic animals. The extreme sites are known to be those mostly exposed to climate change impacts (Sinervo et al., 2010; Artacho et al., 2017; Kirchhof et al., 2017) because local conditions there can overcome the thermal niche edge. In our case, the sites closest to the warm edge of the niche are located in northern Sardinia and southern Corsica (Columbare, Petraiaccio, P. Falcone, P. Colmi, and M. Moro). All of them are coastal sites characterized by large rocky outcrops with no forest vegetation. On the other hand, in the other sites (e.g., Maidopis), irrespective to latitude, warm conditions are buffered by the effect of altitude, hydrography (proximity to water bodies), and/or forest coverage.

The negative effect on thermoregulation effectiveness that we have observed at Columbare could be soon observed in the other sites approaching the warm margin of the species’ niche, with deleterious consequences on individual fitness and population persistence. While this hypothesis requires to be tested with further field studies, the Niche Margin Effect could represent an instrument to detect the earliest effects of the global warming on this endemic species and to identify populations facing higher extinction risk (Wiens, 2016; Bombi et al., 2021).

This study provides the first range-wide characterization of the thermal niche of *Archaeolacerta bedriagae* and highlights a striking geographical pattern of thermoregulation effectiveness at the population level. Thermoregulation effectiveness increases towards the warm niche margin, suggesting an increased thermoregulation effort in environments with lower thermal quality (Niche Margin Effect). Remarkably, in a coastal population under extremely warm conditions we observed the reduction of thermoregulation effectiveness that can indicate a disruption of thermoregulation processes and a potential increase of local extinction risk. In light of the current global warming, we can hypothesize that a similar trend can also occur in other coastal populations, which deserve a special attention for the long-term conservation of the species. In this respect, our approach might represent a useful tool for detecting global warming effects on ectotherms and for identifying priority population. In addition, this approach has the advantage of not requiring the experimental estimation of absolute values of thermoregulation parameters (see e.g., Hetz et al., 1993) because it is based on relative differences among populations and on disclosing geographical patterns of the thermoregulation capacity. Similar approaches have been fruitfully implemented in plants and animals (e.g., Wiens, 2016; Bombi et al., 2017, 2021). Results from this study warrant further exploration of these approaches in animal populations.

Supplementary material. Supplementary material is available online at:
https://doi.org/10.6084/m9.figshare.24968016

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