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Living Beyond the Edge: Impacts of Climate Change on Rock Lizards at the Niche Margin

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ABSTRACT

Ectotherms are particularly threatened by climate change because they are strictly reliant on environmental conditions for homeostasis. Increasing environmental temperatures may approach the species' critical thermal maximum, with deleterious effects on individual thermoregulation capacities. This study tests the hypothesis developed in a recent work that under ongoing global warming populations living in sites at the warm edge of the species' thermal niche will suffer a disruption of the thermoregulation process, with detrimental effects at the individual and population level. We collected individual measurements and temperature data for Mediterranean endemic rock lizards, across the entire distribution range of the species and during two different sampling periods ~20 years apart to compare thermoregulation coefficient (C), body condition index (BCI) and population size under different climatic conditions. We found that C and BCI vary across space and time following a linear pattern along the thermal niche gradient (Niche Margin Effect, NME) until a threshold temperature, beyond which the NME is disrupted. This threshold temperature indicates the warm edge of the species' thermal niche. A slightly higher temperature marks the threshold at which we observed significant population declines over the 20-year study period in the warmest sites. This suggests a lagged response of population trends to climate warming. This study suggests a mechanism of disruption of homeostatic processes when the warm margin of the thermal niche is reached and indicates that individual parameters such as thermoregulation coefficient and body condition, rather than demographic trends, are key indicators for an early detection of population extinction risk. The multipopulation approach implemented in our study allows to identify the niche edge that underlies species' vulnerability to global warming, and to identify populations suffering negative effects of climate change before demographic collapse. This might allow to plan appropriate mitigation measures and management strategies to avoid local extinctions.

1 | Introduction

Climate change has impacts on flora and fauna worldwide, and ectotherms are especially threatened because their capacity for homeostasis is directly related to the thermal quality of the habitat (Hertz, Huey, and Stevenson 1993; Sinervo et al. 2010; Cosendey, Rocha, and Menezes 2023). Locally, species may exhibit three different responses to ongoing climate change: (i) species distributions may shift to more favourable thermal environments, colonising new areas that became suitable; (ii) species may cope with the new climate by acclimation plasticity or adaptive evolutionary responses; (iii) the

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new climatic conditions may drive the species out of its fundamental niche resulting in local extinctions (Diele-Viegas et al. 2020; Sinervo et al. 2018). The latter scenario is more likely for populations located at the warm edge of the species thermal niche exposed to fast climatic changes, because they have reduced possibilities of adaptation (e.g., Bombi et al. 2017). In these marginal sites, temperatures could approach the critical thermal maximum of the species, forcing individuals unable to cope with extreme thermal conditions to inactivity. This, combined with biotic features like competition, determines that populations can have lower density, fitness and genetic diversity (Lawton 1993; Brown, Stevens, and Kaufman 1996; Camacho and Rush 2017; Camacho et al. 2024).

In climatically extreme habitats, ectotherms spend more energy on thermoregulation behaviour because preferred microclimates are less common or less accessible, up to the point that thermoregulation could be less effective and more expensive, pushing its costs to overcome the benefits (Huey and Slatkin 1976; Angilletta 2009; Buckley, Ehrenberger, and Angilletta 2015; Sears and Angilletta 2015; Díaz, Izquierdo-Santiago, and Llanos-Garrido 2022). In addition, water and food availability interact with thermal ecology, influencing thermoregulation costs (Brown and Griffin 2003; Sannolo and Carretero 2019; S'khifa et al. 2020). To avoid overheating, ectotherms, such as lizards, need to retreat in thermal refugia and the time spent in retreat reduces the time available for other activities such as foraging or mating, with negative effects on growth, reproduction and ultimately on population size (Huey 1982; Buckley, Ehrenberger, and Angilletta 2015; Walker, Stuart-Fox, and Kearney 2015; Sinervo et al. 2018). A high thermoregulation effectiveness can buffer the impacts of climate change on lizards' populations in the short term but increases the risk of extinction in the long term (Buckley, Ehrenberger, and Angilletta 2015) because thermoregulation behaviour prevents the evolution of thermal adaptation (Bogert effect; Bogert 1949). However, intraspecific differences in seasonal acclimation were observed (Osojnik et al. 2013), mitigating the potentially increased sensitivity of thermoregulator lizards to long-term climate change effects. A recent study on Mediterranean endemic rock lizards documented a trend of thermoregulation coefficient, which increases when the habitat thermal quality decreases from colder to warmer sites, naming this trend 'Niche Margin Effect' (hereafter NME, Bombi, Calò, and Salvi 2024). A similar pattern was also observed in other species that live in extreme climatic conditions, which deflect energy from thermoregulation to growth and reproduction in thermally favourable environments (e.g., Row and Blouin-Demers 2006; Vickers, Manicom, and Schwarzkopf 2011). Rock lizard populations at the warm edge of the thermal niche show the highest thermoregulation coefficient that might correspond to the maximum thermoregulation effort of which the species is capable. Remarkably, in a coastal population experiencing extremely warm conditions, but similar in terms of habitat structure and reptile assemblage, these authors documented a drop in thermoregulation coefficient (Bombi, Calò, and Salvi 2024). Such a deviation from the NME could indicate a disruption of thermoregulation processes under conditions exceeding the warm edge of the fundamental niche.

Under this hypothesis, in a scenario of global warming, we expect that ectotherm populations living in sites at the warm edge of the niche will be pushed beyond this edge over time and will manifest a disruption of thermoregulation processes that translates into detrimental effects at the population level. The main aim of this study is to test this prediction. Building on the findings of Bombi, Calò, and Salvi (2024), we compared range-wide patterns of thermoregulation coefficient and population condition based on data collected by these authors in 2003–2004 with those based on new data collected in the same sites after two decades (2022–2023). Specifically, under a global warming process, which caused a general worsening of habitat thermal quality across the species range, we expect two different population responses: (i) an increase of thermoregulation coefficient and thermoregulation effort (i.e., NME) for populations inhabiting temperate sites; (ii) a disruption of this pattern for populations inhabiting the warmest sites. As a proxy of increased thermoregulation effort, we used the decrease of individual health status measured by the body condition index (BCI). To assess detrimental effect on populations associated with the disruption of the NME, we estimated population demographic trends. The approach implemented in this study is relevant for the identification of ectotherms' populations facing a higher extinction risk under ongoing global warming.

2 | Materials and Methods

2.1 | Study Species

The Bedriaga's rock lizard, *Archaeolacerta bedriagae* (Camerano, 1885), is confined to large rocky outcrops of Corsica and Sardinia, two large islands in the Mediterranean Sea (Bombi et al. 2009a). This species has high biogeographical and conservation importance because it represents a relict lineage within the Lacertini radiation (Mendes et al. 2016; Garcia-Porta et al. 2019) and is classified as Near Threatened, with a decreasing population trend, in the Red List of the International Union for the Conservation of Nature (Salvi et al. 2024). *Archaeolacerta bedriagae* ranges from the sea level, with typically Mediterranean climate, up to the highest altitudes of these islands (2710 m a.s.l), characterised by cold mountain conditions (Delaugerre and Cheylan 1992; Bombi and Vignoli 2004; Bombi et al. 2009a, 2009b; Salvi et al. 2009a, 2009b; Salvi and Bombi 2010; Salvi et al. 2010; Sindaco et al. 2010; Salvi, Bombi, and Sindaco 2016). Nevertheless, despite its eurizonal range, this species has a strongly fragmented distribution with a significant isolation of some populations, especially in Sardinia, due to environmental temperature, habitat, humidity, presence of competitors. These factors make the species particularly vulnerable to environmental changes and potentially susceptible to local extinctions.

2.2 | Data Collection

We collected individual measurements and temperature data in eight sites spanning the distribution range of *Archaeolacerta bedriagae*. All the sites were sampled between May 2003 and September 2004 (*past samplings*) and five of these sites were also sampled from May 2022 to June 2023 (*new samplings*) in order to compare the same sites in two different periods about 20 years apart. New sampling sites were selected to represent the different areas of the species' distribution range

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and different conditions covered by the thermal niche. During past and new samplings, each site was visited approximatively at the same time of the year. All sampling sites consist of well-delimited rocky outcrops surrounded by Mediterranean vegetation. In each site, we searched for lizards during five consecutive days per sampling period. During each daily session, carried out between 08:00 and 12:00, adult lizards were captured, sexed, measured for snout–vent length (SVL), body mass and body temperature, and temporarily marked before being released in the capture point. In the spot where each lizard was first observed, we collected temperature data for air and rock. During new sampling sessions, we also measured air and rock temperatures at random points across the study sites considering all possible available conditions (i.e., sunny and shady spots, different kinds of soil, vegetation and rock). Overall, 58 lizards were sampled in the past sampling period and 34 lizards in the new sampling period. We collected temperature data to the nearest 0.1°C by using a Delta Ohm HD9218 thermocouple in the past samplings and a Mestek 800C infrared thermometer in the new samplings. The measurement of body temperatures based on infrared thermometers, taken at a close distance (< 5 mm) from the lizard belly and shading both the lizards and the thermometer, is accurate and highly correlated with core body temperature, as shown on lizards of size comparable to *A. bedriagae* (i.e., with an abdominal width ≥ 7 mm) (Pontes-da-Silva et al. 2018; Chukwuka et al. 2019).

2.3 | Thermoregulation Coefficient and Body Condition Index

We used generalised linear mixed models (Breslow and Clayton 1993; Bolker et al. 2009) to estimate the effect of site and of environmental temperatures on lizard body temperatures (T_{body}). We fitted Gaussian GLMMs with T_{body} as response variable, air and rock temperatures (T_{air} and T_{rock} respectively) as fixed effect predictors and sites as random effect predictor. For each population, we estimated the thermoregulation coefficient (C) as $E = 1 - k$; where k is the coefficient of the linear model with T_{body} as response variable and the environmental temperature (T_{air} or T_{rock}) that showed the highest contribution in the GLMMs as predictor (Huey and Slatkin 1976). High C values (close to 1) indicate good thermoregulation strategy, because the body temperature of lizard is less dependent on the environmental temperature. Low C values (close to zero) mean that lizard body temperature follows the environmental temperature, and therefore indicates a thermoconformer strategy. It is important to note that our experimental design is aimed at comparing the coefficient among a network of sites, rather than to estimate absolute value of effectiveness at the individual site (Hertz, Huey, and Stevenson 1993). Doing this, we considered a simplified process, ignoring other factors such as solar radiation, wind convection or water availability.

We used lizard SVL and body mass for the estimation of the mean body condition index (BCI) for each population. We fitted the generalised linear model with lizard body mass as response variable and the interaction between SVL and sex as predictor in order to take into account the sexual dimorphism in size that occurs in the Bedriaga's rock lizard (Salvi et al. 2006), then we calculated the residuals of this model. This residual method separates the effect of body size on the BCI values and thus provides a straightforward proxy of the health status of animals (Jakob, Marshall, and Uetz 1996).

2.4 | Population Size

We estimated lizard population size by applying binomial N-mixture models (Royle 2004) that are particularly suitable for small vertebrates (Ficetola et al. 2018). We used counts performed in each site during the five consecutive days of sampling as repeated visits and each sampling site and sampling period (past and new) as independent sites, obtaining 13 units (eight past sites + five new sites). In the well-delimited sampling sites, we actively searched for lizards and to avoid pseudoreplication in the daily counts, we captured and marked the lizards with a nontoxic and nonpermanent method. We used data about time of the observations, sampling duration, number of samplers and sampling month as covariates for detectability (p) and geographical position (latitude, longitude and elevation of the site), site size, climatic conditions and sampling period (year) as covariates for abundance (N). Various combinations of covariates were tested with a forward stepwise process, and the resulting models were compared by an AIC-based model-selection approach (Akaike 1973). Finally, for five sites, we calculated the variation of population size between past and new samplings as:

$$N_{\text{var}} = \left(\left(N_{\text{new}} - N_{\text{past}} \right) / N_{\text{past}} \right) \times 100$$

where N_{new} is the population size calculated from the new sampling data and N_{past} is the population size calculated from the past sampling data.

2.5 | Niche Margin Effect and Threshold Test

To clarify the effects of the climate on lizard populations, we used data on two bioclimatic variables at the sampling sites. We considered the ‘Maximum Temperature of the Warmest Month’ (Bio5) and the ‘Mean Temperature of the Warmest Quarter’ (Bio10) at two different time slices. We selected these two variables because they bring information about seasons when lizards' activity is highest and because they may be critical for thermoregulation (Bombi, Calò, and Salvi 2024). Field data collected during the past samplings (2003–2004) were analysed with bioclimatic variables for the period 1970–2000, downloaded from the WorldClim high spatial resolution databank (version 2.1; Fick and Hijmans 2017) with a resolution of 30 arc-seconds. Field data from the new samplings (2022–2023) were analysed with bioclimatic variables produced under the Coupled Model Intercomparison Project Phase 6 (CMIP6) by 23 modelling infrastructures for the period 2021–2040 according to the Shared Socioeconomic Pathway 5-8.5 (SSP5-8.5).

The two bioclimatic variables were used to explore the variation of thermoregulation coefficient (C), BCI and population trends across the thermal niche gradient. We fitted generalised linear models using population traits (C and BCI) as response variable and the

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climate (Bio5 and Bio10) as predictor. In addition, we tested the presence of a threshold temperature above which lizard populations begin to show differences in the *C* and BCI trends. We built 23 different datasets, one for each available climate prediction. We tested a range of different threshold temperatures, both for Bio5 and Bio10 and we selected threshold temperature that maximises the significance of the GLM fitted with below-threshold data (i.e., data from sites having climatic temperatures falling below the selected threshold). Finally, we estimated the threshold temperature for the population size variation as the temperature value related to a change from moderate ($<30\%$) to large ($>60\%$) variations of population size during the 20-year period, considering a variation that exceeds 60% as a directional trend.

In addition, to test the reliability of the site coefficients, we used an approach based on null models (Gotelli and Graves 1996). Site thermoregulation coefficients were calculated 1000 times randomising the temperature data and the relative relation between climate and thermoregulation coefficient was recalculated with the new values. The proportion of times that the simulated *p*-value (derived from permutations) was lower than the observed *p*-value (from original, nonpermutated data) was calculated and used as an aggregate *p*-value, indicating the probability that the final pattern derives by chance from random data.

Similarly, we tested whether the estimated threshold values improved the explanation of the observed patterns, by using a null-model approach (Gotelli and Graves 1996) to verify that the difference between the significance of the prethreshold GLMs (fitted on prethreshold data only) and the significance of the total GLMs (fitted on the entire dataset) was not due to chance. We compared the observed difference, from the original data, with the frequency distribution of the simulated differences, from 1000 random permutations of the climate data. The proportion of times that the simulated difference was higher than the observed difference indicates the probability that the increase of significance obtained assuming the existence of the threshold derives by chance from random data.

2.6 | Microhabitat Scale

We used the field-sampled temperature data to describe the thermal niche of *A. bedriagae* at the microhabitat scale. Air and rock temperatures measured in random points through the sampling sites define the available thermal conditions, while the temperatures measured in the points where each lizard was firstly observed indicate the conditions used by lizards. Available and used temperatures were compared through binomial GLMs and GLMMs. In addition, to clarify whether the thermal conditions used by lizards changed over time, we compared the used temperatures measured in new and past samplings.

3 | Results

Most of the variance associated with the relationship between T_{body} and the environmental temperatures is explained by T_{rock} ($R^2_{\mathrm{GLMM(fixed)}} = 0.15$, $p < 0.001$), a small portion of variance is explained by the random effect of sites ($R^2_{\mathrm{GLMM(random)}} = 0.07$) and a negligible variance portion is associated with the effect of T_{air} ($R^2_{\mathrm{GLMM(fixed)}} = 0.0001$, $p = 0.43$). Therefore, the thermoregulation coefficient (*C*) was calculated using T_{rock} as predictor. In line with the GLMMs results, *C* changed from site to site (see Figure 1 and Table 1). The populations with the highest mean *C* were Petraiaccio-Past ($\mathrm{PET}_{\mathrm{past}}$) and P. Colmi (PCO) and those with the lowest mean *C* values were Petraiaccio-New ($\mathrm{PET}_{\mathrm{new}}$), P. Falcone-New ($\mathrm{PFA}_{\mathrm{new}}$) and Maidopis-New ($\mathrm{MAI}_{\mathrm{new}}$). Thermoregulation coefficient changed remarkably between past and new samplings in the same sites. PET, PFA and MAI had a steep decrease, from good (MAI) or excellent (PET and PFA) thermoregulators to moderate thermoregulators; *M. Moro* (MMO) site had similar *C* between the two sampling periods, while Ortachis (ORT) was the only population that improved its *C*-value. Lizard body temperatures ranged from 26.8°C to 40°C with a mean value of 32.16°C.

The BCI, used like a proxy of the health status of the lizard populations, ranged from −0.83 in $\mathrm{PET}_{\mathrm{past}}$ to 1.00 in Columbare (COL) (see Table 1). The BCI increased from the past to the new samplings in all the resampled sites and was not affected by sampling season (p-value $= 0.87$). Population size analysis showed that *A. bedriagae* is a species with low detectability (Figure 2). This parameter ranged between 0.01 (in $\mathrm{PET}_{\mathrm{new}}$) and 0.2 (in COL) with a mean value of 0.12. Probability of detection was positively affected by the sampling effort (sampling duration and the number of samplers) while the sampling period and the time of the observations were less important (see Table S1 for details). The largest estimated population size was found in $\mathrm{MAI}_{\mathrm{past}}$ ($N = 84.85$) while in $\mathrm{PFA}_{\mathrm{new}}$ the lowest ($N = 12.68$). Population size slightly changed between past and new samplings in MAI (−3.6%), MMO (+27.6%) and ORT (−28.7%), while it strongly decreased in PET (−62.7%) and PFA (−62.1%).

The relationships between the thermoregulation coefficient and the two bioclimatic variables were not significant if all the data were considered (Figure 3A,B); but it became significant if sites with bioclimatic values above the predefined thresholds were excluded. The best threshold values for Bio5 ranged between 28.45°C and 29.00°C (mean = 28.85°C), depending on the considered climate scenario, with a mean *p*-value of 0.006 for the prethreshold regressions. For Bio10, the best thresholds ranged between 22.05°C and 23.4°C (mean = 23°C), with a mean *p*-value of 0.01 for the prethreshold regressions (Supporting Information S3 for details about pre- and postthreshold regressions). The thermoregulation coefficient in prethreshold sites increased when approaching the threshold value indicating the warm margin of the species thermal niche. The BCI decreased from cold sites to sites at the warm edge of the species thermal niche (Figure 3C,D). Regressions followed a linear decreasing pattern until the threshold temperature beyond which the relationships between BCI and thermal variables were disrupted. The best threshold values ranged from 28.7°C to 29.7°C (mean = 29.16°C) for Bio5 and from 21.55°C to 23.20°C (mean = 22.66°C) for Bio 10, with mean *p*-values for the prethreshold regressions of 0.04 and 0.05 respectively (Table S3). Over the 20 years' time span, population size showed moderate changes ($<30\%$) in three sites (MMO, MAI and ORT) and major declines ($>60\%$) in two sites (PFA and PET) (Figure 3E,F). The threshold values separating these two groups of sites (moderate vs. large changes) ranged from 28.95°C to 31.00°C (mean = 30.05°C) for Bio5 and from 24.55°C to 26.30°C (mean = 25.38°C) for Bio 10.

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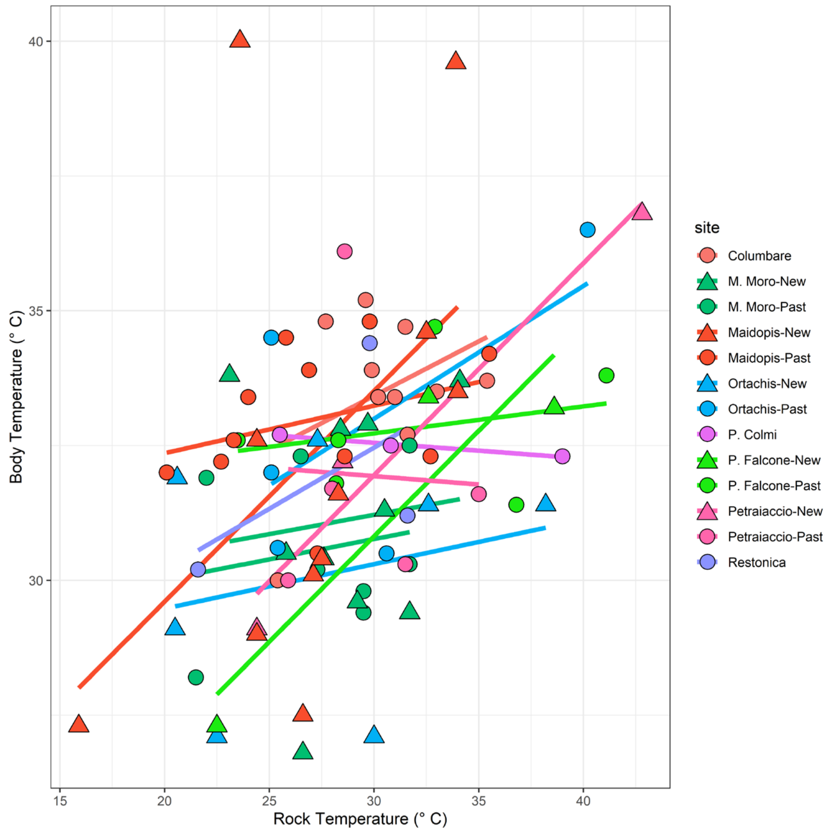

FIGURE 1 | Thermoregulation coefficient of the studied populations of *Archaeolacerta bedriagae*. Relationship between lizard body temperature and rock temperature of the points where lizards were firstly observed.

TABLE 1 | Thermoregulation coefficient (C) for each site and the relative p-values and R^2 of the fitted linear models.

Sites	C	p	R^2	BCI
Columbare	0.7978	0.2777	0.1449	1.0082
M. Moro-Past	0.9245	0.6406	0.0386	−0.3448
M. Moro-New	0.9288	0.7837	0.0099	0.2183
Ortachis-Past	0.8085	0.2661	0.2942	−0.2465
Ortachis-New	0.9176	0.6056	0.0572	−0.1049
P. Colmi	1.0292	0.0785	0.9848	0.5889
P. Falcone-Past	0.9499	0.6184	0.0677	−0.4107
P. Falcone-New	0.6088	0.2587	0.8436	1.0069
Petraiaccio-Past	1.0311	0.9428	0.0020	−0.8334
Petraiaccio-New	0.6067	0.1258	0.9614	−0.0912
Maidopis-Past	0.9118	0.3584	0.0942	−0.7896
Maidopis-New	0.6092	0.1394	0.2260	−0.4480
Restonica	0.7452	0.3976	0.3628	0.8650

Note: The ‘BCI’ column indicates the mean body condition index of the populations.

Tests based on null models support the reliability of thermoregulation coefficients. The aggregate p-value, derived from the 1000 prethreshold regressions recalculated using the simulated values of C is equal to 0.043 and 0.048 for Bio5 and Bio10 respectively. This indicates that the observed pattern is not due to chance.

Assuming the existence of a threshold temperature value improved the explanation of the observed pattern, that is, we observed an increase of significance in linear models considering the threshold temperature relative to models without the threshold (i.e., based on the whole dataset.). Such increase of significance was observed in all tested relationships and these increases were not due to chance (null model p-value <0.05). The p-values relative to the increase of significance of C were 0.04 and 0.018 for Bio5 and Bio 10 respectively; the p-values relative to the increase of significance of BCI were 0.038 and 0.046 for Bio5 and Bio10 respectively.

The difference between used and available microenvironmental temperature in the resampled sites (Figure 4) is mostly explained by the random effect of the sites ($R^2_{\text{GLMM(random)}} = 0.25$), with a limited amount of variance explained by the environmental temperatures ($R^2_{\text{GLMM(fixed)}} = 0.07$) mainly due to the effect of the air temperature ($p<0.01$). Three sites showed significant differences between available and used air temperatures: PFA ($R^2=0.11$, $p<0.05$), MAI ($R^2=0.05$, $p<0.05$) and ORT ($R^2=0.08$, $p<0.01$). The latter site also showed a significant difference between available and used rock temperatures ($R^2=0.05$, $p<0.05$). The used air temperatures measured in the new samplings were significantly higher than those from the past samplings ($R^2=0.317$, $p<<0.001$), whereas the used rock temperatures were not significantly different between past and new samplings ($R^2=0.003$, $p=0.473$). The available rock

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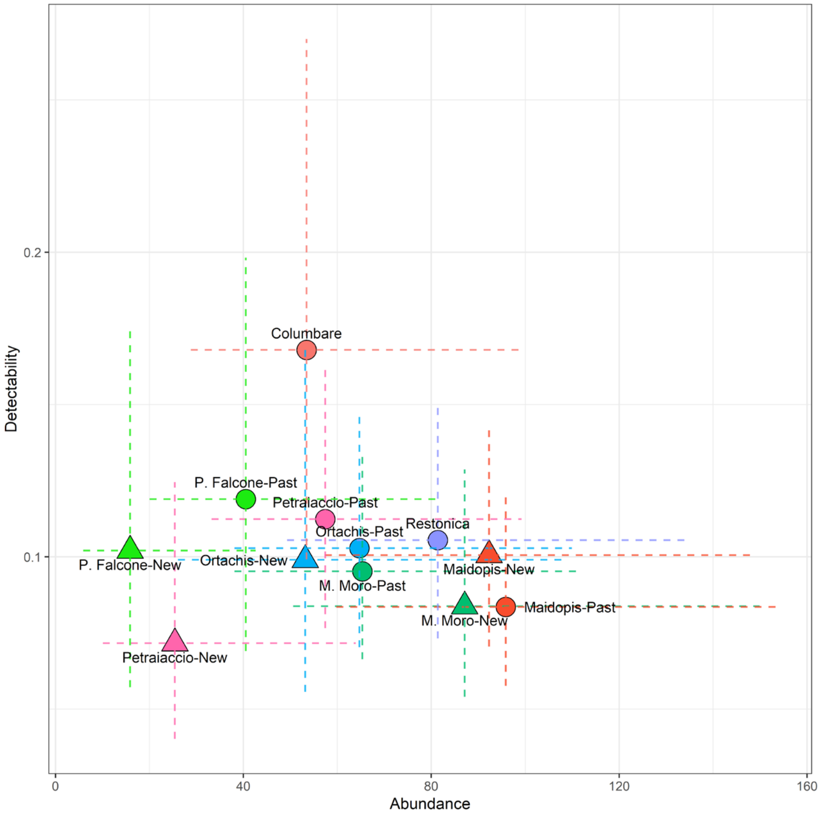

FIGURE 2 | Population size and detection probability for *Archaeolacerta bedriagae* in the different sites.

temperatures measured in the new samplings ranged from 9.4°C to 52.1°C (mean = 27.88°C), while available air temperatures ranged from 14.9°C to 39.2°C (mean = 29.86°C). These values were significantly different among sites (ANOVA $F_{\text{rock}} = 82.88$, $p_{\text{rock}} << 0.001$; $F_{\text{air}} = 121.03$, $p_{\text{air}} << 0.001$). Overall, considering both past and new samplings, the used temperatures ranged from 15.9°C to 42.8°C (mean = 28.96°C) for rock and from 12.0°C to 38.6°C (mean = 25.75°C) for air.

4 | Discussion

Understanding the relationship between the thermal quality of the environment and the ability of ectotherms to maintain their body temperature closer to the preferred range is crucial to predict the effects of climate warming on population survival (Ortega, Mencía, and Pérez-Mellado 2016; Alés et al. 2017). An increase of thermoregulation effort and coefficient with the reduction of habitat thermal quality from colder to warmer sites (NME) was documented in rock lizard populations (Bombi, Calò, and Salvi 2024) and other reptile species (e.g., Row and Blouin-Demers 2006; Vickers, Manicom, and Schwarzkopf 2011). However, deviations from this NME and detrimental effects on populations were recently observed in extremely warm sites (Bombi, Calò, and Salvi 2024), suggesting a disruption of thermoregulation processes under conditions exceeding the warm edge of the species' fundamental niche. This starting hypothesis is fully supported by our results. As expected under this hypothesis, we observed (i) the increase of thermoregulation coefficient and thermoregulation effort in populations inhabiting temperate sites (NME), (ii) the disruption of this pattern for populations inhabiting warmer sites that were pushed beyond the niche edge and (iii) the demographic collapse for populations in the warmest sites as a consequence of a negative cascade effect that propagates from individual to population level. Findings from this study provide insights into the thermal ecology of the study species, as they allow us to define its thermoregulatory strategy and to pinpoint the warmer limit of its fundamental thermal niche, as well as on conservation biology, because it allows to identify populations at greatest risk of extinction due to climate change before they show irreversible demographic decline.

4.1 | Thermoregulatory Strategy and Thermal Niche Limits in Bedriaga's Rock Lizards

Bedriaga's rock lizards are active in microhabitats with air temperature ranging between 12°C and 39°C and rock temperature between 16°C and 43°C. When these conditions are not available across the site, lizards take shelter in rock crevices. Under the 20-year interval studied, from past to new samplings, air temperatures used by lizards changed over time, following the global trend of increasing temperatures; in addition, it also changed over space, from site to site, according to the local conditions. On the contrary, used rock temperatures did not vary between sampling periods and across sites, suggesting both a major influence of rock temperatures on thermoregulation mechanisms and a lack of seasonal acclimation in this species, differently from the two potential competitors *Podarcis tiliguerta* and *Podarcis siculus* (Van Damme et al. 1990; Van Damme et al. 1989).

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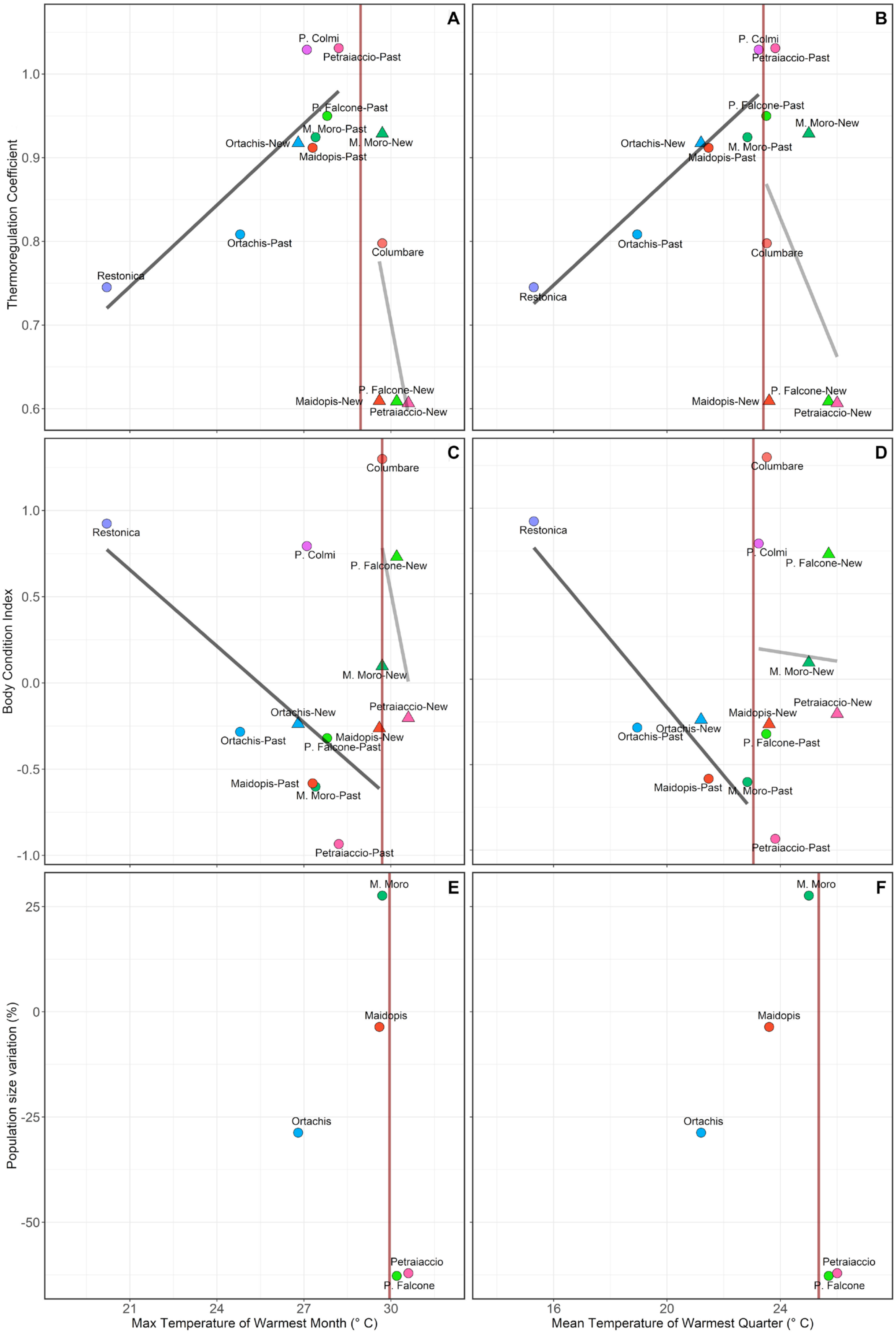

FIGURE 3 | Relationship between thermoregulation coefficient (A and B), body condition index (C and D) and population size variation (E and F) with climate. The red vertical lines represent the thresholds after which the niche margin effects are disrupted, indicating the thermal niche margin. In these plots, only the climatic prediction closest to the mean value is considered for clarity, the complete figure, with all the climatic predictions is shown in Figure S2.

Results of the GLMMs indicate that Bedriaga's rock lizards thermoregulate mainly by using microhabitats with suitable rock temperatures, with a marginal effect of the air temperature. This is coherent with the evidence of a stricter influence of rock temperatures on thermoregulation mechanisms, as discussed above. These results are in line with

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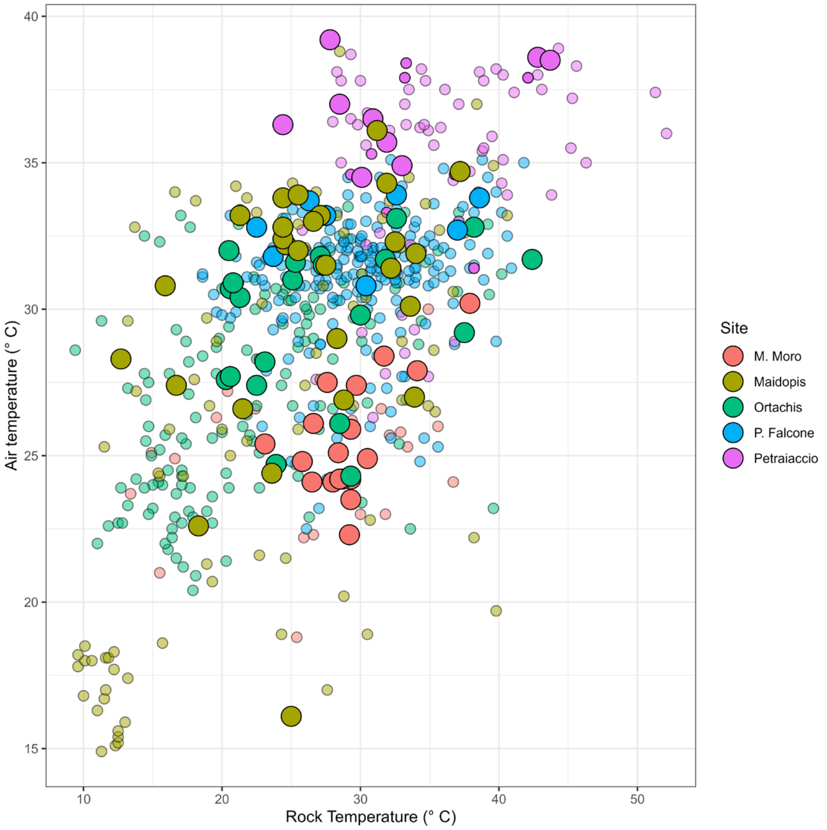

FIGURE 4 | Thermal niche of *Archaeolacerta bedriagae* at the microhabitat scale. Large points represent the selected temperatures of air and rock in the points where lizards were firstly observed. Small points represent the available conditions measured in random points across the study sites.

previous studies on lizards indicating that surface temperature represents the best predictor of lizard body temperature under warm and dry climatic conditions (Belliure and Carrascal 2002; Blais et al. 2023; Rivera-Rea et al. 2023). These conditions are particularly strong in rocky habitats, where the effect of high temperatures and lack of water typical of summer in Mediterranean climates are exacerbated. These results suggest that rock lizards have a thigmotherm thermoregulatory strategy (Pough and Gans 1982), gaining heat by conduction from the substrate.

4.2 | Thermoregulation Coefficient up to and Beyond the Niche Limit: Niche Margin Effect Disruption and Its Consequences

The coefficient of the thermoregulation process in rock lizards varies across space and time (from site to site and from past to new samplings) and suggests an effect of site-specific features associated with the habitat thermal quality. Several previous studies showed that: (i) changes of environmental conditions (e.g., hydric and thermal conditions, availability of shade and sun patches) over years or across space cause variations in the habitat thermal quality and influence thermoregulation effort, behavioural adjustments and coefficient of lizard thermoregulation (Gvoždík 2002; Artacho et al. 2017; Rozen-Rechels et al. 2021; Díaz, Izquierdo-Santiago, and Llanos-Garrido 2022) and (ii) thermoconformity is not the preferred strategy for reptile species in habitats with low thermal quality (e.g., Row and Blouin-Demers 2006; Vickers, Manicom, and Schwarzkopf 2011; Artacho et al. 2017). Under these conditions, the availability of suitable microhabitats is necessary to avoid climatic extremes (Diele-Viegas and Rocha 2018; Sunday et al. 2014). Our results are in agreement with these studies and corroborate previous observations on *A. bedriagae* by Bombi, Calò, and Salvi (2024). We found that rock lizards inhabiting sites with environmental temperatures closer to the warm margin of the species' thermal niche show increased thermoregulation coefficient. This pattern, named Niche Margin Effect (NME; Bombi, Calò, and Salvi 2024), holds until reaching a threshold (about 29°C for Bio5 and about 23°C for Bio 10) that identifies the niche edge. Beyond this threshold, thermoregulation coefficient collapses, suggesting that at exceedingly high environmental temperatures, the thermoregulation effort is no longer sufficient for guaranteeing an efficient control of body temperature.

To disclose possible effects of environmental thermal conditions on individual health status of lizards, we used the body condition index as it is related to storage and expenditure of energy and can reveal the effect of stress or limitations on individuals. Our results evidenced that, despite similar reptiles' community, the BCI is different across sites and sampling periods, showing an increase in the new sampling sites, and following a very similar pattern of variation along the climatic gradient as the thermoregulation coefficient, but with opposite values. Indeed, BCI decreases from colder to warmer sites until a similar threshold, after which BCI varies across sites without a direct linkage with climate. The reduction of BCI closer to the warm margin of the species niche can be explained by increased thermoregulation effort at the expenses of other activities like foraging.

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This is coherent with a process of 'metabolic meltdown' (Huey and Kingsolver 2019) and in agreement with previous studies on lizards that observed reduced BCI in response to climatic events (Waye and Mason 2008), habitat characteristics (e.g., Gabirot et al. 2013; Gallego-Carmona, Castro-Arango, and Bernal-Bautista 2016; Stark et al. 2022; Macdonald et al. 2023) or demographic fluctuations that influenced the intraspecific competition (Moore et al. 2007). The decreasing trend observed for the BCI until the niche margin, particularly its disruption beyond this climatic threshold, can be explained as a consequence of the increasing energetic cost associated with thermoregulation in hot conditions.

As suggested by the cost–benefit model of the thermoregulation (Huey and Slatkin 1976; Blouin-Demers and Nadeau 2005), lizards tend to become thermoconformers when the costs of efficient thermoregulation behaviour outweigh the benefits, in these cases body condition and fitness should be maximised with a not perfect thermoregulation (Neel 2023). In this respect, BCI can be interpreted as a proxy of the energetic cost paid by lizards for thermoregulating. The observed trends of thermoregulation coefficient and BCI in populations beyond the niche margin suggest that outside the thermal niche limit, an efficient thermoregulation is too expensive, and we can hypothesise that the consequential change in thermoregulation strategy (i.e., from thermoregulator to thermoconformer) allows lizards to reduce energy expenditure. We could speculate that such a reduction of the costs might explain the increased BCI observed in populations beyond the thermal niche limit.

Population size varies among sites and over time during the studied time frame of ~20 years. Our results show two groups of sites with distinct demographic trends: three sites with limited/moderate demographic variations and two sites with significant demographic decline. These two latter sites are those experiencing the most extreme climatic conditions. Remarkably, the climatic threshold separating the two groups of sites is slightly higher than the thresholds marking the disruption of the NME for thermoregulation coefficient and BCI. This indicates that population demographic effects appear later than (and are a likely consequence of) individual physiological effects due to reduced thermoregulation ability. These consequential effects indicate that the individual inability to cope with extreme climatic conditions could lead, in the long term, to demographic collapse, and ultimately to local extinction.

In line with previous studies, we observed a very low probability of detection for lizards (e.g., Ficetola et al. 2018), as expected for small vertebrates that have many potential predators and also a high availability of rock crevices where they can hide. In these cases, caution is needed when interpreting population estimates as absolute values, because uncertainty in *N*-mixture models increases with low detectability (McIntyre et al. 2012; Yamaura, Kéry, and Andrew Royle 2016). However, our comparative approach is based on the comparison of population size estimates among sites and between sampling years, rather than on absolute estimates of population size.

The consequential relation between NMEs and population reductions corroborates the conclusions by Sagarin and Gaines (2002) that the 'abundant centre' distribution is not a general biogeographical rule. Indeed, population size does not decrease until the niche margin is reached and, as a consequence, population decline is a late indicator of the detrimental effect of global warming on ectotherms. This implies that demographic studies alone, even if robust and based on long-term data, do not allow to detect NMEs and thus to recognise whether populations are getting closer to the niche margin. On the other hand, indicators such as individual thermoregulation capacities and/or body conditions are promptly sensitive to NMEs and provide an early warning system to predict potential demographic impacts. Therefore, monitoring programmes should rely on these kinds of indicators, rather than on demography alone, to identify populations facing the greatest risk of extinction due to global warming. In addition, a multipopulation approach allows to identify where the effects of climate change are already occurring and where they are expected in the near future.

4.3 | Conservation Implications

This study verifies the predictions of the Niche Margin Effect (Bombi, Calò, and Salvi 2024) and provides support for a mechanism of disruption of individual and populational homeostatic processes when the warm margin of the thermal niche is reached. Negative physiological effects related to thermoregulation ability and body index emerge at remarkably similar thermal conditions and are followed by the collapse of the population. The approach implemented in our study allows to identify the niche edge that underlies the brink of collapse. This corresponds to the environmental conditions at which the detrimental effects of exceedingly hot climate on individual thermophysiology and body condition translate into demographic impacts that might anticipate local extinction. It is important to remark that because of the time-lagged response of populations to climate warming, the observation of a demographic decline might indicate an already advanced stage towards the extinction vortex. Therefore, individual thermophysiology parameters such as thermoregulation coefficient represent a key indicator for an early detection of population extinction risk.

Ectotherms are bioindicators of the environmental quality because of their tight dependence on environmental conditions, and several studies have demonstrated that human activities, habitat modification and global change are the main causes of their decline (e.g., Gibbons et al. 2000; Huey et al. 2012; Lara-Reséndiz et al. 2015; Wang et al. 2016; Doherty et al. 2020). Nowadays many ectotherms' populations are living on (or close to) the edge of their thermal tolerance. Identifying the niche margin and detecting NMEs in some population traits allows to identify and forecast which sites are prone to demographic collapses. This might allow to plan appropriate mitigation measures and management strategies to avoid local extinctions.

Author Contributions

P.B. and F.C. conceived the ideas and designed the methodology; P.B., D.S. and F.C. collected the data; P.B. and F.C. analysed the data; P.B., D.S. and F.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

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