RESEARCH ARTICLE

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Heat tolerance is more variable than cold tolerance across species of Iberian lizards after controlling for intraspecific variation

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Abstract

1. The widespread observation that heat tolerance is less variable than cold tolerance ('cold-tolerance asymmetry') leads to the prediction that species exposed to temperatures near their thermal maxima should have reduced evolutionary potential for adapting to climate warming. However, the prediction is largely supported by species-level global studies based on single estimates of both physiological metrics per taxon.

2. We ask whether cold-tolerance asymmetry holds for Iberian lizards after accounting for intraspecific variation in critical thermal maxima (CT_{max}) and minima (CT_{min}). To do so, we quantified CT_{max} and CT_{min} for 58 populations of 15 Iberian lizard species (299 individuals). Then, we randomly selected one population from each study species (population sample = 15 CT_{max} and CT_{min} values), tested for differences between the variance of both thermal metrics across species, and repeated the test for thousands of population samples as if we had undertaken the same study thousands of times, each time sampling one different population per species (as implemented in global studies).

3. The ratio of variances in CT_{max} to CT_{min} across species varied up to 16-fold depending on the populations chosen. Variance ratios show how much CT_{max} departs from the cross-species mean compared to CT_{min}, with a unitary ratio indicating equal variance of both thermal limits. Sampling one population per species was six times more likely to result in the observation of greater CT_{max} variance ('heat-tolerance asymmetry') than cold-tolerance asymmetry. The probability of obtaining the data (given the null hypothesis of equal variance being true) was twice as likely for cases of cold-tolerance asymmetry than for the opposite scenario.

4. Range-wide, population-level studies that quantify heat and cold tolerance of individual species are urgently needed to ascertain the global prevalence of cold-tolerance asymmetry. While broad latitudinal clines of cold tolerance have been strongly supported, heat tolerance might respond to smaller-scale climatic and habitat factors hence go unnoticed in global studies. Studies investigating physiological responses to climate change should incorporate the extent to which thermal traits are characteristic of individuals, populations and/or species.

1 | INTRODUCTION

Our understanding of how climate change impacts biodiversity has been notably improved through macrophysiological analyses that describe patterns of organismal heat and cold tolerance over large spatial and temporal scales (Chown & Gaston, 2016). The predictive power of such approaches has recently prompted the creation of a dataset of species' thermal traits across the tree of life and the different biomes on Earth (Bennett et al., 2018). These data resources are bound to fuel a wealth of future research because the modelling of latitudinal clines of global thermal tolerance typically relies on georeferenced, species-level data (e.g. Deutsch et al., 2008; Gunderson & Stillman, 2015; Huey et al., 2009; Sunday, Bates, & Dulvy, 2010).

A fundamental prediction from global patterns of thermal tolerance is that many species currently exposed to temperatures close to their upper thermal limits might have exhausted the potential to unfold further tolerance to warming (Araújo et al., 2013; Grigg & Buckley, 2013; Gunderson & Stillman, 2015; Hoffmann, Chown, & Clusella-Trullas, 2013). This prediction rests on the consistent and widespread observation of 'thermal niche asymmetry' (sensu Herrando-Pérez, 2013) whereby cold tolerance is more variable than heat tolerance in hundreds of species of plants, ectotherms and endotherms (Araújo et al., 2013). Lizards are abundant and easy to study and ecologists accumulate an encyclopaedic knowledge of their life histories and ecophysiology (Camargo, Sinervo, & Sites, 2010), so they have been widely used to investigate the eco-evolutionary consequences of thermal niche asymmetry. Thus, Grigg and Buckley (2013) showed that critical thermal maxima (CT_{max}) were more phylogenetically conserved across 254 species of lizards than were critical thermal minima (CT_{min}), thereby backing that heat tolerance should show less variability than cold tolerance across species. Such conservatism implies that the evolution of heat tolerance could require more pronounced functional shifts in physiological performance and genetic make-up than the evolution of cold tolerance (Hoffmann et al., 2013), the lack of which could weaken adaptive responses to warming (Stillman, 2004) such as the heat-shock response (Stillman & Tagmount, 2009).

Tests for thermal niche asymmetry generally incorporate the thermal traits of only one population per species (see papers using >100 species in Table 1), thereby assuming that interspecific variation overrides intraspecific variation or that population-level variation might have negligible impacts on overall patterns (Schou, Mouridsen, Sørensen, & Loeschcke, 2016). Here, we explicitly test this assumption by querying the extent to which intraspecific variability in thermal limits can change the frequency and direction of thermal-tolerance asymmetries using CT_{max} and CT_{min} from 58 populations of 15 species of Iberian lizards. This is an important area of enquiry because intraspecific variation in thermal tolerance of ectotherm fauna (see Clusella-Trullas & Chown, 2014; Sinclair et al., 2016) is a major component structuring biological communities (Violle et al., 2012), can improve our forecasts of biodiversity responses to environmental change (Artacho, Saravia, Perret, Bartheld, & Galliard, 2017; Kolbe, Kearney, & Shine, 2010; Lancaster, 2016; Valladares et al., 2014) and, if disregarded, result in rival predictions of the amount of time over which environmental temperatures might exceed a species' CT_{max} (Herrando-Pérez, Ferri-Yáñez, et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Field and laboratory work

We sampled 15 species of lacertid lizards by noosing 299 adult males from 58 Spanish and Portuguese mainland populations in the spring and early summer of 2013 and 2014 (mapped in Figure S1). The species set (listed in Table 2) represents all of the major lineages of Iberian lacertids (see Pyron, Burbrink, & Wiens, 2013). Sampling effort totalled 2–5 populations per species (median = 4 populations/species with 90% interquartile ranges of [3, 4]), and 3–10 males/population (5 [5, 6]). A minimum sample size of three males per population should accurately capture the mean population CT_{max} estimated from larger sample sizes (Herrando-Pérez, Ferri-Yáñez, et al., 2019), and is within the range of published work (e.g. Beal, Lattanzio, & Miles, 2014; Muñoz et al., 2016). Our populations were identical to those used by Herrando-Pérez, Ferri-Yáñez, et al. (2019)—barring one Spanish population of the common wall

TABLE 1 Treatment of intraspecific variability of thermal tolerance in papers supporting cold-tolerance asymmetry (heat tolerance less variable than cold tolerance) across >100 terrestrial species. N (sample size) indicates the number of species (N_{sp}) and the median number of populations per species (with 90% interquartile ranges). Literal quotations are italicized

Reference	Taxa	N_{sp}	N_{pop}	Thermal metric	Treatment of intraspecific variability	Statistical approach and pattern support
Addo-Bediako et al. (2000)[a]	arthropods	250	1	CT_{max} LLT SCP ULT	*Where a species was examined more than once, either in a single paper or by different authors, the record with the highest ULT or CT_{max} was selected. If a species was entered twice or more with the same ULT or CT_{max}, then the record from the geographical location which was least represented in the database was selected*	Visual inspection of scatter diagrams (published figure 2a) of latitude in abscissas (also controlling for altitude, published figure 2c) against species' thermal tolerances (one data point per species and tolerance estimate) in ordinates. Analyses support that heat tolerance experiences less geographical variation than cold tolerance (published figure 3)
Araújo et al. (2013)[b]	amphibians arthropods birds mammals reptiles	26 461 70 157 164	1[1,1] 1[1,4] 1[1,1] 1[1,1] 1[1,2]	CT_{max} CT_{min} LCT LLT UCT ULT	For species examined several times (i.e. in different studies or experimental treatments), authors selected the lowest and highest metrics of cold and heat tolerance, respectively	Visual inspection of boxplots of heat vs. cold tolerance in broad taxonomical groups (published figures 2, 3, 4), and linear regression of thermal tolerance in response to ambient temperatures (including controls for body size, published figure 5). Analyses support greater variation in cold than in heat tolerance, and correlation of ambient temperature with cold tolerance alone
Grigg and Buckley (2013)[c]	reptiles	401	1[1,1]	CT_{max} CT_{min} Tb TTB	*Data were reviewed and corrected when multiple measurements were recorded for the same species in a given location. For example, duplicate rows were deleted and separate Tb recordings for male and females at a given location were either combined or not used*	A variance–covariance matrix of heat and cold tolerance (separately) as response modelled against phylogenetic, spatial and residual effects via phylogenetic independent contrasts (published figure 2a, 2b). Models support much larger residual effects on variation in cold relative to heat tolerance
Gunderson and Stillman (2015)	amphibians arthropods reptiles	68 46 29	1[1,4] 1[1,3] 1[1,1]	CT_{max} CT_{min}	*If acclimation capacity was reported for multiple ages or developmental stages in a population, we always chose data for the oldest or most developmentally advanced group... if plasticity values were measured across categories such as sex or season for a population, as a rule we always chose data for the group that demonstrated the greatest plasticity*	CT_{max} and CT_{min} as responses in separate linear mixed-effects models with phylogenetic relatedness as random factor, and habitat type and acclimation time and latitude or seasonality as predictors. Analyses support that plasticity in heat tolerance is unrelated to latitude or thermal seasonality, whereas cold tolerance is related to seasonality (published tables 1, 2, figures 1, 2)
Hoffmann et al. (2013)[d]	arthropods reptiles	176 238	1[1,2] 1[1,1]	CT_{max} CT_{min} HCT LLT SCP ULT	*If data for several populations were reported for the same species and the criteria above[e] did not favour one study over another, an arithmetic mean was calculated for the species* (Clusella-Trullas, Blackburn, & Chown, 2011)	Levene's homoscedasticity test (published table 1), visual data inspection (published figure 1) following (Addo-Bediako et al., 2000), and phylogenetic-least squares models of heat and cold tolerance (separately) as response against mean ambient temperature (published table 2, figure 2). Analyses support greater variation in cold over heat tolerance, and model support for geographical variation in cold tolerance alone

(Continues)

TABLE 1 (Continued)

Reference	Taxa	N_{sp}	N_{pop}	Thermal metric	Treatment of intraspecific variability	Statistical approach and pattern support
Sunday et al. (2010)[f]	amphibians arthropods reptiles	30 79 128	1[1,1] 1[1,1] 1[1,1]	T_{max} T_{min} TTB	*Where separate studies of the same species were encountered (n = 19 cases), a single study was selected that most closely met the following criteria: it either (i) documented thermal tolerance temperatures in both summer and winter, (ii) included the greatest range of high and low acclimation temperatures or (iii) if it was a 'no acclimation' study, it had the largest sample size*	Mixed-effects model of cold and heat tolerance (separately) as response against acclimation history, habitat, hemisphere and latitude as fixed effects (individually and in combination) and phylogeny as random effect (published table 1, figure 4). Models support stronger variation in cold over heat tolerance across latitude only in terrestrial species

Abbreviations: CT_{max}, critical thermal maxima; CT_{min}, critical thermal minima; HCT, heat coma temperature; LCT, lower critical temperature; LLT, lower lethal temperature; SCP, supercooling point; Tb, activity body temperature; T_{max}, upper thermal limit; T_{min}, lower thermal limit; TNZ, thermal neutral zone; TTB, thermal tolerance breadth; UCT, upper critical temperature; ULT, upper lethal temperature.

[a]Unpublished dataset so median and interquartile ranges could not be calculated—See Hoffmann et al. (2013) below[d].

[b]Plant species excluded from counts for consistency with the other studies reported, which exclusively focus on animal species.

[c]Grigg and Buckley (2013) collated CT_{max}, CT_{min} and TTB for 113 species from Sunday et al. (2010).

[d]Hoffmann et al. (2013) collated arthropod and reptile metrics from Addo-Bediako et al. (2000) and Clusella-Trullas et al. (2011), respectively.

[e]Criteria after Clusella-Trullas et al. (2011): *In cases where more than one study was found for the same species, priority was given to (i) studies that measured CT_{max}, CT_{min}, and T_p (preferred body temperature) (or CT_{max} and CT_{min}) for the same population; (ii) field-fresh individuals over those given short-term acclimations and short-term acclimated individuals over those given long-term acclimations; (iii) data taken during active phases (i.e. daytime for diurnal and nighttime for nocturnal species) and active seasons; (iv) data taken in a fasted state over a fed state; (v) photothermal and thigmothermal gradients for heliothermic and thigmothermic species, respectively; (vi) arithmetic mean over median T_p (due to the higher availability of the former); (vii) the loss of righting response over the onset of spasms (OS) as the end point of CT_{max} and CT_{min} (due to the paucity of OS usage across species; Lutterschmidt & Hutchison, 1997); and (viii) acclimation at 20° or 25°C when only studies with acclimated individuals were available; if data at these temperatures were not available, the arithmetic mean of acclimation groups was used.*

[f]Sunday et al. (2010) regarded both lethal and critical lower limits as T_{min}, and collated one estimate per species (including aquatic species as in Gunderson and Stillman (2015)).

lizard *Podarcis muralis* from Moncayo (Soria), which we excluded because only CT_{max} data were available. Owing to the amount of field-work required, our sampling scheme was designed to cover a grid of localities maximizing species richness with minimum travelled distance, and capturing at least half of the length of the climate gradients occupied by each species (described by Herrando-Pérez, Ferri-Yáñez, et al., 2019). Thus, for most of our study species, their climatic ranges vary over regions experiencing a gradient from high Spring-to-Autumn precipitation to high Summer temperatures.

After sampling each population in the field, we transported all lizards to the 'Ventorrillo Field Station' in Madrid (Spain) and housed them in individual terraria at 25°C (08:00–18:00 hr, lights-on) and 15°C (18:00–08:00, lights-off) for 14 days. We fed lizards daily with house crickets and spring water in a Petri dish. Following the acclimation period, we measured critical temperatures by inserting a wired thermocouple probe 1–2 cm (depending on body size) into the cloaca and placing each individual in a thermal chamber. CT_{min} was estimated first, for which we decreased body temperature by cooling the chamber at ~1°C/min until reaching body temperatures of 15°C, and thereafter at 0.5°C/min. On the following day, we measured CT_{max} by exposing each lizard to a 150-watt red bulb from a distance of ~30 cm and ramping body temperature at ~1.0°C/min up to 39°C, and thereafter at 0.5°C/min. CT_{max} and CT_{min} were the body temperatures at which lizards lost their righting response (Huey & Stevenson, 1979; Lutterschmidt & Hutchison, 1997). We maintained a single rate across

individuals for comparative purposes, so without making adjustments in cooling or heating rates (Terblanche, Deere, Clusella-Trullas, Janion, & Chown, 2007). After the cold shocks, individuals ate, drank and behaved normally. And immediately after the heat shocks, we held each lizard for 30 s in a bath of tap water up to their necks to prevent physiological/physical damage. On completion of experiments, we provided water and food ad libitum to all lizards for up to five consecutive days and ultimately freed them at their point of capture.

2.2 | Data analyses

All statistical analyses and plotting were done in *R* (R Core Team, 2019) and we cite all packages and functions used in the Supporting Information. Throughout, we estimated the CT_{max} and CT_{min} of each population as the mean values over all male lizards sampled from a given locality (our analyses yielded equivalent results using population medians). Hereafter, we define a 'population sample' as 15 CT_{max} and 15 CT_{min} estimates obtained by randomly selecting one population from each study species. Our statistical analyses consisted of a three-step protocol as follows: (a) we took one population at random to represent the heat and cold tolerance of each species, as done routinely in the literature (Table 1; see Section 1), (b) we tested for zero differences between CT_{max} and CT_{min} variability across species (null hypothesis, see below) and (c) we applied the same statistical

TABLE 2 Ecophysiological summary of 15 species, 58 populations and 294 male lizards (Family Lacertidae) including sample sizes, and means (variances) of population critical thermal maxima (CT_{max}) and minima (CT_{min}) within species (across population means) and within populations (means across individuals). Populations used in Figure 1a are superindexed (ca = cold-tolerance asymmetry, ts = tolerance symmetry, ha = heat-tolerance asymmetry)

Species	Populations	Individuals	Species		Populations		Site
			CT_{min} (°C)	CT_{max} (°C)	CT_{min} (°C)	CT_{max} (°C)	Coordinates (lat/long)
Acanthodactylus erythrurus	Matalascañas[ha]	5	7.3 (0.6)	46.0 (1.8)	6.8 (0.5)	47.4 (0.8)	37.0/−6.6
	Collado Mediano	5			7.7 (1.7)	45.9 (2.6)	40.7/−4.0
	Los Santos	5			7.2 (1.0)	45.9 (1.1)	40.5/−5.8
	Ontígola[ca,ts]	7			7.6 (0.3)	44.6 (0.2)	40.0/−3.6
Algyroides marchi	Tranco	5	5.7 (0.8)	42.0 (0.2)	6.5 (1.6)	42.2 (0.3)	38.2/−2.8
	Mundo	5			5.7 (0.1)	42.4 (0.0)	38.5/−2.4
	Borosa[ca,ts]	5			4.3 (0.2)	42.2 (0.1)	38.0/−2.8
	Guadalquivir[ha]	5			6.3 (0.6)	41.4 (0.4)	37.8/−3.0
Iberolacerta cyreni	Puerto Morcuera	5	5.7 (4.2)	42.2 (0.1)	4.3 (0.0)	42.8 (0.1)	40.8/−3.8
	Peña Negra	5			5.9 (0.7)	42.2 (0.1)	40.4/−5.3
	Navalhorno[ca]	5			8.5 (1.1)	41.9 (0.3)	40.8/−4.0
	Valdesquí[ts]	5			4.3 (2.8)	41.8 (0.2)	40.8/−4.0
	Plataforma[ha]	5			5.6 (0.5)	42.2 (0.4)	40.3/−5.2
Iberolacerta monticola	Cabeza Manzaneda[ha]	4	5.2 (1.6)	41.4 (0.0)	6.7 (0.8)	41.5 (0.5)	42.3/−7.3
	Serra Estrela	10			4.8 (0.3)	41.2 (0.1)	40.3/−7.6
	Parada[ts]	5			4.4 (4.1)	41.2 (0.0)	42.6/−7.1
	Ancares[ca]	5			5.0 (1.0)	41.5 (0.3)	42.8/−6.9
Lacerta bilineata	Moncayo	5	4.4 (1.1)	41.4 (0.2)	4.6 (0.5)	41.2 (0.3)	41.8/−1.9
	Camino del Hayedo[ha]	5			5.8 (1.0)	41.2 (0.3)	41.9/−2.7
	Canfranc[ca,ts]	5			3.3 (0.2)	42.2 (0.2)	42.8/−0.5
	Refugio	3			4.0 (0.2)	41.1 (0.1)	42.8/−0.7
Lacerta schreiberi	Rebollar[ha]	5	5.2 (1.5)	41.7 (0.3)	6.5 (1.0)	42.1 (0.8)	40.3/−6.6
	Alameda del Valle[ca]	5			6.0 (0.5)	42.1 (0.2)	40.9/−3.8
	Plataforma	5			4.1 (0.3)	41.5 (0.5)	40.3/−5.2
	Valdesquí[ts]	5			4.0 (0.2)	41.1 (0.2)	40.8/−4.0
Podarcis muralis	Navaleno[ha]	5	5.1 (1.7)	43.0 (0.9)	6.3 (0.2)	42.8 (0.4)	41.8/−3.0
	Cercedilla[ts]	5			4.9 (2.9)	43.7 (0.9)	40.8/−4.0
	Lozoya[ca]	5			4.2 (0.9)	42.5 (0.4)	41.0/−3.8
Podarcis liolepis	Candasnos[ha]	6	7.3 (0.9)	43.0 (1.8)	6.6 (0.5)	44.8 (0.2)	41.5/0.1
	Noviercas[ts]	5			7.0 (0.3)	44.0 (1.3)	41.7/−2.0
	Gésera	5			7.1 (0.3)	41.9 (0.3)	42.4/−0.3
	Valle de Hecho[ca]	5			8.1 (0.5)	42.6 (0.5)	42.8/−0.8
	Cuellar	5			7.8 (6.6)	41.9 (1.8)	41.4/−4.3
Podarcis carbonelli	Esmoriz[ca]	5	7.2 (0.1)	44.9 (0.2)	7.1 (0.4)	44.7 (0.2)	41.0/−8.6
	Matalascañas[ts,ha]	5			7.3 (0.5)	45.1 (0.4)	37.0/−6.6
Podarcis hispanicus sensu stricto	Puebla Salvador[ts]	4	5.2 (1.2)	43.5 (0.2)	4.2 (4.7)	44.1 (0.3)	39.6/−1.7
	Ciudad Encantada	5			5.7 (0.5)	43.4 (0.4)	40.2/−2.0
	Guadalquivir[ha]	5			5.8 (0.8)	43.3 (0.7)	37.8/−3.0
	Cazorla[ca]	5			5.1 (1.4)	43.2 (0.4)	37.9/−3.0

TABLE 2 (Continued)

Species	Populations	Individuals	Species CT$_{min}$ (°C)	Species CT$_{max}$ (°C)	Populations CT$_{min}$ (°C)	Populations CT$_{max}$ (°C)	Site Coordinates (lat/long)
Podarcis guadarramae	Segovia[ca,ts]	5	6.7 (0.1)	43.4 (0.4)	7.2 (2.1)	43.1 (0.6)	41.0/−4.1
	Navalcán	5			6.4 (0.2)	43.2 (0.5)	40.0/−5.1
	Hoyos del Espino	5			6.6 (0.2)	43.0 (0.6)	40.4/−5.2
	Alto del León[ha]	5			6.6 (0.2)	44.2 (0.0)	40.7/−4.1
Podarcis vaucheri	Matalascañas[ts]	5	6.2 (1.2)	44.0 (0.5)	7.6 (0.1)	45.3 (0.5)	37.0/−6.6
	La Barrosa[ca]	5			5.1 (0.3)	43.3 (0.3)	36.4/−6.2
	La Sauceda	5			5.3 (0.5)	43.6 (0.1)	36.5/−5.6
	Villaluenga Rosario[ha]	5			7.0 (1.0)	43.8 (0.0)	36.7/−5.4
Podarcis virescens	Aranjuez[ts,ha]	5	5.4 (0.9)	42.6 (0.4)	6.5 (2.6)	42.1 (0.6)	40.0/−3.6
	Évora[ca]	5			4.2 (0.4)	42.0 (0.1)	38.6/−7.9
	Fuertescusa	5			5.3 (1.0)	43.5 (0.5)	40.5/−2.2
	Borosa	5			5.5 (0.9)	42.8 (0.5)	38.0/−2.9
Psammodromus algirus	Matalascañas	5	6.8 (0.0)	43.1 (0.1)	7.4 (1.2)	43.1 (0.1)	37.0/−6.6
	Navacerrada	5			6.7 (0.4)	43.5 (0.3)	40.7/−4.0
	Navacepeda de Tormes[ca,ts]	10			7.0 (0.5)	42.9 (0.3)	40.4/−5.3
	Trujillo[ha]	5			6.2 (1.5)	42.7 (0.8)	39.5/−5.9
Psammodromus hispanicus	Aranjuez[ca]	5	6.6 (0.1)	45.2 (1.9)	6.7 (6.2)	43.8 (1.4)	40.0/−3.6
	El Espinar	5			6.8 (1.5)	45.6 (1.1)	40.7/−4.3
	Riópar[ts,ha]	5			6.3 (0.6)	46.1 (0.7)	38.5/−2.4

test for batches of 1×10^3, 1×10^4, 1×10^5, 1×10^6 and 1×10^7 different population samples—we sketch the resampling procedure in Figure S2.

To test for differences in CT$_{max}$ vs. CT$_{min}$ variability across species, prior authors have used disparate approaches, namely visual inspection of (box)plots, homoscedasticity tests, and linear regression with and without phylogenetic and geographical controls (Table 1). Here, we use homoscedasticity tests because their outputs are easily comparable across thousands to millions of population samples. We were interested in overall statistical patterns, so we dispensed with *post hoc* corrections for multiple testing. For each population sample, we applied the F_{max} test (Hartley, 1950) in the R package STATS to contrast the (null) hypothesis of homoscedasticity (CT$_{max}$ variance = CT$_{min}$ variance) with the (alternative) hypothesis of heteroscedasticity (CT$_{max}$ variance ≠ CT$_{min}$ variance) across our 15 study species. This test quantifies the ratio of the variance of each of two groups of measurements (CT$_{max}$ variance vs. CT$_{min}$ variance), whereby a ratio close to 1 implies homogeneity of variances. We evaluated the consistency of our results by applying four additional homoscedasticity tests, namely Barlett (R package STATS), Levene (*car*), Brown–Forsythe (*vGWAS*) and PERMDISP (*vegan*) tests. Succinctly, the Barlett test is based on a χ^2 statistic computed from the logarithm of the among-group weighted variances (Bartlett, 1937). The Levene test is based on a single-classification ANOVA between the means of the deviations of single observations from group medians. The Brown–Forsythe is akin to the Levene test except that the ANOVA

is applied to the medians of the deviations of single observations from group medians (Brown & Forsythe, 1974). Finally, PERMDISP is a multivariate analogue to the Levene test, where group dispersion is measured as the Euclidean distance of single observations to group centroids or medians (Anderson, 2006)—for the latter, we used group medians, though group centroids gave equivalent results.

In our study, the rejection of the null hypothesis of equal variance by the F_{max} test could occur in rival scenarios representing two different alternative hypotheses: (a) 'cold-tolerance asymmetry' for population samples where CT$_{max}$ variance < CT$_{min}$ variance as opposed to (b) 'heat-tolerance asymmetry' for population samples where CT$_{max}$ variance > CT$_{min}$ variance (examples of those scenarios shown in Figure 1a). Therefore, for each of the five batches of population samples (1×10^3 to 1×10^8, see above), we counted the times both outcomes occurred and the associated *probability* (*p*) of the observed data given the null hypothesis (homoscedasticity). To control for the fact that the number of individuals sampled per population varied, which could bias our population estimates of thermal-tolerance variance, we replicated the entire analyses using (a) the full dataset with all individuals, and (b) the CT$_{max}$ and CT$_{min}$ from three individuals randomly selected from each population/species for each population sample. Our expectation is that, if cold-tolerance asymmetry is a predominant phenomenon across species in our study area (see Section 1), it should not depend on lizard population identity, so the number of population samples statistically supported for CT$_{max}$ variance < CT$_{min}$ variance must
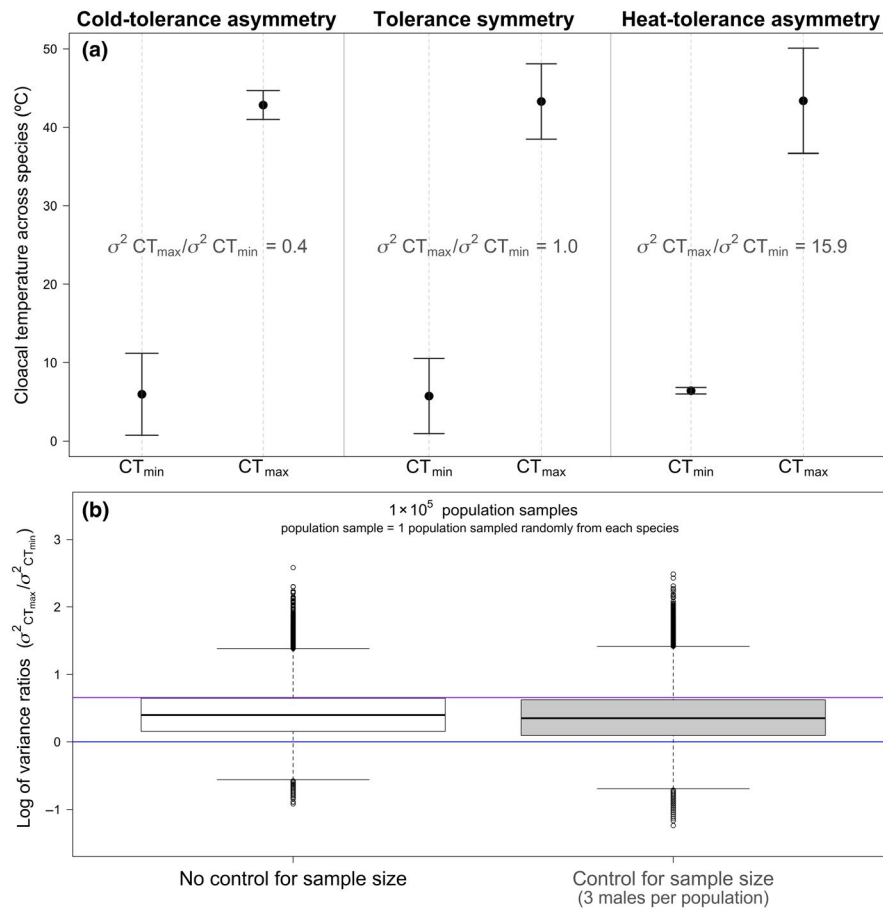
FIGURE 1 Variance (σ^2) in critical thermal maxima (CT_{max}) and minima (CT_{min}) across 15 Iberian lizard species. Upper plots (a) show three alternative scenarios*, where each species is represented by one population (populations used to generate the plots superindexed in Table 2). Black circles are means ± 2 times the variance. Boxplots (b) show CT_{max} σ^2/CT_{min} σ^2 ratios on a logarithmic scale for each of 10^5 population samples based on 58 study populations (2–5 per species, see Table 2). Data points represent a population sample including 1 population taken randomly from each of the 15 study species, and the horizontal blue and purple lines indicate ratios of (unlogged) 1.0 (CT_{max} σ^2 = CT_{min} σ^2) and 1.9 (maximum population CT_{max} and minimum population CT_{min} selected from each species), respectively. The three panels in the upper plot (a) are three examples of the full set of data points in the boxplots (b)**. CT_{max} and CT_{min} were the average of the CT_{max} and CT_{min} of all males sampled (3–10 per population; white box), or three males taken randomly from each study population (grey box). *The F_{max} probability of homoscedasticity between both thermal limits was 0 for cold- and hot-tolerance asymmetry, and 1 for tolerance symmetry. **The example of heat-tolerance asymmetry was obtained from a batch of 1×10^7 population samples (Figures S2, S3)

outnumber those supported for CT_{max} variance > CT_{min} variance. Throughout, we have deliberately avoided the use of the term 'significant' (and derivatives) because of its semantic vagueness and lack of biological meaning (Johnson, 1999). Consequently, we report each *p* value following McCarthy (2007) such that it represents the probability of obtaining the data (e.g. an observed difference in an ANOVA test or, in our case, an observed variance ratio in a F_{max} test) if the null hypothesis is true (e.g. a zero difference between treatment means in an ANOVA test or, in our case, a unitary variance ratio in a F_{max} test).

Homoscedasticity tests do not quantify the amount of variation in CT_{max} and CT_{min} across species that can be attributed to population differences alone, nor control for allometric effects. Given our a priori expectation of the prevalence of cold-tolerance asymmetry (see above), we also expected differences in CT_{max} to be weaker than differences in CT_{min} among species after accounting for population variation in both thermal limits.

We addressed this question through a nested analysis of variance in a generalized linear mixed-effects model with populations (random effects) nested within species (fixed effects) for each physiological metric separately (CT stands for CT_{max} or CT_{min} in the formula below). Since our experimental design was unbalanced (different number of populations per species, see Section 2), we used a Restricted Maximum Likelihood fitting procedure (Searle, Casella, & McCulloch, 2008) in the R package NLME. We ranked model support, based on the Akaike's information criterion adjusted to finite sample size (AIC_c) (Sugiura, 1978), by means of model probabilities ($wAIC_c$, which are scaled to a 0–1 interval) and evidence ratios of $wAIC_c$ of the top-ranked model to the $wAIC_c$ of every other model in the set (Burnham & Anderson, 2002) for four models capturing (a) species and population effects: *CT ~ spe, random = ~1 | pop*, where *pop* is a categorical factor representing the study populations nested in *spe* as the categorical factor representing the 15 study species, (b) body-size and population

effects: *CT ~ body, random = ~1 | pop*, where *body* is a continuous variable measuring the weight in grams of each lizard individual, (c) body size, species and population effects: *CT ~ body + spe, random = ~1 | pop* and (d) population effects (null model): *CT ~ 1, random = ~1 | pop*. The residuals of our best-supported model were normally distributed and randomly scattered across fitted values for both CT_{max} (Table S2) and CT_{min} (Table S3), hence we assumed Gaussian errors. Through the R package MuMIn, we extracted the variance explained by the fixed (*f*) and random (*r*) factors after Nakagawa, Johnson, and Schielzeth (2017) following the formulas $R_f^2 = \sigma_f^2/(\sigma_f^2 + \sigma_r^2 + \sigma_o^2)$ and $R_r^2 = (\sigma_f^2 + \sigma_r^2)/(\sigma_f^2 + \sigma_r^2 + \sigma_o^2) - R_f^2$, respectively, where the observation-level variance (σ_o^2) is the variance over individual data points.

3 | RESULTS

Median lizard thermal tolerances were 42.7°C with 90% interquartile ranges of [40.9, 46.0] for CT_{max} and 6.2°C [3.4, 8.6] for CT_{min} across individuals (Table 2). A total of 52 and 50 populations had mean CT_{max} and CT_{min} variances < 1, respectively—the variance measures how much a thermal limit departs from its mean. The medians of the population variances of CT_{max} and CT_{min} were 0.4

[0.0, 1.3] and 0.5 [0.2, 4.2] across all 58 populations, respectively. The two highest intraspecific variances (across population means) were 1.8 for both the spiny-footed lizard *Acanthodactylus erythrurus* and the Catalonian wall lizard *Podarcis liolepis* for CT_{max}, and 1.7 and 4.2 for the common wall lizard *P. muralis* and the Cyren's rock lizard *Iberolacerta cyreni* for CT_{min}, respectively (Table 2).

We quantified the ratio of CT_{max} variance to CT_{min} variance across our 15 study species by randomly sampling one population per species (population sample), and repeated the former calculation for batches of 1×10^3, 1×10^4, 1×10^5, 1×10^6 and 1×10^7 different population samples (see Section 2 and Figure S2). The cross-taxa median ratio of CT_{max} variance to CT_{min} variance was 1.6 [0.8, 2.8] based on the batch of 1×10^3 population samples, and 1.5 [0.8, 2.8] indistinctly for the other batches of 1×10^4 to 1×10^7 population samples (Figure 1b; Figure S3). A median ratio above 1 indicates that CT_{max} variance surpassed CT_{min} variance across species, while variance ratios should be conceptualized as the relative magnitude of departure of each thermal limit from the mean value across species. Indeed, for all batches of population samples, CT_{max} variance was larger than CT_{min} variance (heat-tolerance asymmetry: 86%–87% of the population samples) six to seven times more frequently than when CT_{max} variance was smaller than CT_{min} variance (cold-tolerance asymmetry: 13%–14%
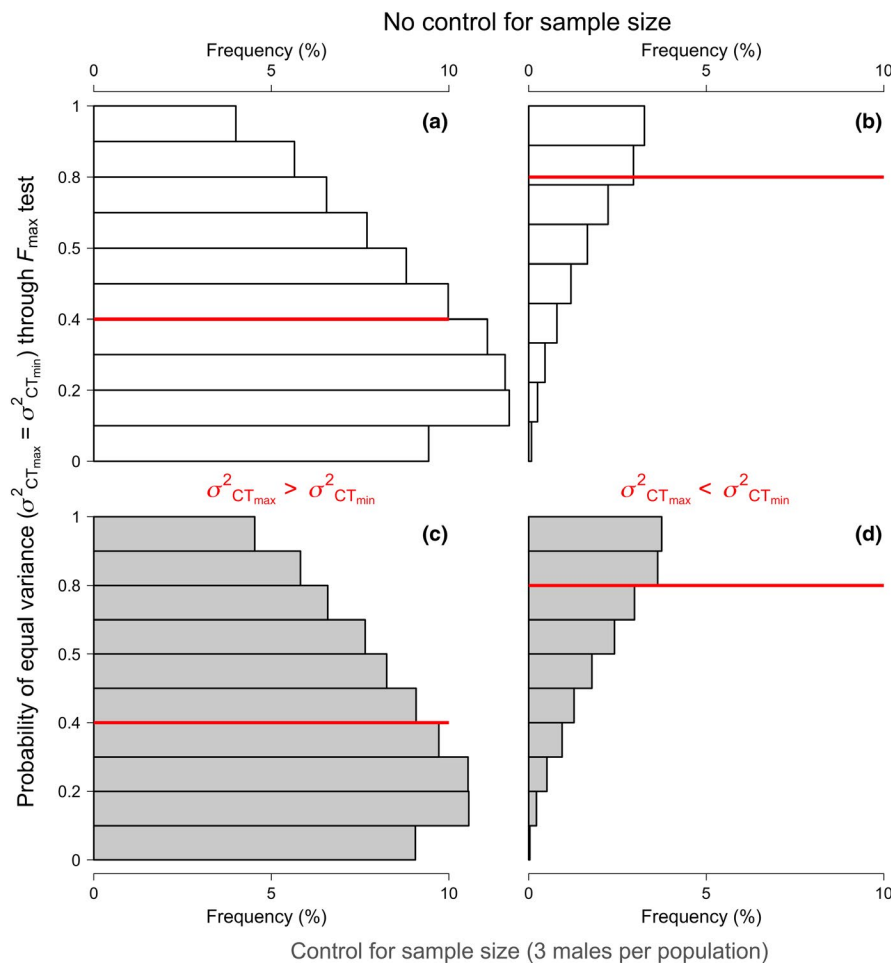

FIGURE 2 Homoscedasticity tests (the null hypothesis being that CT_{max} variance = CT_{min} variance, F_{max} test) across 15 lizard species for each of 1×10^5 population samples, where a population sample includes one population taken randomly from each study species (2–5 available per taxon). CT_{max} and CT_{min} from each study population were the average of the CT_{max} and CT_{min} of all males sampled (a, b: 3–10 per population), or three randomly taken individuals (c, d). In both cases, probabilities are broken down for population samples where CT_{max} variance > CT_{min} variance (a, c: heat-tolerance asymmetry) vs. CT_{max} variance < CT_{min} variance (b, d: cold-tolerance asymmetry). Red lines indicate median probabilities

TABLE 3 Probability of the data given the null hypothesis of equal variance (median [90% interquartile ranges]) across 15 lizard species for each of (left to right) 1,000, 10,000, 100,000, 1,000,000, 10,000,000 population samples (N), where a population sample includes one population taken randomly from each study species (2–5 populations available per taxon, 58 populations in total, see Table 2). Probabilities are reported for five different tests for population samples where CT_{max} variance was smaller than, equal to, or larger than CT_{min} variance. For each study population, CT_{max} and CT_{min} were the average of the CT_{max} and CT_{min} of all males sampled from each population (3–10 per population)

		Probability		
N	Test	$CT_{max}\,\sigma^2 < CT_{min}\,\sigma^2$	$CT_{max}\,\sigma^2 = CT_{min}\,\sigma^2$	$CT_{max}\,\sigma^2 > CT_{min}\,\sigma^2$
1×10^3	*Population samples =*	*141*	*4*	*855*
	F_{max}	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Barlett	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Brown–Forsythe	0.7 [0.2,1.0]	0.9 [0.7,1.0]	0.5 [0.1,1.0]
	Levene	0.7 [0.2,1.0]	0.9 [0.7,1.0]	0.5 [0.1,0.9]
	PERMDISP	0.7 [0.2,1.0]	0.9 [0.7,1.0]	0.5 [0.1,1.0]
1×10^4	*Population samples =*	*1,231*	*69*	*8,700*
	F_{max}	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Barlett	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Brown–Forsythe	0.7 [0.3,1.0]	0.9 [0.6,1.0]	0.5 [0.1,1.0]
	Levene	0.7 [0.3,1.0]	0.9 [0.6,1.0]	0.5 [0.1,0.9]
	PERMDISP	0.7 [0.3,1.0]	0.9 [0.6,1.0]	0.5 [0.1,1.0]
1×10^5	*Population samples =*	*12,869*	*655*	*86,746*
	F_{max}	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Barlett	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Brown–Forsythe	0.7 [0.3,1.0]	0.8 [0.6,1.0]	0.5 [0.1,1.0]
	Levene	0.7 [0.3,1.0]	0.8 [0.6,1.0]	0.5 [0.1,1.0]
	PERMDISP	0.7 [0.3,1.0]	0.9 [0.6,1.0]	0.5 [0.1,1.0]
1×10^6	*Population samples =*	*127,740*	*6,088*	*866,172*
	F_{max}	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Barlett	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Brown–Forsythe	0.7 [0.3,1.0]	0.8 [0.6,1.0]	0.5 [0.1,1.0]
	Levene	0.7 [0.3,1.0]	0.9 [0.6,1.0]	0.5 [0.1,0.9]
	PERMDISP	0.7 [0.3,1.0]	0.8 [0.6,1.0]	0.5 [0.1,1.0]
1×10^7	*Population samples =*	*1,275,488*	*60,875*	*8,663,637*
	F_{max}	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Barlett	0.8 [0.4,1.0]	1.0 [0.9,1.0]	0.4 [0.1,0.9]
	Brown–Forsythe	0.7 [0.3,1.0]	0.8 [0.6,1.0]	0.5 [0.1,1.0]
	Levene	0.7 [0.3,1.0]	0.9 [0.6,1.0]	0.5 [0.1,0.9]
	PERMDISP	0.7 [0.3,1.0]	0.8 [0.6,1.0]	0.5 [0.1,1.0]

Italics denote sample size from information about statistical results.

of the population samples). CT_{max} variance equalled CT_{min} variance (unitary variance ratio) in <0.7% of the population samples. Overall, the former indicates that heat-tolerance asymmetry is more likely to be detected than cold-tolerance asymmetry using one population per species in our study area.

Our finding was further supported by the frequency of extreme variance ratios. So, for all batches, CT_{max} variance was two times larger than CT_{min} variance in 21%–22% of the population samples, and CT_{min} variance was two times larger than CT_{max} variance only in <0.1% of the cases. And the highest CT_{max} variance-to-CT_{min} variance ratio across species for any given population sample was

16, while the top CT_{min}-to-CT_{max} variance ratio was 3 (Figure 1b; Figure S3). Additionally, if we selected the population with the highest CT_{max} and the population with the lowest CT_{min} per species, as sometimes applied in the literature (Table 1), again CT_{max} variance was nearly two times larger than CT_{min} variance across species (Figure 1b). For comparison, the global database *GlobTherm* (Bennett et al., 2018) collates paired CT_{max} and CT_{min} ratios for 161 squamate reptiles with an overall CT_{min}-to-CT_{max} variance ratio across species of 1.58 (cold-tolerance asymmetry, Figure 1a). In contrast, in our dataset, for population samples with heat-tolerance asymmetry the cross-species CT_{max} variance-to-CT_{min}

TABLE 4 Probabilities, evidence ratios and variance explained for generalized linear mixed-effects models[a] equating critical thermal maxima (CT_{max}) or minima (CT_{min}) as a function of population (*pop* = random effect), *species* and *body* weight (= fixed effects). The study includes 15 study lizard species with 2–5 populations per species and 3–10 individuals per population (sample sizes reported in Table 2)

Models	Model probability ($wAIC_c$)	Evidence ratio (ER)	% variance explained (fixed effects)	% variance explained (random effects)
$CT_{max} \sim spe, random = \sim1 \mid pop$	0.98	1	65	17
$CT_{max} \sim body + spe, random = \sim1 \mid pop$	0.02	61	65	17
$CT_{max} \sim body, random = \sim1 \mid pop$	0.00	2E+14	4	76
$CT_{max} \sim 1, random = \sim1 \mid pop$	0.00	5E+13	–	81
$CT_{min} \sim spe, random = \sim1 \mid pop$	0.96	1	31	28
$CT_{min} \sim body + spe, random = \sim1 \mid pop$	0.04	27	31	28
$CT_{min} \sim body, random = \sim1 \mid pop$	0.00	5E+14	6	53
$CT_{min} \sim 1, random = \sim1 \mid pop$	0.00	3E+04	–	56

[a]Model probabilities ($wAIC_c$) and evidence ratios (ER = $wAIC_c$ of top-ranked model to $wAIC_c$ of any given model) obtained through the Akaike's Information Criterion adjusted for finite sample size (AIC_c), and variance explained (coefficient of determination) estimated by linear models with Gaussian errors (see Tables S2, S3).

variance ratio exceeded the *GlobTherm* ratio in >3 of every four population samples (heat-tolerance asymmetry, Figure 1a), and for population samples with cold-tolerance asymmetry the cross-species CT_{min}-to-CT_{max} variance ratio exceeded the *GlobTherm* ratio in <1 of every 10 populations samples (cold-tolerance asymmetry, Figure 1a).

Using variance ratios, we used the F_{max} test to query the statistical support for homoscedasticity given the two alternative scenarios of unequal cross-taxa variances of CT_{max} vs. CT_{min} (see Section 2)—both without and with control for the number of male lizards per population (Figure 2; Figure S3; see Section 2). For all batches, when CT_{max} variance > CT_{min} variance (Figure 1a: heat-tolerance asymmetry), the median probability of the observed variance ratio given the null hypothesis (CT_{max} variance/CT_{min} variance = 1) was 0.4 [0.06, 0.9] across all population samples (Figure 2; Figure S4). In contrast, when CT_{max} variance < CT_{min} variance (Figure 1a: cold-tolerance asymmetry), the median probability of the observed variance ratio given the null hypothesis (CT_{min} variance/CT_{max} variance = 1) was 0.8 [0.4, 1.0] across all population samples (Figure 2; Figure S4). Therefore, based on the F_{max} test, the data were twice as probable under the null hypothesis (variance ratio = 1 or variance symmetry) for population samples showing cold-tolerance asymmetry than for those showing heat-tolerance asymmetry. We found equivalent, relative statistical support for the two alternative scenarios through four additional homoscedasticity tests (Table 3; Table S1) including Barlett's (Figure S5), Brown–Forsythe's (Figure S6), Levene's (Figure S7) and PERMDISP (Figure S8).

We quantified differences in thermal limits across species by contrasting likelihoods in a set of four models using generalized linear mixed-effects modelling (species and body size = fixed effects, population = random effects; see Section 2). The model encapsulating species and population effects on CT_{max} or CT_{min} was 61 and 27 times more likely than the model also incorporating allometric effects, respectively, and 4–14 orders of magnitude more likely than the models including allometric or population effects alone (Table 4).

Additionally, species coefficients (fixed effects) on CT_{max} were two times larger than those on CT_{min}. These coefficients indicate mean differences in CT_{max} (Table S2), or CT_{min} (Table S3), between the first species listed in the dataset (*A. erythrurus*) and each of the other species, while the species *p* values represent the probabilities of the observed effects under the null hypothesis that a given species coefficient is 0. Thus, the median species effect on CT_{max} was 2.9 [0.9, 4.5]°C with 11 of the 15 study species scoring fixed effects ≥2.5°C, while the median probability of those coefficients being 0 was negligible (= 5.3E−07 [2.1E−11, 1.4E−01]). In contrast, the median species effect on CT_{min} was 1.5 [0.1, 2.4]°C with only 1 of the 15 study species scoring fixed effects >2.5°C, while the median probability of those coefficients being 0 was 0.02 [9.2E−5, 0.9]. Fixed (species) and random (populations) effects explained 65 and 17% of the variation in CT_{max} (totalling 82%), and 31 and 28% of the variation in CT_{min} (totalling 59%), respectively (Table 4).

4 | DISCUSSION

Using CT_{max} and CT_{min} from multiple populations of 15 lizard species from the Iberian Peninsula, we show that the frequency, magnitude, direction of, and statistical support for thermal-tolerance asymmetries (CT_{max} varying more *or* less strongly than CT_{min} across species), depend on the individual population taken to represent each species in cross-taxa comparisons. We found that CT_{max} was more variable than CT_{min} in >80% of the random population samples investigated, while cross-species effects were two times stronger on CT_{max} than on CT_{min}, respectively, after controlling for body size and intraspecific variation. In other words, had we repeated our study thousands of times, each time sampling one different population per species, we would have found heat-tolerance asymmetry more likely than cold-tolerance asymmetry. This result contrasts with the view that cold tolerance is more variable than heat tolerance using single estimates of both metrics across hundreds of species from tropical to temperate and boreal climates (Table 1).

Arthropod reaction norms indicate that plasticity in cold tolerance enhances adaptation to cold temperatures, while plasticity in heat tolerance can lead to beneficial, detrimental or null adaptive potential across species (Schou et al., 2016). Those reaction norms would support the observation that broad latitudinal clines of cold tolerance have been found to covary linearly with climate much more strongly than heat tolerance in both invertebrate and vertebrate ectotherms (Addo-Bediako, Chown, & Gaston, 2000; Sunday et al., 2010). However, if some species decreased heat tolerance over large-scale spatial gradients while others increased it, linear responses of heat tolerance to latitude would not be detected. Indeed, our study is restricted to Iberia, but studies focusing on global latitudinal variation in CT_{max} vs. CT_{min} cover wide environmental gradients encompassing tropical, temperate and/or boreal climate zones (see Table 1). At such broad scales, complex interactions of climate and heat tolerance occurring at smaller spatial scales might not be discernible (see below).

Additionally, large-scale studies generally rely on coarse climatic data such as mean air temperatures, while for small ectotherms CT_{max} and CT_{min} are bound to correlate locally to a complex suite of nuanced environmental cues. Indeed, lizard populations of the same species are often exposed to contrasting climate variation due to habitat heterogeneity and associated opportunities for shelter and thermoregulatory behaviour (see Sears & Angilletta, 2015). This seems unsurprising given that the thermal environment experienced by lizards can vary by up to 20°C as a result of the landscape heterogeneity imposed by vegetation, topography and geology (Sears, Raskin, & Angilletta, 2011), and such thermal variation compares well with the magnitude of warming expected in the most pessimistic scenarios of future climate change (Suggitt et al., 2011). Without population-level data and quantitative methods incorporating population-level trait variation (discussed by Herrando-Pérez, Ferri-Yáñez, et al., 2019), coarse climatic indices can fail to capture how heat and cold tolerances of species interact with regional climatic shifts (Garcia, Allen, & Clusella-Trullas, 2019; Sears & Angilletta, 2015) in both the cold and warm margins of species distributions (Nadeau & Urban, 2019). For instance, latitudinal clines of thermal tolerance for several beetle species are more pronounced for heat tolerance in the southern (hot) margins of species distributions than for cold tolerance in the northern (cold) margins (Calosi, Bilton, Spicer, Votier, & Atfield, 2010). The investigation of asymmetries in heat and cold tolerance over multiple spatial scales thus represents a critical area of future development in macroecological research, and warrants future efforts towards the collation of global databases covering already available population- *and* species-level metrics of thermal performance (see Bennett et al., 2018).

Differentiating evolutionary adaptation and phenotypic plasticity under a changing climate remains challenging (Merilä & Hendry, 2014), but even in the simplest scenario of plasticity being equal among populations of a single species, both heat and cold tolerance are expected to be shaped by different evolutionary processes (Hoffmann et al., 2013), and can also evolve rapidly—though

examples from wild populations are scant. For instance, selection for decreased CT_{min} was detected in lizards following an extremely cold winter (Campbell-Staton et al., 2017) or an introduction to a climate colder than native conditions (Leal & Gunderson, 2012). And selection for increased CT_{max} has been predicted in fruit flies (Blackburn, Heerwaarden, Kellermann, & Sgrò, 2014) and found in a lake invertebrate over four decades (Geerts et al., 2015) but remains elusive for terrestrial ectotherms (but see Logan, Cox, & Calsbeek, 2014; Skelly et al., 2007). Working with ants, Baudier, D'Amelio, Malhotra, O'Connor, and O'Donnell (2018) found stronger correlation of CT_{max} (relative to CT_{min}) with local elevational and temperature ranges, and postulated that such contrast could be signalling that temperature anomalies are driving CT_{max} variation alone in an adaptive manner. If this was the case in our study area, the larger variation in CT_{max} across our study lizard species could be indicative of modern microevolutionary responses to the ongoing increase in the frequency and severity of heatwaves (Dasari, Salgado, Perdigao, & Challa, 2014) and droughts in the Mediterranean basin (Araújo, Thuiller, & Pearson, 2006; Marvel et al., 2019; Russo, Gouveia, Dutra, Soares, & Machado Trigo, 2019).

For small vertebrate ectotherms with limited dispersal capacity (i.e. virtually all temperate species of terrestrial lizards), it is plausible that where benign microhabitats abound, thermoregulation might relax selective forces (e.g. extreme climatic events) acting differentially on one or the two thermal limits (Diamond, 2017; Gunderson & Stillman, 2015; Huey, Hertz, & Sinervo, 2003). For instance, lizard cold tolerance can be adjusted to nocturnal temperatures but thermoregulation should play no role in such adjustments and only limit exposure to diurnal temperatures approaching the limits of heat tolerance for diurnal species (Domínguez–Guerrero et al., 2019; Muñoz & Bodensteiner, 2019). Consequently, complex biogeographic patterns of variation in heat and cold tolerance could emerge regionally depending on the opportunities for effective thermoregulation, the prevalence of which could prevent microevolutionary adaptation despite its potential to buffer lizards against heat stress in regions such as the Iberian Peninsula (Aguado & Braña, 2014; Ortega, Mencía, & Pérez-Mellado, 2016a).

Along those lines, geographical variation in both CT_{max} and CT_{min} is expected to be stronger for thermoconformer than for thermoregulatory lizards but, critically, for temperate species living in relatively hot regions (where thermoregulation is less effective) only CT_{max} might be modified by evolutionary shifts (Buckley, Ehrenberger, & Angilletta, 2015; Sears et al., 2016). The efficiency of thermoregulation can, therefore, drive higher (plastic and/or adaptive) variability in heat tolerance relative to cold tolerance, though the functional mechanisms underlying such variability might differ widely among species. For example, among Iberian lizards, it can be expected that generalist thermophilic lizard species should have higher thermoregulation efficiency than cold-adapted specialists living in high altitudes (Ortega, Mencía, & Pérez-Mellado, 2016b), but generalists will invariably occupy wider distributional ranges and face much higher variation in climatic and microhabitat conditions leading to larger variance in thermal performance under

heat stress. A cascading effect could be that open-habitat basking species with relatively high CT_{max} might potentially displace low-CT_{max} species adapted to alpine or shady environments as environmental warming progresses as proposed for tropical lizards (Huey et al., 2009). This scenario could be exacerbated if warming imposed restrictions on the time of activity of shade-loving species (but see Kearney, 2013). Such scenario can be relevant for Iberian high-altitude species (*Iberolacerta* spp.) and, particularly, the endangered Spanish algyroides *Algyroides marchi* by virtue of its confined distribution to the Alcaraz, Cazorla and Segura mountain ranges, low CT_{max} (comparable to that of high-altitude species; see Table 2; Herrando-Pérez, Ferri-Yáñez, et al., 2019) and preference for shady, humid environments (Rubio & Martín, 2017).

Many of our study species are cosmopolitan and/or occupy broad climatic gradients in the Iberian Peninsula (Araújo, Guilhaumon, Neto, Pozo, & Gómez, 2015). For that reason, even if our dataset represents one of the largest one-off regional surveys of lizard thermal tolerances undertaken globally to date, the number of populations per species (2–5, see Section 2) precludes biologically meaningful modelling of correlations between environmental and thermal-tolerance variances. Overall, we require studies of phenotypic plasticity and microevolution in heat and cold tolerance over the entire distribution of individual species (discussed by Herrando-Pérez, Ferri-Yáñez, et al., 2019), while novel climatic reconstructions must be developed to match the multidirectionality of climate change (Garcia, Cabeza, Rahbek, & Araújo, 2014; VanDerWal et al., 2013) and the spatial scales that are relevant to the life history of the species under investigation (Bonebrake et al., 2018; Lembrechts, Nijs, & Lenoir, 2019). The former approaches should, for instance, validate predictions that species extinctions can be largely buffered by the availability of microhabitats (Suggitt et al., 2018) and shading (Kearney, 2013) or even poorly driven by physiological limits (Cahill et al., 2013) under climate change.

A different caveat is how much variance in CT_{max} and CT_{min} can arise from methodological uncertainties. In that respect, we note that in our study we applied the same acclimation regime to all study individuals and populations in contrast with published cross-taxa research selecting thermal limits from multiple sources where population and species acclimation history is not controlled for (Table 1). Additionally, the magnitude of thermal limits depends on heating and cooling rates (Kingsolver & Umbanhowar, 2018; Terblanche et al., 2007), and thermal limits can be interpreted by different behaviours like onset of body spams, or loss of coordinated movement or righting response (Lutterschmidt & Hutchison, 1997; Terblanche et al., 2007). A more biologically sound approach would be to measure the thermal thresholds at which cell, membrane or protein damage occurs by means of molecular biomarkers, and to validate how the former relate to the wide variety of metrics of heat and cold tolerance, among which CT_{max} and CT_{min} are just one option (Clusella-Trullas & Chown, 2014; Sinclair et al., 2016). These developments are occurring in the fields of comparative physiology (Somero, 2011) and extremophile biology (Clarke, 2014) and await incorporation in (macro)ecological and physiological research integrating the molecular, cellular and whole-organism levels of biological organization (Pörtner et al., 2006). Overall, those efforts could shed light on a conceptually fundamental question that has been surprisingly poorly tested when it comes to correlating behaviour, physiology and life history (Montiglio, Dammhahn, Dubuc Messier, & Réale, 2018): are thermal tolerances truly individual, population and/or species traits? Albeit apparently strictly methodological, such a question poses the need for a quantitative assessment of the relative effect of individual vs. population vs. species variances (Calosi et al., 2013; Pörtner et al., 2006) on adaptive and functional responses to environmental change.

AUTHORS' CONTRIBUTIONS

S.H.-P. conceived the idea, designed and run the statistical analyses and wrote the first draft of the manuscript. M.B.A. and C.M. designed the project and experiments. C.M., V.G. and W.B. conducted the field and experimental work. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

CT_{max} and CT_{min} data along with body weights, locality names and latitude and longitude have been deposited in the Dryad Digital Repository (23/11/2019) and update the first version of the dataset https://doi.org/10.5061/dryad.1553pc3 (Herrando-Pérez, Monasterio, et al., 2019).

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SUPPORTING INFORMATION

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