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Intraspecific variation in lizard heat tolerance alters estimates of climate impact

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Abstract

1. Research addressing the effects of global warming on the distribution and persistence of species generally assumes that population variation in thermal tolerance is spatially constant or overridden by interspecific variation. Typically, this rationale is implicit in sourcing one critical thermal maximum (CT_{max}) population estimate per species to model spatiotemporal cross-taxa variation in heat tolerance. Theory suggests that such an approach could result in biased or imprecise estimates and forecasts of impact from climate warming, but limited empirical evidence in support of those expectations exists.
2. We experimentally quantify the magnitude of intraspecific variation in CT_{max} among lizard populations, and the extent to which incorporating such variability can alter estimates of climate impact through a biophysical model. To do so, we measured CT_{max} from 59 populations of 15 Iberian lizard species (304 individuals).
3. The overall median CT_{max} across all individuals from all species was 42.8°C and ranged from 40.5 to 48.3°C, with species medians decreasing through xeric, climate-generalist and mesic taxa. We found strong statistical support for intraspecific differentiation in CT_{max} by up to a median of 3°C among populations. We show that annual restricted activity (operative temperature > CT_{max}) over the Iberian distribution of our study species differs by a median of >80 hr per 25-km^2 grid cell based on different population-level CT_{max} estimates. This discrepancy leads to predictions of spatial variation in annual restricted activity to change by more than 20 days for six of the study species.
4. Considering that during restriction periods, reptiles should be unable to feed and reproduce, current projections of climate-change impacts on the fitness of

ectotherm fauna could be under- or over-estimated depending on which population is chosen to represent the physiological spectra of the species in question. Mapping heat tolerance over the full geographical ranges of single species is thus critical to address cross-taxa patterns and drivers of heat tolerance in a biologically comprehensive way.

KEYWORDS
climate change, critical thermal maxima, ectotherm, physiology, plasticity, thermal biology

1 | INTRODUCTION

The response of individuals to climate warming and, ultimately, the combined effects on populations and species, is mediated through interactions between physiology and behaviour (Pörtner & Farrell, 2008; Somero, 2012; Sunday et al., 2014). Organisms eat, move and reproduce within a thermal window bounded by their thermal tolerance, or performance limits, generally known as critical thermal maximum (CT_{max}) and minimum (CT_{min}) (Cowles & Bogert, 1944; Huey & Stevenson, 1979). When environmental temperatures are at or around critical limits, biological activity is constrained and, if temperature extremes are prolonged, they might compromise individual and population survival (Clarke, 2014; Somero, 2011). The policy consequences of these interactions, in the context of both impacts and adaptation, have been stressed by the Intergovernmental Panel on Climate Change in its Fifth Assessment Report: "…surpassing temperature thresholds means going into time-limited tolerance, and more extreme temperature changes lead to exceedance of thresholds that cause metabolic disturbances and ultimately onset of cell damage" (Field et al., 2014).

Thermal metrics, including upper thermal limits, have been documented for many species and compiled into global databases (Bennett et al., 2018). Collectively, these data constitute a valuable resource for research aiming at determining how clines in thermal tolerance might affect biotic responses to local, regional and global environmental change (Angilletta, 2009; Deutsch et al., 2008; Sunday, Bates, & Dulvy, 2012; we review examples focusing on climate change in Supporting Information Table S1). For instance, conservatism of CT_{max} implies that many species might have exhausted the evolutionary potential for developing further tolerance to climate warming (Araújo et al., 2013; Grigg & Buckley, 2013; Hoffmann, Chown, & Clusella-Trullas, 2013). And extinction risk due to increased temperatures is expected to peak in the tropics because tropical species seem to be closer to their upper thermal limits than temperate species (Deutsch et al., 2008; Gunderson & Stillman, 2015; Sunday, Bates, & Dulvy, 2010). Such research is based on sizeable datasets, typically collated from

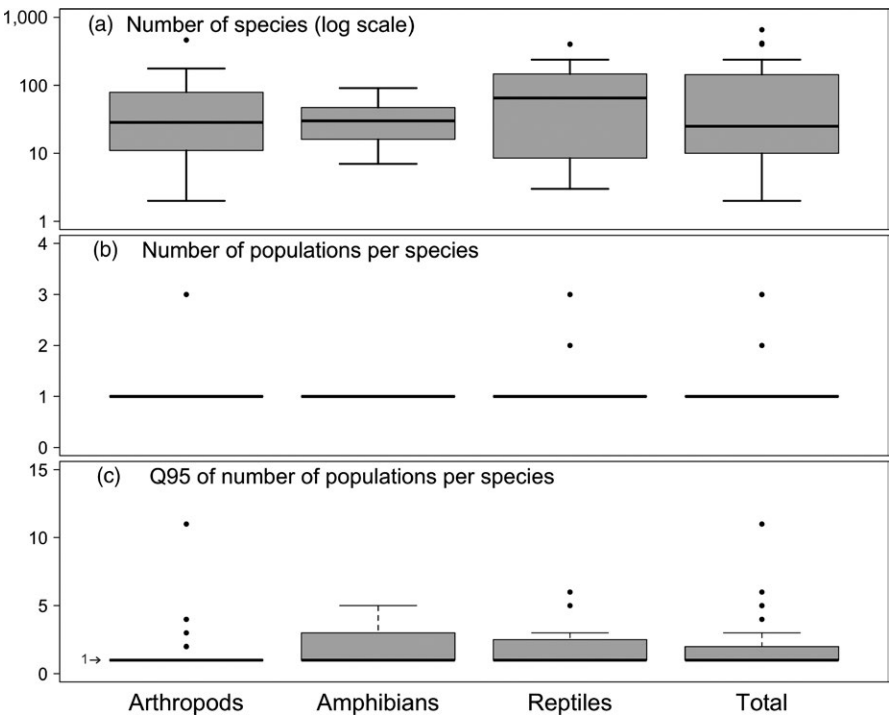

FIGURE 1 Species and population sample sizes in climate-change studies using critical thermal maxima (CT_{max}) of multiple species of three groups of terrestrial ectotherms. Thick lines in boxes indicate medians across all studies (n = 38) for broad taxa separately (arthropods, amphibians, reptiles) and all taxa together (total). Q95 is the 95% interquartile range. Studies comprise primary literature where CT_{max} has been estimated by the "dynamic method" (see Materials and Methods; taxa, hypotheses and conclusions summarized in Supporting Information Table S1). We assume that one population represents one species in the minority of cases in which a species' CT_{max} is taken to be the average of the CT_{max} of several populations

multiple primary-literature sources, whereby the thermal tolerance of individual species is most often characterized based on one population (Figure 1). The approach is based on the implicit working assumption that interspecific variation is larger than intraspecific variation or, the least, that variation among populations is so small as to have negligible impact on overall patterns. Invariably, a potentially large source of physiological variation at the species level has been to date rarely considered to forecast biological responses to environmental change (Valladares et al., 2014; see below). This aspect is important because spatial mosaics of thermal tolerance might reduce the vulnerability of species to climate warming, consequently altering estimates of impact and plans for conservation and management (Cochrane, Yates, Hoyle, & Nicotra, 2015; Sears, Raskin, & Angilletta, 2011).

The thermal performance of species along environmental gradients is expected to vary considerably across both altitude and latitude and might include ontogenic and evolutionary components (Clusella-Trullas & Chown, 2014; Sinclair et al., 2016). Theoretical developments have demonstrated that incorporating intraspecific variability in life-history traits into modelling could substantially improve forecasts of how species ranges might respond to environmental shifts such as climate change (Ikeda et al., 2017; Valladares et al., 2014). This has been corroborated in a few applied studies, particularly with plants (Benito Garzón, Alía, Robson, & Zavala, 2011; Cochrane, Hoyle, Yates, Wood, & Nicotra, 2015; Smith, Alsdurf, Knapp, Baer, & Johnson, 2017), and including thermal traits in ectotherms such as insects (Lancaster, 2016), reptiles (Artacho, Saravia, Perret, Bartheld, & Le Galliard, 2017) and amphibians (Kolbe, Kearney, & Shine, 2010). However, little effort has been made to quantify the magnitude and the likely predictive importance of population differences in CT_{max} for multiple species in a common biogeographical context. To address this issue, we quantify intraspecific variability in CT_{max} across 59 populations of 15 species of Iberian lizards, and determine the extent to which among-population variability is likely to modify forecasts and predictions of annual restricted activity when environmental temperatures exceed CT_{max}.

2 | MATERIALS AND METHODS

2.1 | Sampling

Through spring and summer 2013 and 2014, we sampled 304 adult males from 59 populations and 15 Iberian species of lacertid lizards (Table 1). Our study populations comprised wide- and restricted-range taxa (nine endemic to the Iberian Peninsula) covering all of the major climatic regions through Spain and Portugal (Supporting Information Figures S1 and S2). Given the substantial sampling effort involved, sampling was tailored to cover a grid of localities maximizing species richness, minimizing travelled distance (see sampling map in Supporting Information Figure S2), and capturing in most cases more than 50% of the length of the climate gradient occupied by each species in the Iberian Peninsula (climate gradients reconstructed in Supporting Information Figure S3).

Individuals were caught by noosing. We sampled two to five populations per species (median = 4 populations per species with 90% interquartile ranges of [3, 5]), and 3–10 males per population (Table 1). The former intrapopulation sample size is within the range of that used in many studies of lizard thermal tolerance (e.g., Beal, Lattanzio, & Miles, 2014; Muñoz et al., 2016). However, we assessed optimal sample size from six datasets, including population CT_{max} from 8 to 25 adult lizards from the Americas, Asia and Europe (Andrango, Sette, & Torres-Carvajal, 2016; Belasen et al., 2016; Buckley, Ehrenberger, & Angilletta, 2015; Huang & Tu, 2008; Muñoz et al., 2014; and unpublished data), and concluded that a sample size of three males should accurately capture the mean population CT_{max} estimated from larger population sizes (Supporting Information Table S2; Figures S4–S9).

2.2 | CT_{max} estimation

To minimize local-ambient effects prior to CT_{max} estimation, all lizards were housed at 25°C (8:00–18:00 hr, lights-on) and 15°C (18:00–8:00 hr, lights-off) for 14 days. Throughout, lizards were kept individually in terraria layered with coconut fibre and a ceramic brick for shelter. We fed lizards daily with house crickets (*Acheta domesticus*) and provided them daily with spring water in a Petri dish. Following the former acclimation period, we determined CT_{max} through the "dynamic method" after Lutterschmidt and Hutchison (1997) as follows. We inserted a thermocouple some 1–2 cm (depending on body size) into the cloaca of each lizard—to avoid internal damage, the thermocouple was covered with pure vaseline and the apical sensor was rounded with a minute drop of dry nail polish. The thermocouple was wired to a HH-25TC Omega Thermometer via a 1-m-long cable made up of flexible polytetrafluoroethylene. For each lizard, we fastened a 2 × 5 cm^2 strip of parafilm that immobilized the distal part of the cable (equipped with the thermocouple) ventrally against the cloacal and genital area. Thereafter, lizards were kept some 30 cm from a red-light lamp, and body temperatures were ramped up at 1°C × min^{-1}. Throughout each trial, we monitored body temperature and behaviour, and ultimately estimated CT_{max} as the cloacal temperature at which a lizard lost its righting response (Lutterschmidt & Hutchison, 1997). Ramping rates affect CT_{max} estimation (Terblanche, Deere, Clusella-Trullas, Janion, & Chown, 2007), so we controlled for this factor by using a single rate across all individuals examined. Immediately after thermal shocks, we immersed lizards down to their necks in a bath of cool water to prevent physiological/physical damage, thereafter providing water and food ad libitum to all individuals for up to five consecutive days following the day of CT_{max} estimation. We released all individuals at their point of capture.

2.3 | Modelling

2.3.1 | Linear model: locality vs. region effects on CT_{max}

We ranked statistical support for two models through the Akaike's information criterion adjusted to finite sample size (Sugiura, 1978),

TABLE 1 Intraspecific variability in critical thermal maxima (CT_{max}, °C) and annual restriction times (RT, hours per 5 × 5 km^2 grid cell) based on 59 populations from 15 Iberian species of lacertid lizards[a]. Species listed in order of decreasing median CT_{max}. See description of variables below[b]

Study species	Populations (individuals)	CT_{max} median	CT_{max} range	RT median	RT range	Broad climate type	Precipitation	Temperature
Acanthodactylus erythrurus	4 (22)	45.6 [44.5, 47.3]	3.1	475 [379, 524]	163	Dry, warm	46 [15, 83]	22.6 [6.5, 25.0]
Podarcis carbonelli	2 (10)	45.0 [44.7, 45.3]	0.6	87 [61, 112]	57	Generalist	64 [25, 97]	19.6 [18.3, 22.1]
Psammodromus hispanicus	3 (15)	44.7 [43.1, 46.2]	3.3	127 [87, 164]	86	Generalist	53 [17, 107]	22.0 [169, 234]
Podarcis vaucheri	4 (20)	43.7 [43.4, 44.8]	1.6	522 [493, 621]	150	Dry, warm	18 [14, 31]	22.8 [193, 241]
Podarcis hispanicus	4 (19)	43.6 [43.2, 44.2]	1.1	265 [238, 281]	46	Generalist	54 [23, 103]	22.4 [4.8, 24.9]
Podarcis guadarramae	4 (20)	43.3 [42.9, 44.2]	1.5	244 [203, 263]	66	Generalist	73 [45, 132]	19.5 [16.2, 23.3]
Psammodromus algirus	4 (25)	43.1 [42.1, 43.6]	1.6	592 [574, 615]	43	Generalist	58 [18, 142]	21.9 [3.6, 25.1]
Podarcis virescens	4 (20)	43.0 [42.3, 43.4]	1.2	572 [464, 670]	232	Generalist	36 [19, 72]	23.2 [19.7, 25.7]
Podarcis muralis	4 (20)	42.8 [42.3, 43.9]	1.7	57 [34, 73]	44	Mesic, cold	159 [96, 248]	16.6 [11.0, 19.1]
Podarcis liolepis	5 (26)	42.4 [42.1, 44.8]	2.3	160 [111, 274]	188	Generalist	112 [58, 209]	16.8 [19.0, 22.5]
Algyroides marchi	4 (20)	42.2 [41.5, 42.4]	1.0	202 [177, 247]	81	Mesic, warm	61 [38, 74]	21.2 [19.7, 23.4]
Iberolacerta cyreni	5 (25)	42.1 [41.9, 42.7]	0.9	320 [283, 326]	49	Mesic, cold (alpine)	78 [53, 96]	17.6 [16.1, 21.5]
Lacerta schreiberi	4 (20)	41.7 [41.0, 42.1]	1.1	683 [607, 712]	119	Mesic, cold	121 [47, 176]	17.9 [15.2, 22.3]
Iberolacerta monticola	4 (24)	41.3 [40.8, 41.5]	0.2	97 [72, 145]	83	Mesic, cold (alpine)	138 [94, 176]	16.7 [13.7, 18.9]
Lacerta bilineata	4 (18)	41.2 [41.0, 41.9]	1.0	553 [495, 631]	150	Mesic, cold	161 [108, 245]	17.0 [27.0, 19.1]

Notes. [a]*Podarcis hispanicus* and *Psammodromus hispanicus* are recently redefined species that keep the names of former species complexes (Speybroeck, Beukema, Bok, Van Der Voort, & Velikov, 2016). [b]First data column shows number of populations (total number of individuals) sampled per species. Second and third data columns show the grand median CT_{max} (among population medians), and the RT median (obtained through a biophysical model); both are reported along with 90% interquartile limits. CT_{max} ranges are the differences between maximum and minimum median population estimates, and RT ranges are the difference between maximum and minimum population restriction times for each species. Broad climate types, in which each species is found in the Iberian Peninsula, follow Speybroeck et al. (2016). Precipitation and temperature (median and 90% interquartile ranges over all 10 × 10 km^2 grid cells in the Iberian distribution of each species) are rainfall of the wettest quarter (mm) and temperature of the hottest quarter (°C) from the "Bioclim" suite (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

using model probabilities ($wAIC_c$, which are scaled to a 0–1 interval), and evidence ratios of $wAIC_c$ of the first-ranked model to the $wAIC_c$ of the other model (Burnham & Anderson, 2002). For each species separately, the model set contrasted the hypothesis that CT_{max} varies according to the geographic location of populations (locality effect: CT_{max} ~ *loc*, i.e., a unique intercept or mean CT_{max} for each population, with *loc* being a categorical variable coding for population identity) against the alternative (null) hypothesis that CT_{max} is homogeneous across all populations studied (region effect: CT_{max} ~ *1*, i.e., a unique intercept or mean CT_{max} across all populations within a species). Throughout, we assumed Gaussian errors (corroborated in the saturated model [CT_{max} ~ *loc*] by means of Q-Q and fit-versus-residual plots) and discarded heteroscedasticity effects using Bartlett's tests (Bartlett, 1937). The "lm" function in the *R* package "stats" was used for the linear models, and all data plots hereafter were generated in "graphics" (*R* Development Core Team 2016).

Since we sampled 3–10 males per population (Table 1, see above), statistical support for our two models might be influenced by different sample sizes among populations. We controlled for this factor by sampling randomly three individuals per population (the minimum sample size collected from any one population) and contrasting our model set for each study species (locality vs. region effects on CT_{max} as above), and repeating this procedure 100 times each including a different triplet of individuals per population.

2.3.2 | Biophysical model: restriction times based on CT_{max}

To assess the extent to which single-population estimates generate varying predictions of lizard responses to climatic variation, we used activity restriction times as the biological response. Sinervo et al. (2010) defined "restriction time" for lizards as the amount of time per day in which "operative temperatures" (T_e, see below) are above preferred body temperatures. We use a more conservative metric whereby "restriction time" equates with the amount of hours over which a lizard's T_e exceeds CT_{max}; this metric is biologically realistic because diurnal lizards are bound to be active when T_e surpasses their preferred temperature (Gunderson & Leal, 2015). Effectively, our metric equates with *diurnal* restriction times because there is no solar radiation, nor (in our species set) lizard activity, at night. Overall, our purpose was to generate a metric of restriction time that is biologically meaningful and comparable among populations, rather than to construct a fully parameterized model of the thermal niche (e.g., Kearney & Porter, 2004), or a model characterizing the magnitude of the erosion of the thermal niche (e.g., Sinervo et al., 2010).

Prior to calculating restriction times, we estimated T_e by solving the biophysical model by Porter, Mitchell, Beckman, and DeWitt (1973), namely $Q_E = (Q_S + Q_I) - (Q_T + Q_C)$, which includes climate (fluxes of ground radiation, air temperature and wind speed) and biological (e.g., skin emissivity and absorbance) information. Succinctly, this model formulates the heat flow between an organism and its environment (Q_E) as a function of the solar shortwave (Q_S) and infrared (Q_I) radiations absorbed by an individual, minus the heat the animal exchanges by thermal radiation (Q_T) and convection (Q_C). T_e is one of the factors in the four-order equation for Q_T given the surface area (S) and emissivity (ε) of the animal, and the Stefan–Boltzmann constant (σ), that is, $Q_T = S \times \varepsilon \times \sigma \times T_e^4$. Equations and variables are fully described in Supporting Information Table S4.

For each population, we estimated T_e every hour daily for an entire calendar year, resulting in 8,784 maps (24 hr per day × 366 days per year, where 366 days account for leap years in our model of regional climate, see below) using the *R* package "RnetCDF" (Michna & Woods, 2013). To do so, we obtained hourly estimates of the climate variables (averaged over the period 1955–2010) from a "Regional Climate Model" specifically elaborated for the Iberian Peninsula at a 5 × 5 km^2 grid-cell resolution (Dasari, Salgado, Perdigao, & Challa, 2014); the former represents an improvement for the study area relative to other datasets with coarser resolution and global scope (e.g., Kearney, Isaac, & Porter, 2014). For every 5 × 5 km^2 grid cell, we summed the number of hours when T_e was larger than CT_{max} for each population separately (= annual restriction time) using the "Climate Data Operators" package (Kaspar, Schulzweida, & Mueller, 2010). The resulting maps were clipped to the geographical distribution of each species and converted to geo-tiff format through the package "GDAL/OGR" (GDAL/OGR Contributors 2016). Species distributions (presence–absence data in 10 × 10 km^2 grid cells) were obtained from Araújo, Guilhaumon, Neto, Pozo, and Calmaestra (2011) and from additional sources for recently described species (see Supporting Information). We therefore downscaled species distribution data to 5 × 5 km^2 grid cells to match the resolution of the climate data, and standardized annual restriction times by the total number 5 × 5 km^2 grid cells occupied by each species in the *R* packages "raster" (Hijmans & Etten, 2012) and "rgdal" (Keitt, Bivand, Pebesma, & Rowlingson, 2010).

3 | RESULTS

The median CT_{max} across all 304 individuals (59 populations, 15 species) was 42.8°C with 90% interquartile limits of [41.0, 46.0]. The CT_{max} across all individual lizards varied by 8°C, from 40.2°C (Catalonian wall lizard *Podarcis liolepis* from Cuellar, Segovia-Castilla and León) to 48.3°C (spiny-footed lizard *Acanthodactylus erythrurus* from Matalascañas, Huelva-Andalucía) (Figure 2a). The median of the population CT_{max} medians varied from 41.2 [41.0, 41.9] in the western green lizard *Lacerta bilineata* to 45.6 [44.5, 47.3] °C in *A. erythrurus* (Table 1). CT_{max} medians tended to decrease from arid- to mesic-adapted species, with climate generalists in between (Table 1).

We found strong statistical support for the hypothesis that CT_{max} differed among populations within each species separately (locality effect: different mean CT_{max}), against the alternative hypothesis that CT_{max} did not differ (region effect: same mean CT_{max} among populations)—we report AIC metrics per species in

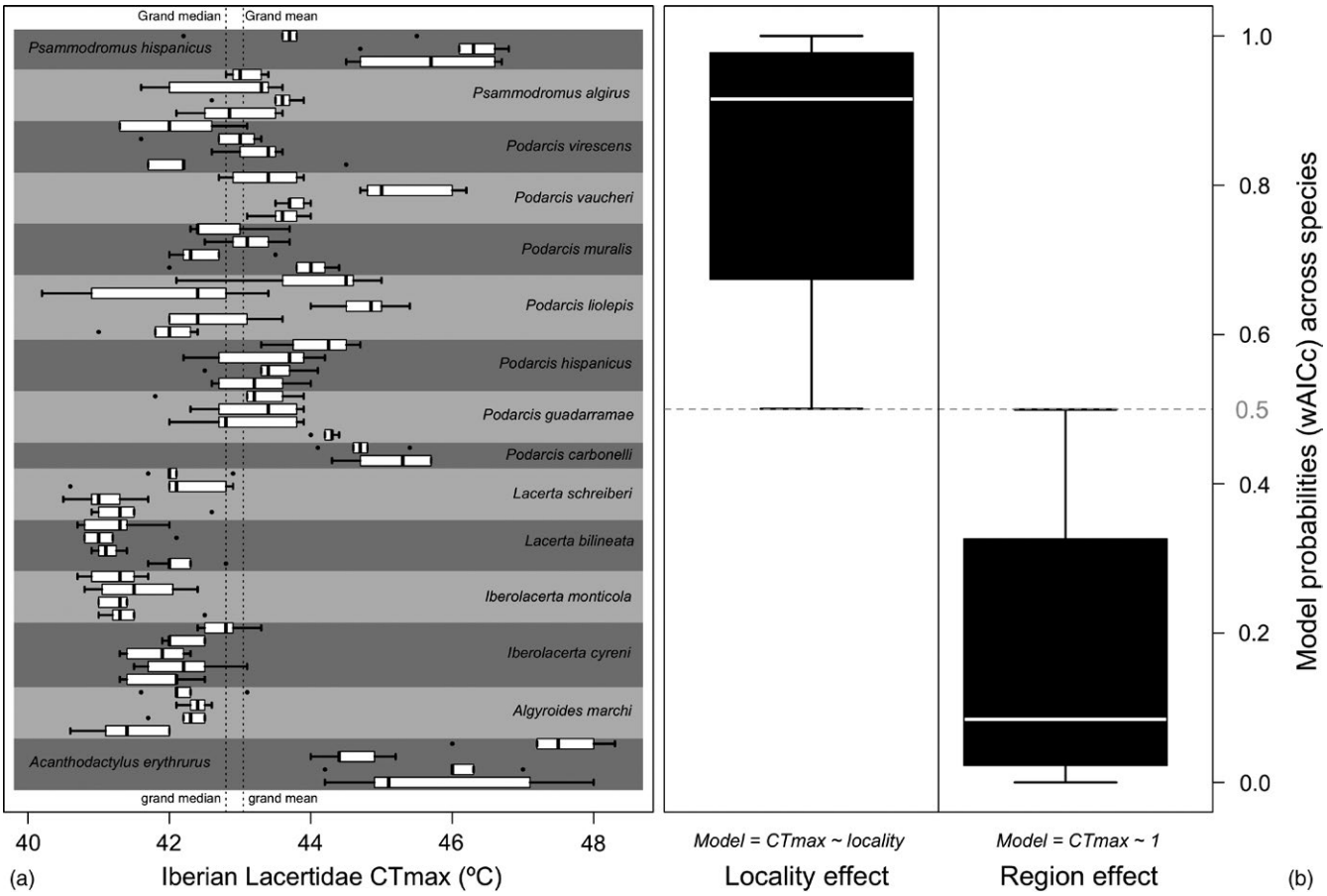

FIGURE 2 Population-level critical thermal maxima (CT_{max}) of 15 Iberian species of lacertid lizards. Left panel (a) shows CT_{max} over 304 adult male lizards from 59 populations of the 15 study species. Single boxplots represent discrete populations, sample-size median per population is five adult males with 90% interquartile ranges of [5, 6], and dashed lines indicate mean and median CT_{max} across all individuals. In the right panel (b), black boxplots represent cross-species median model probabilities ($wAIC_c$) of two models: CT_{max} varies with population locality vs. CT_{max} does not vary among populations. AIC metrics per species reported in Supporting Information Table S3

Supporting Information Table S3. Across species, the locality- and region-effect hypotheses had a median probability of 0.83 [0.52, 0.96] and 0.17 [0.04, 0.48], respectively (Figure 2b), and we obtained similar support for both models when we controlled for intrapopulation sample size (see Materials and Methods, Supporting Information Figure S10). The locality-effect model explained up to 32% of the variation in CT_{max} and scored between 2 and 32 times higher model probabilities ($wAIC_c$, see Materials and Methods) than the region-effect model for 12 of the 15 study species (Supporting Information Table S3). Both models had similar support for the Vaucher's wall lizard *Podarcis vaucheri*, the Geniez's wall lizard *Podarcis virescens* and the Spanish large psammodromus *Psammodromus algirus* (Supporting Information Table S3). Median and mean differences in CT_{max} between populations remained mostly between 1 and 3°C (Table 1).

The median annual restriction time across the 59 sampled populations was 281 [63, 670] hr per 5 × 5 km^2 grid cell (Figure 3) in the known Iberian distribution of the 15 study species. Assuming an average daily activity of 7 hr, those restriction times mean lack of diurnal activity due to overheating over 40 [9, 96] days in a calendar year. Annual restriction times across the 59 populations varied from 31 (common wall lizard *P. muralis* from Navacerrada, Madrid) to 596 (Schreiber's green lizard *Lacerta schreiberi* from Gata, Caceres-Extremadura) hours per grid cell. Within species, the median population-level range of restriction times was 83 [43,201], varying from 43 (*P. algirus*) to 232 (*P. virescens*) hours per grid cell (Table 1). In particular, for 6 of the 15 study species (*A. erythrurus*, *L. schreiberi*, *P. virescens*, *L. bilineata*, *P. liolepis*, *P. vaucheri*) predicted annual restriction times differed by > 140 hr per grid cell among populations (Table 1, Figure 3); for the former species, therefore, depending on which population-level CT_{max} was included in the biophysical model, intraspecific discrepancies of > 20 days in the number of seven-hour days free of lizard activity could result. Additionally, for the four study species with the lowest predicted annual restriction times (median among populations < 90 hr per grid cell; *P. muralis*, Carbonell's wall lizard *Podarcis carbonelli*, Iberian rock lizard *Iberolacerta monticola*, Spanish psammodromus *Psammodromus hispanicus*), the range of restriction times among populations was larger or nearly equal to the smallest restriction time estimated for a single population (Table 1, Figure 3).

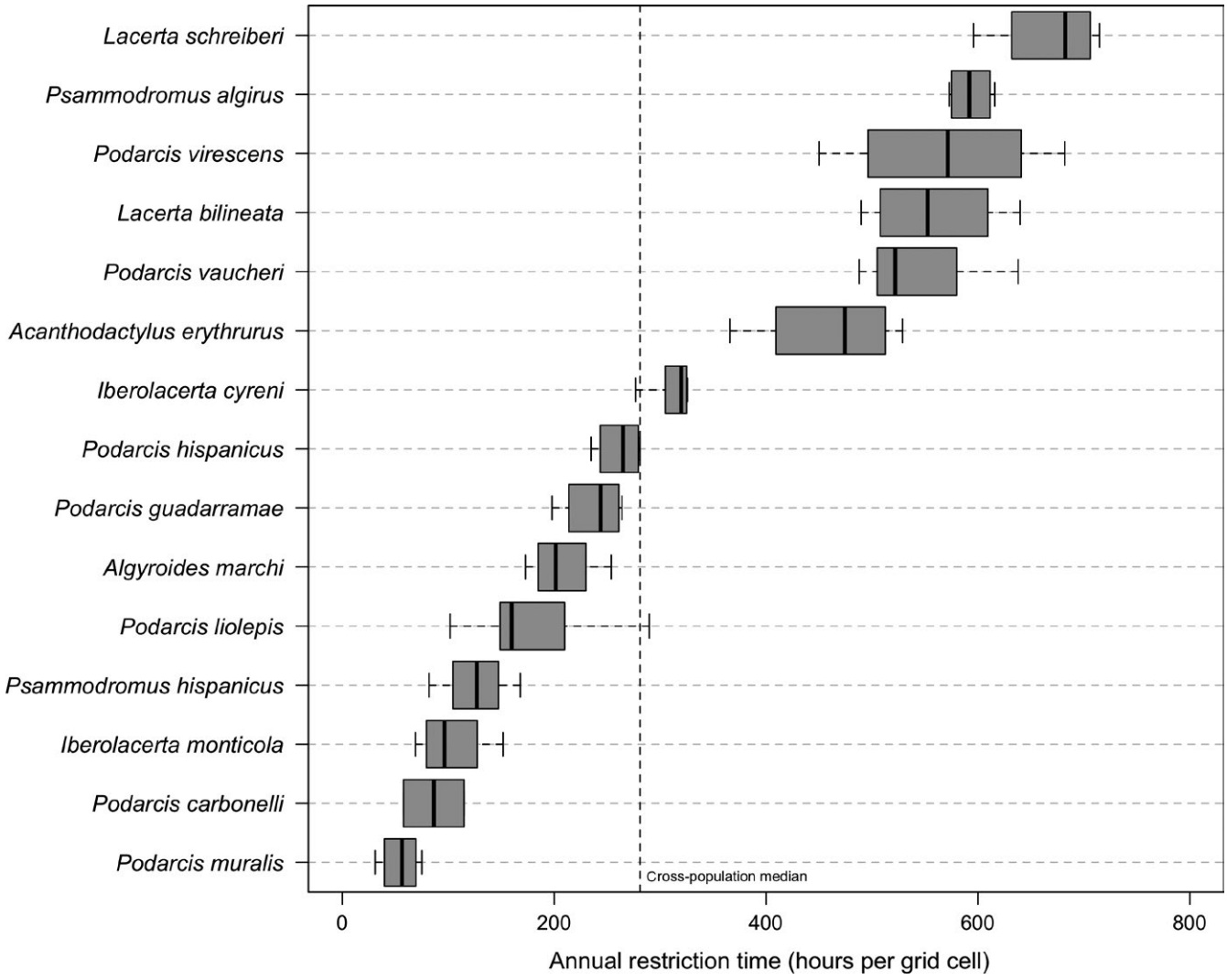

FIGURE 3 Prediction of annual restriction times from 59 populations of Iberian species of lacertid lizards (ordered by median values). Each box represents intraspecific variation in predictions based on the median CT_{max} of single populations. Restriction time defined as number of diurnal hours over a calendar year when operative temperatures are above the population CT_{max} per 5 × 5 km^2 grid cell within the known Iberian distribution of each species. Sample sizes reported in Table 1

4 | DISCUSSION

We show that intraspecific heat tolerance varies considerably across the Iberian Peninsula, with CT_{max} differences of up to 3°C (median) among populations of single lizard species. Those differences comprise ~75% of the CT_{max} range observed across our 15 study species (Table 1). This pattern holds true across Iberian lineages of lacertids—all represented in our species set (see Pyron, Burbrink, & Wiens, 2013).

In contrast, whenever multiple population data are available, in those studies that have related heat tolerance to climate change across multiple ectothermic species (Figure 1, Supporting Information Table S1), authors often average or take the maximum CT_{max} of a limited number of populations (e.g., Araújo et al., 2013; Clusella-Trullas, Blackburn, & Chown, 2011; Sinervo et al., 2010), or otherwise use several CT_{max} values for some species and, mostly, only one for others (e.g., Gunderson & Stillman, 2015; Hoffmann et al., 2013; Huey et al., 2009). Our results demonstrate, however, that the population, or population estimate, taken to represent a full species can result in starkly different cross-taxon patterns of heat tolerance, be they for CT_{max} or, potentially, any of its composites such as thermal performance curves (Sinclair et al., 2016), "safety margins" (e.g., Gunderson & Stillman, 2015; Sunday et al., 2014) or "warming tolerance" (e.g., Deutsch et al., 2008; Hoffmann et al., 2013). The rationale behind a "one species, one thermal trait" approach (Sinclair et al., 2016) is partly the fact that thermal limits have been estimated only once for most species whose thermal physiology has been investigated and partly because popular statistical methods to analyse those datasets while accounting for phylogenetic relatedness among species (e.g., phylogenetic least-squares regression) were originally designed to deal with one data point per species. However, from a purely analytical viewpoint (see Ives, Midford, & Garland, 2007; Stone, Nee, & Felsenstein, 2011), the effect of heterogeneous sampling can be as

important as phylogenetic bias and should be considered in comparative studies (Garamszegi & Møller, 2010).

For six of the 15 study species, our prediction of annual restriction times, using different population-level CT_{max} estimates, translated into species-level variation of 20 days, and longer, during which environmental (operative) temperatures would be above CT_{max}. This variation can dramatically modify inferences about behavioural patterns and fitness (Adolph & Porter, 1993) and, therefore, estimations of climate impacts accounting for trait (Cochrane, Yates, et al., 2015) or niche (Pearman, D'Amen, Graham, Thuiller, & Zimmermann, 2010) variation within species. For instance, phenotypic and species distributions can track different aspects of climate change (e.g., temperature vs. precipitation) and both complement impact assessments (Smith et al., 2017), climate effects can be masked by thermoregulation interacting with topography (Sears et al., 2011) and spatial scale (Barton, Clusella-Trullas, & Terblanche, 2018), latitudinal enhancement of heat tolerance might signal recent poleward range expansions (Lancaster, 2016), while species distribution models can fail to detect constrains in population expansion (Kolbe et al., 2010) or area of occupancy (Benito Garzón et al., 2011) owing to trait plasticity. To illustrate this point, we predicted annual restriction times of 596, 668, 697 and 715 hr per 5 × 5 km^2 grid cell using the CT_{max} of each of four populations of the Schreiber's green lizard *L. schreiberi* (CT_{max} range = 40.5–42.9°C across individuals, and 41.0–42.1°C among population medians). This species is endemic to the Iberian Peninsula, where it is mostly restricted to riparian shrubs in mountain ranges and low temperate forests close to mountain slopes (Monasterio, Shoo, Salvador, Iraeta, & Díaz, 2013). Our population-based modelling variation above would imply differences in predicted annual restriction times for the species from 85 to 102 seven-hour days per grid cell during which individuals would be forced to shelter from overheating. This is biologically important because body growth and reproductive rates are compromised by high temperatures in this species (Monasterio et al., 2013), while extended periods of shelter might come at the expense of feeding and reproductive opportunities for ectothermic fauna (Sinervo et al., 2010).

Our study supports the idea that single populations are bound to represent a snapshot of the continuum of phenotypic variability in species' heat tolerances, and reinforces the proposition that intraspecific variability in thermal limits is a key factor to project reliably how species might respond to climate warming (Valladares et al., 2014). Physiological flexibility represents an important mechanism by which species can persist in variable environments (Chevin & Hoffmann, 2017) and adapt to environmental change (Chown et al., 2010). This is a major area of research with regard to the ways in which species responses to climate change are mediated by the interplay between microevolutionary processes and plasticity (Gienapp, Teplitsky, Alho, Mills, & Merila, 2008). Considering the heterogeneity of climatic conditions across the Iberian Peninsula and within the range of most Iberian lacertids, and the projected loss of climate space (higher temperatures, lower precipitation) for reptiles in the south-west of Europe (Araújo, Thuiller, & Pearson, 2006), it is unsurprising that current and future variability in CT_{max} might be the result of natural selection and adaptation at the population level. The genetic basis of this variation in lizards still needs to be disentangled. Heritability of some thermal traits may be low (Logan, Cox, & Calsbeek, 2014; Martins, Kruuk, Llewelyn, Moritz, & Phillips, 2019), and determining how common such low heritability might be requires wider taxonomical coverage and larger sample sizes. Recent studies do illustrate that ectotherm thermal limits can evolve in a few generations in response to climate events (Campbell-Staton et al., 2017; Geerts et al., 2015), while rapid climate change can also elicit complex evolutionary patterns combining directional (Gilbert & Miles, 2017; Logan et al., 2018) and correlational (Artacho, Saravia, Ferrandière, Perret, & Le Galliard, 2015; Gilbert & Miles, 2017) selection across populations (Logan et al., 2014; Martins et al., 2019). These mechanisms can shed light on the role of plasticity and evolutionary forcing in high vs. low latitudes (Lancaster, 2016), and at the margins of the distribution of species where extinction and dispersal processes in response to environmental change might be most frequent and intense (Valladares et al., 2014).

It is also unclear whether intraspecific variability in heat tolerance could buffer proposed rates of extinction of ectothermic species under climate change (see Sinervo et al., 2010), and interact with other life-history traits to constrain activity times and elicit concomitant effects on population fitness (Kearney, 2012, 2013). For instance, in insects intraspecific variation in thermal breadth (CT_{max} – CT_{min}) seems latitudinally invariant only for stable and declining species, so those taxa currently not experiencing range expansions might be unfit to tolerate further warming at high altitudes, especially in the case of insular, endemic or, overall, narrowly distributed species (Lancaster, 2016). An assessment of the biological implications of this phenomenon seems highly relevant for the ecology and conservation of species, particularly those with long generation times and slow genetic responses to rapid environmental change (Hoffmann & Sgrò, 2011), and could be integrated into modelling approaches available for the study of climate-change impacts on biodiversity (Pacifici et al., 2015). The generation of novel physiological data for more species from the tree of life is indeed a pressing endeavour (Pörtner & Farrell, 2008). Thus, the recent collation of the *GlobTherm* database (Bennett et al., 2018: species-level metrics of thermal tolerance for 2133 taxa globally) highlights voids of knowledge in the most diverse eukaryotic groups (algae, plants, invertebrates) and in vast stretches of northernmost Africa, America and Eurasia. Bennett et al. (2018) foresaw the inclusion of intraspecific variation in future versions of the dataset, and those updates will quantify the existing bias in thermal-trait information for species vs. populations. All the same, acquiring estimates of thermal traits over broader expanses of the geographical ranges of single species seems essential (Chown & Gaston, 2016) before we might be able to address cross-taxa patterns and drivers of heat tolerance in a biologically comprehensive way. This endeavour could be logistically prohibitive for very wide-ranging species (which are an uncommon phenomenon), but could be realized for species with restricted distributions, and represents an important area of future development.

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AUTHORS' CONTRIBUTIONS

S.H.P., D.R.V. and M.B.A. conceived the idea. M.B.A. and C.M. designed the project and the full set of experiments. C.M., V.G. and W.B. did field and experimental work. S.H.P. run hypothesis contrasts and assessed optimal sample size, F.F.Y. modelled restriction times, and W.B. generated polygon data of species distributions. S.H.P. led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All physiological data associated with this study (CT_{max} for 304 male lizard individuals) have been deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.1553pc3 (Monasterio et al., 2018). As further data analyses are in progress, release of data has been embargoed for 1 year from the date of publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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