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Does heat tolerance actually predict animals' geographic thermal limits?

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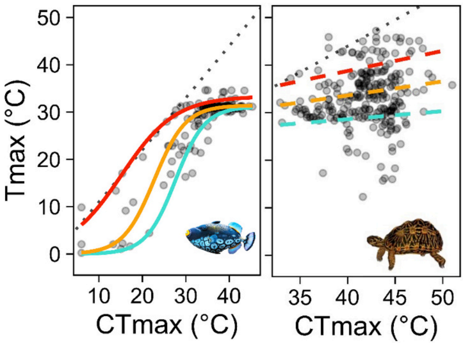
HIGHLIGHTS

- Heat tolerance's constraining effects on animals' warm range edges remain uncertain.
- We discovered that it depends on the taxon and the heat tolerance parameter used.
- Heat tolerance restricts warm range edges more when they are hotter for species.
- At warm range edges, heat challenges have multiple causes.

GRAPHICAL ABSTRACT



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ABSTRACT

The "climate extremes hypothesis" is a major assumption of geographic studies of heat tolerance and climatic vulnerability. However, this assumption remains vastly untested across taxa, and multiple factors may contribute to uncoupling heat tolerance estimates and geographic limits. Our dataset includes 1000 entries of heat tolerance data and maximum temperatures for each species' known geographic limits (hereafter, Tmax). We gathered this information across major animal taxa, including marine fish, terrestrial arthropods, amphibians, non-avian reptiles, birds, and mammals. We first tested if heat tolerance constrains the Tmax of sites where species could be observed. Secondly, we tested if the strength of such restrictions depends on how high Tmax is relative

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Thermoregulation
Warm edges

to heat tolerance. Thirdly, we correlated the different estimates of Tmax among them and across species. Restrictions are strong for amphibians, arthropods, and birds but often weak or inconsistent for reptiles and mammals. Marine fish describe a non-linear relationship that contrasts with terrestrial groups. Traditional heat tolerance measures in thermal vulnerability studies, like panting temperatures and the upper set point of preferred temperatures, do not predict Tmax or are inversely correlated to it, respectively. Heat tolerance restricts the geographic warm edges more strongly for species that reach sites with higher Tmax for their heat tolerance. These emerging patterns underline the importance of reliable species' heat tolerance indexes to identify their thermal vulnerability at their warm range edges. Besides, the tight correlations of Tmax estimates across on-land microhabitats support a view of multiple types of thermal challenges simultaneously shaping ranges' warm edges for on-land species. The heterogeneous correlation of Tmax estimates in the ocean supports the view that fish thermoregulation is generally limited, too. We propose new hypotheses to understand thermal restrictions on animal distribution.

1. Introduction

Describing the global relationships between a species' heat tolerance and environmental temperatures is crucial for comprehending the boundaries of its geographical distribution and its susceptibility to climate-related challenges (Bennett et al., 2021; Comte and Olden, 2017; Deutsch et al., 2008; Gaston et al., 2009; Khaliq et al., 2017; Kingsolver et al., 2013; Sinervo et al., 2010; Sunday et al., 2014; Terblanche et al., 2008). This research line is grounded in the climate extremes hypothesis (Pither, 2003; Sunday et al., 2019), which posits that physiological tolerance plays a pivotal role in shaping the edges of a species' geographical range by restricting the temperatures at which individuals can disperse, survive, and reproduce. This hypothesis has been tested in an array of contexts (see discussion, Andersen et al., 2015; Bennett et al., 2021; Comte and Olden, 2017; Khaliq et al., 2017; Pinsky et al., 2019; Pither, 2003; Rezende et al., 2020; Sunday et al., 2014, 2019; Moore et al., 2023). However, only a few studies have examined whether heat tolerance can effectively predict the warm boundaries of species' distributions within particular taxonomic groups (e.g., Anurans, as in Diaz-Ricaurte et al., 2020; Gouveia et al., 2014; although Khaliq et al., 2017 explored this for Endotherms). Conversely, many heat tolerance measures have been proposed for evaluating thermal restrictions on animals' distributions (e.g., Hertz et al., 1993; Huey et al., 2009; Sinervo et al., 2010; Camacho et al., 2018; Van Heerwaarden and Sgrò, 2021). Evaluating the restrictive capacity of different heat tolerance parameters seems particularly important at the warm edges of species ranges. Namely, the rear or trailing edges of species ranges that are shifting due to climate change (Ex. Hampe and Petit, 2005; Fredston-Hermann et al., 2020; Moore et al., 2023). These are the hottest regions of each species' geographic distribution and are particularly prone to warming-induced extinctions (Wiens, 2016). In this context, a fundamental assumption of the climate extremes hypothesis justifies the worldwide utilization of heat tolerance metrics in studies of thermal vulnerability or read-edge dynamics. This assumption posits that, insofar as it is measured, individuals' heat tolerance generally constrains the highest environmental temperatures that populations can withstand at species' warm range edges (Tmax).

Many factors, ranging from biological to purely methodological, could blur the restrictions of heat tolerance on Tmax across species. Biological factors, such as local adaptation (Geerts et al., 2015) and plasticity (i.e., acclimation, Morley et al., 2019), may lead to intraspecific geographic variation in heat tolerance (e.g., Clusella-Trullas and Chown, 2014; Sasaki et al., 2022) and in thermal risk (Bennett et al., 2019). This means that heat tolerance at warm edges might be different than at the sites of experimental measurement. Thermoregulatory behavior can also decouple individuals' body temperatures from too high environmental temperatures (Buckley et al., 2013; Meiri et al., 2013; Sunday et al., 2014) and even prevent the evolution of heat tolerance itself (Huey et al., 2003; Muñoz and Bodensteiner, 2019). In parallel, species interactions might restrict geographic ranges before the heat does so (e.g., Amundrud and Srivastava, 2020; Paquette and Hargreaves, 2021). This could prevent species from realizing their fundamental thermal niche, making them unable to reach sites where the local climate actually challenges tolerance (Moore et al., 2023). Besides biological factors, methodological ones could also blur heat tolerance-Tmax relationships by leading to inaccurate estimates of both variables. To cite some examples: the incorrect estimation of heat tolerance (e.g., Camacho and Rusch, 2017; Wolf et al., 2017), the scale-dependent variability in estimates of environmental temperatures (Garcia et al., 2019), the duration of stressful heat exposures (Rezende et al., 2014; Guevara-Molina et al., 2020; Lima et al., 2021; Camacho et al., 2023), or the lack of knowledge on species' distributions (Hortal et al., 2015).

Such an extensive list of species-specific problems could overcome the restrictive effect of heat tolerance on Tmax (see above). If this is the case, heat tolerance, or at least some of the ways in which it is represented, should be less generally helpful in identifying limits to species' geographic distribution and populations' thermal vulnerability. Alternatively, if robust relationships emerge within/across major taxa, they should justify using heat tolerance parameters for identifying heat-defined limits to species distributions.

The generality and sensitivity of the heat tolerance-Tmax assumption can be observed by testing it across several major sources of variation in both measures. Firstly, across multiple types of heat tolerance indexes which can be sorted into three main groups, ranging from higher/acute to lower/chronic stress indexes (Hochachka and Somero, 2002). In this sense, we herein sorted them into thermal limits, upper limits to optimal physiological temperatures, and indexes of behavioral tolerance (See methods). Secondly, these heat tolerance indexes have been applied across large taxa, such as marine fish, arthropods, amphibians, non-avian reptiles, birds, and mammals (Bennett et al., 2021). Therefore, we can observe the taxon-dependency of the heat tolerance-Tmax assumption. Thirdly, since the environmental history of animal lineages influences their current heat tolerance (Bennett et al., 2021), extant species could be more or less challenged by heat stress at their current warm edges. In this context, separating species based on how their heat tolerance relates to their current Tmax should help characterize how heat tolerance limits animals' warm range edges. Still, this procedure has not been done in studies relating heat tolerance with environmental temperatures.

Finally, maximum environmental temperatures measured at exposed sites (i.e., exposed soils, water surface) often exceed animals' heat tolerance across their geographic ranges, so they have been proposed as a measure of thermal risk (Sunday et al., 2014). However, thermoregulating animals typically avoid these temperatures using thermal refuges like shaded or underground microhabitats (see same study). Thus, at their warm range's edge, their heat tolerance could be more related to resisting high temperatures when they are already sheltered. Therefore, correlating heat tolerance with Tmax estimates made at different microhabitats seems necessary to evaluate the robustness of the heat tolerance-Tmax assumption. Besides, correlating Tmax estimates across species ranges' warm edges could inform on the thermal challenges experienced by animal populations at these sites, as shown for latitudinal patterns in thermal risk (Ex. Sunday et al., 2014).

In this meta-analysis, we accounted for multiple sources of variation in testing the heat tolerance-Tmax assumption. Specifically, we tested a) whether species' heat tolerance restricts Tmax estimated in different microhabitats, b) whether heat tolerance-Tmax correlations are stronger for species whose heat tolerance is more challenged by Tmax, and c) whether Tmax estimates correlate across animal species.

2. Methods

2.1. Estimation of Tmax for each species

Herein, Tmax represents the species' geographic thermal limit. It is calculated as the maximum environmental temperatures registered at each species' hottest known location. The location where it was registered is the species' warm edge (i.e., its trailing edge under a climatic warming scenario, Donelson et al., 2019; Pinsky et al., 2019; Stuart-Smith et al., 2017). Tmax is calculated as the mean of maximum

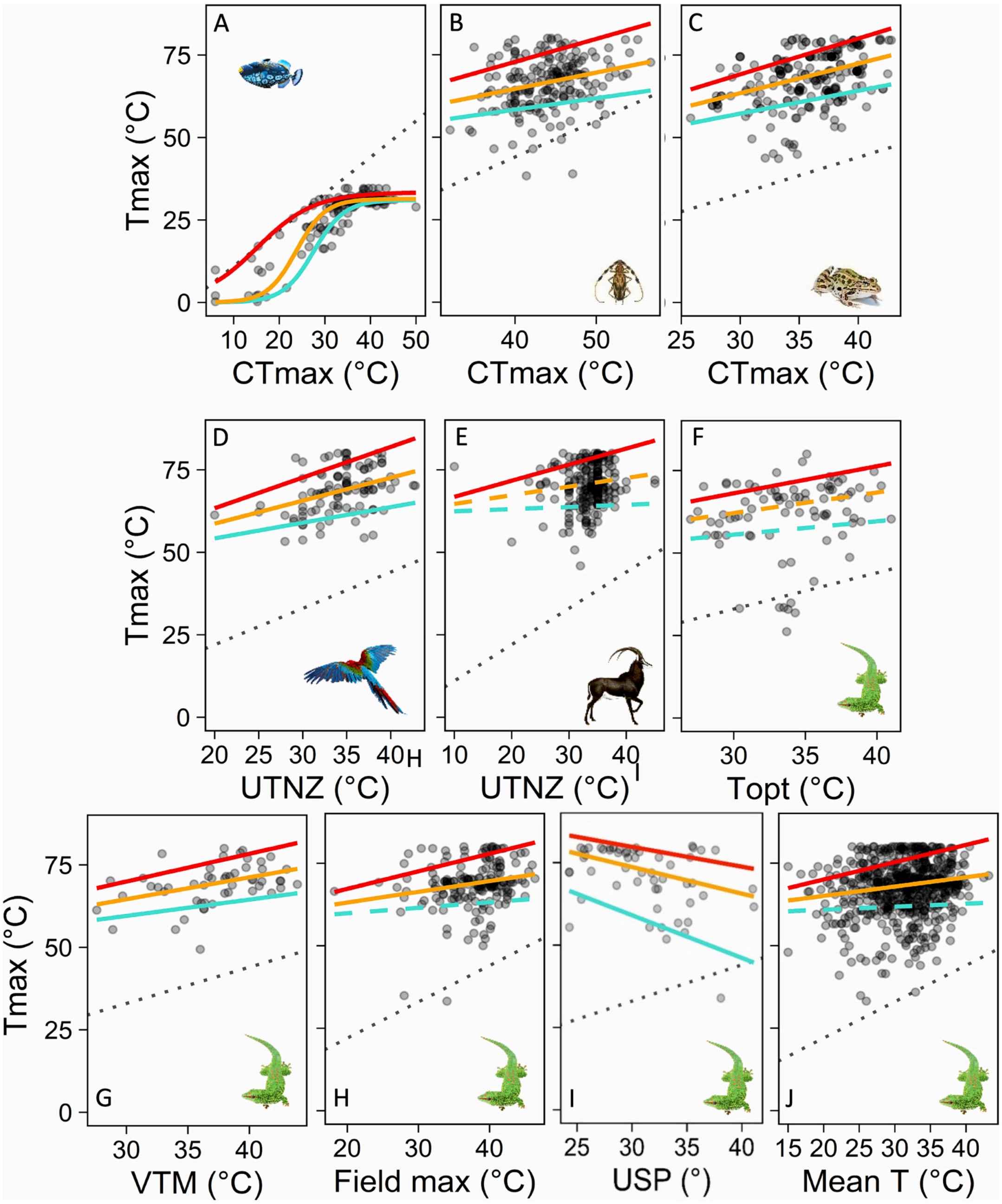

Fig. 1. Taxonomically detrended relationships between heat tolerance and Tmax (Maximum temperature available at exposed sites of animal species' warm edges. A-C). Thermal limits as measured in marine fish, terrestrial arthropods, and amphibians. D-F). Upper limits of physiologically optimal temperatures measured in birds, mammals, and lizards. G-J). Indexes of behavioral thermal tolerance measured in reptiles (see definitions in Table 1 and methods). The dotted line represents a 1:1 relationship between thermal tolerance and the geographic thermal limit. Solid lines represent the slopes of taxonomically detrended predictions of Tmax based on thermal physiology. Red, orange, and blue lines represent predicted 90th, 50th, and 10th conditional percentiles of Tmax on thermal tolerance, respectively. Slashed lines represent non-significant associations. Error ribbons are not included due to the small size of SE (see Table 2). relative to the axis scale. Supporting Figs. S2 A, B, and C contain graphs for all relationships between heat tolerance and Tmax indexes.

temperatures registered during each year's hottest month, also averaged across 20 recent past years. This method for summarizing extreme temperatures is known as bioclim 5 (Fick and Hijmans, 2017). We used the highest spatial resolution available for each Tmax estimate.

For on-land species, Tmax exp. (temperatures measured at sun-exposed soil) and Tmax prot (measured at 20 cm under shaded soil) were extracted from the microclim dataset (5 min resolution, Kearney et al., 2014). Additionally, we obtained Tmax air (measured in shaded air at around 1.5 m high) from the CHELSA dataset (30-s resolution).

For marine fish, we obtained Tmax surf, representing sea surface temperatures from the MARSPEC database (30-s resolution). We also obtained Tmax surf and Tmax mid-depth from the Bioracle database (5 min resolution; Assis et al., 2018). Tmax mid-depth represents temperatures at the middle of the water column and thus varies depending on the ocean depth, from a couple of meters at the coasts to hundreds of meters in the open sea. Although datasets with different scales may lead to different Tmax estimates (Garcia et al., 2019), we found that Tmax estimates from different scales led to similar patterns (see discussion).

To find each species' Tmax and their warm edge, we extracted bioclim5 values for every species' known location, obtained from the Global Biodiversity Information Facility (GBIF). We only used locations associated with specimens deposited in scientific collections to ensure their safe identification. Following Hijmans and Elith (2013), all locations were cleaned for likely captivity sites (e.g., zoos), long/lat zeroed records, mirrored records, records in the sea for terrestrial species, and vice versa. Outliers were identified by the interquartile range method and manually deleted. We followed suggestions by Sunday et al. (2014) and show results for Tmax exp. and Tmax surf (temperatures for exposed soil and sea surface) in the main text and Fig. 1.

Previous studies relating heat tolerance with the local thermal environment have relied on either one measure of environmental temperature (e.g., air temperatures measured in the shade, Huey et al., 2009; Khaliq et al., 2017) or estimates of body temperatures (e.g., operative temperatures for an individual of 5 g with idealized shape for all species., Sunday et al., 2014). Ideally, to account for variation in body size and thermoregulation options, studies should represent the distribution of operative temperatures for every species at the hottest time of the year, when individuals are exposed to stressful temperatures. Yet, this is not practical for a large diversity of body sizes, shapes, and habits. Thus, following Bakken and Angilletta Jr (2014), we represented thermal heterogeneity at each species' warm edge by bracketing the range of environmental temperatures available at warm edges (i.e., from Tmax exp. to Tmax prot). We discussed the robustness of our findings using different Tmax indexes.

2.2. Indexes of heat tolerance

Our heat tolerance indices represent a continuous gradient of heat stress intensity (Hochachka and Somero, 2002, pp.: 331), namely, from indices that represent acute and extreme stress (i.e., kills in minutes to hours) to ones that induce heat stress only after chronic exposure (i.e., kills or hampers reproduction after hours to days of exposure. Appendix A contains all the data and sources used herein, which were sorted into three groups.

Our first group represents upper physiological thermal limits. These represent temperatures that block individuals' locomotion and can kill during short exposures (i.e., minutes). They are often termed CTmax, from Critical Thermal Maximum (Lutterschmidt and Hutchison, 1997), and have been extensively measured in ectothermic animals. We obtained them for 193 terrestrial arthropods, 220 adult amphibians, and 298 non-avian reptiles (squamates and tortoises, heretofore simplified as "reptiles"). We also obtained CTmax data for marine fish, usually estimated by measuring the temperature that causes loss of equilibrium (LOE, 121 species) or the lethal limit (63 species). This latter measure represents the mean of the first temperature treatment that causes death in a fish during experimental heating (Comte and Olden, 2017).

Our second group of indexes represents the upper thermal limits for optimal physiological performance. Among endotherms, these limits are represented by the Upper Thermoneutral Zone limits (UTNZ), which refer to the environmental temperature over which metabolic and water loss costs sharply increase (McNab and Morrison, 1963). We used measures for 98 birds and 231 mammals (Khaliq et al., 2017). Across lizards, upper limits to optimal performance (Martin and Huey, 2008) have most often been measured as the body temperature that maximizes sprint speed (Topt, Huey et al., 2009), and this was assessed for 84 species in our dataset.

Our third group of indices comprehends several measures of body temperatures voluntarily tolerated by lizards, a widely studied taxon in thermal physiology. In this group, heat tolerance has been represented in multiple ways. We obtained data for panting temperatures (i.e., temperatures that induce panting to reduce head temperature, Heatwole et al., 1973). We also compiled the maximum body temperatures measured in active lizards, which can be measured in several ways affecting their values (Camacho and Rusch, 2017). We separated data obtained in the field (Field max temperatures, 179 species, Brattstrom, 1965; Cowles and Bogert, 1944), in laboratory thermal gradients (PBT max, for maximum preferred body temperatures, 63 species) and heating chambers (Voluntary Thermal Maximum or VTMax, 51 species, 23 from the literature and 28 new data from a field trip to Mozambique, see methodological details in Appendix B). Other studies have used either the 75th percentile (54 species, Hertz et al., 1993; Sinervo et al., 2010) or the mean of body temperatures measured in active lizards (657 species, Meiri et al., 2013). To avoid misrepresenting voluntary limits in field maximum temperatures, we excerpted maximum field temperatures measured in less than ten individuals per species.

Most of these datasets come from previous compilations made for adult animals (Brattstrom, 1965; Bennett et al., 2021; Comte and Olden, 2017; Curry-Lindahl, 1979; Diele-Viegas et al., 2018; Heatwole et al., 1973; Huey et al., 2009; Khaliq et al., 2017; Meiri et al., 2013; Sinervo et al., 2010; Sunday et al., 2014). We also added new data such as Fangue et al., 2011; Garcia-Robledo et al., 2018; Vinagre et al., 2019. When assessing heat tolerance within a species using a specific method, multiple tolerance values may be available. We always selected the highest value for the heat tolerance index in such cases. Creating a fully comprehensive dataset on thermal tolerance is not the aim of this study; interested users may find other large data compilations in the literature (e.g., GlobTherm, Bennett et al., 2018). While we provide data on heat tolerance for dozens to hundreds of species more, depending on the index, and seven more parameters of heat tolerance (limits to optimal temperatures, behavioral tolerance parameters for squamates, and species' Tmax), they bring up more data on experimental contexts. In addition, we provide new data on Tmax for different microhabitats at species' warm range edges.

2.3. Quantile correlations between Tmax and heat tolerance indexes

We applied quantile mixed models to test whether heat tolerance measures may constrain Tmax values. For that, we obtained correlation parameters for the 10th, 50th, and 90th percentiles of Tmax conditional on thermal tolerance. Here, lower percentiles (10th, 50th) represent species less challenged by maximal temperatures at their ranges' warm edges. In the analysis of marine fish, we initially tested whether the different approaches to measuring CTmax (LOE and lethal limit) yielded identical patterns. Given that they did (as shown in Appendix C, Fig. S1), we subsequently analyzed them jointly and hereafter refer to them as CTmax.

We initially considered linear and non-linear models to represent heat tolerance-Tmax relationships. For this, we fitted both linear (LQMM, Geraci and Bottai, 2014) and logistic nonlinear quantile mixed models (NLQMM, Geraci, 2019b). To control for phylogenetic relatedness in the absence of phylogenetic information, we specified the random effects at the genus level, as this produced a better fit than correcting by family level. Standard errors and 95 % confidence intervals were obtained via Bootstrap with 199 iterations. The analysis was conducted in R version 4.0.0 (R Core Team, 2013) using the "lqmm" (Geraci, 2014), "nlqmm" (Geraci, 2019a, b), and "aqmm" (Geraci, 2019c) packages.

A taxonomic detrending using random effects has already been successfully used to control for taxonomic relatedness (e.g., Sunday et al., 2014). Nonetheless, we also used standard phylogenetic correlations on subsets of species with available phylogenetic data (see Appendix B).

We could not add more factors to these correlations (i.e., effects of acclimation temperature, ramping rates, or exposure duration). Including additional factors may improve the fit of correlations, but they did not change geographical patterns in thermal tolerance in a previous study (Sunday et al., 2019). Besides, estimates for these factors' effects are rare and species-specific (Camacho and Rusch, 2017; Clusella-Trullas and Chown, 2014). Further, various acclimation and exposure times to deleterious temperatures are possible in natural conditions, depending on the local thermal conditions and thermoregulatory behavior (see discussion). Thus, as is typical in correlative studies, non-included factors comprise part of the model's random error term. Nonetheless, we discuss the impact of lacking factors in our models.

By repeating the above-explained correlations for each Tmax estimate (i.e., Tmax exp., Tmax air, and Tmax prot), we accounted for the possibility that either significant correlations or a lack of them for any group studied would derive from species generally using or avoiding one of these microhabitats.

2.4. *Test of differences in effect sizes across quantile correlations of Tmax-Heat tolerance*

We also tested if heat tolerance is more important to reaching higher Tmax for species' whose tolerance is more heat-challenged at their ranges' warm edges. In statistical terms, we tested if the effect size of correlations varied systematically across the three observed quantiles, accounting for our multiple estimates of Tmax (our response variable). Specifically, we conducted a three-level meta-analysis of multiple outcomes (Van den Noortgate et al., 2015) to compare slopes and their associated standard error using linear mixed models. Here, the response variable was the regression slope of the tests described in 2.3, and the fixed factor was the quantile of each regression. For the case of non-linear correlations across fish species, we compared the scale across quantiles instead of the slope. The two grouping variables were: 1) "Tmax dataset", which allowed us to compare effect sizes within the same Tmax estimate. For terrestrial groups, the levels were Tmax exp., Tmax air, and Tmax prot. For marine fish, we used two estimates of Tmax surf (MARSPEC and BIORACLE) and one of Tmax mid-depth (BIORACLE). 2) The grouping variable "Group" allowed us to compare size effects within each of the thirteen groups of taxa and their associated heat tolerance indexes. We performed this test using the rma. mv function from the metafor package (Viechtbauer, 2010). Statistical significance for the fixed effect was calculated through a Wald test with Knapp and Hartung's (2003) adjustment.

2.5. *Correlations of Tmax indices across species*

To perform these correlations, we applied the same model used for correlating Tmax with heat tolerance, described in 2.3. For terrestrial species, we correlated Tmax exp. with Tmax prot, Tmax exp. with Tmax air, and Tmax prot with Tmax air. For marine fish, we correlated Tmax surf with Tmax mid-depth, both from the Bio-Oracle dataset.

3. Results

3.1. *Quantile correlations between Tmax and heat tolerance indexes*

Physiological thermal limits (hereafter CTmax) constrain Tmax across marine and terrestrial ectotherms, except reptiles (Fig. 1; Appendix C, Figs. S2: A, B, C; Table 1). While CTmax-Tmax relationships were robust to changes in Tmax indexes for Marine fish, for terrestrial taxa, CTmax was often not significantly related to Tmax prot (Appendix C: S2A, B, and D; Appendix C S2 A, B, C, See methods). Also, unlike for terrestrial taxa, the heat tolerance-Tmax relationship is better described by a non-linear trend for Marine fish (AIC difference over 23 units, Appendix E, Table D). Thus, we described the relationships using the best-fitting model for each taxon. Phylogenetic analyses relating CTmax and Tmax but without estimating quantiles rendered similar (reptiles, birds, and mammals) or different results (amphibians) (Appendix E: D).

Upper limits for optimal body temperatures predicted Tmax for endotherms robustly across Tmax indexes. In contrast, squamates again showed weak to no correlations between their optimal temperatures and Tmax (see Fig. 1, Table 1, Appendix C: Figs. S2 A, B, C, and Appendix D: Tables S2, A, B, and C). When applying phylogenetic correlations without quantiles, relationships for endotherms remained, and significant correlations arose for lizards' Topt with Tmax exp. and Tmax air (Appendix F).

Only some behavioral traits robustly predicted Tmax for reptiles across heat tolerance indexes and Tmax estimates (Fig. 1 and Appendix C S2 A, B, C; Table 1 and Appendix D: S2 A, B, C). The weakest predictors were panting temperatures and the maximum preferred temperatures measured in laboratory gradients. In contrast, the strongest predictors of Tmax were the voluntary thermal maximum, the maximum field body temperatures, and the mean preferred body temperatures. Yet, the last shows visibly weaker relationships with Tmax and smaller slopes (Fig. 1, Table 1, Appendix C: S2 A, B, C; Tables Set 2: S2, A, B, C). Strikingly, the upper set point of preferred temperatures correlated strongly but negatively with Tmax (Fig. 1I, Table 1, and Appendix D: S2, A, B, C). Phylogenetic correlations led to different results, depending on the estimate of Tmax and behavioral index of heat tolerance. Yet, they remained significant for the VTmax and mean body temperatures (Appendix E).

3.2. *Comparison of correlations' effect sizes across quantiles*

Correlations' effects sizes were larger for higher quantiles across all the taxa/heat tolerance index groups (three-level meta-analysis: $df = 115$, $z = 8.247$, $p < .0001$, Fig. 2, Appendix D: S2 D. This indicates that for various animal taxa, the higher the maximum temperatures at their geographic boundaries, the more crucial a higher heat tolerance becomes for the expansion of the species' range toward warmer areas.

The patterns found were robust to changes in the scale of climatic datasets. For instance, among Fish, CTmax x Tmax surf correlations led to similar results using 30 s and 5 min databases (Fig. 2). Likewise, CTmax x Tmax air (30 s) rendered similar patterns and intermediate effect sizes compared to Tmax exp. and Tmax prot (5 min), as expected if they came from the same scale.

3.3. *Correlations among Tmax estimates across species*

On land, Tmax estimates from different microhabitats (i.e., at exposed soil, shaded air, and under moist, shaded soil) were strongly correlated across species' warm edges (Figs. 3A. Appendix F: S3 A, B, C and Set 4: S4E). In the sea, Tmax surf and Tmax mid-depth correlate with large heteroscedasticity (Fig. 3B). In concrete, the scatter indicates smaller differences among Tmax estimates at the hottest and the coldest warm edges in the ocean. These are tropical and polar coasts, as known from geographic occurrences (Appendix A). Phylogenetic correlations led to similar results (Appendix E).

Table 1

Relationships between Tmax exp. and Heat tolerance across animals. Describes parameters, standard errors (SE), and *P*-values from nonlinear (marine fish) and linear (other animal groups). Quantile mixed models for the 10th, 50th, and 90th percentiles of Tmax exp. conditional on indices of thermal tolerance. CTmax, critical thermal maximum; UTNZ: upper thermoneutral zone limit; Topt: optimal temperature for sprint speed; Panting T: body temperature that induces panting; VTM: voluntary thermal maximum, body temperature that induces retreat; Field max: maximum temperature observed in the field; PBT max: maximum preferred body temperature measured in a laboratory thermal gradient; USP: Upper Set Point 75th percentile of preferred temperatures; Mean T: mean body temperature of active individuals; Par. = Parameter, Asy. = Asymptote, Inf. = Inflection point, Sca. = Scale, Slo. = Slope, N = species number per analysis. See methods for definitions of tolerance indexes. Correlations' intercepts can be observed in Table S1. Colors relate to quantiles shown in Fig. 1—Tmax exp. sources: Microclim for terrestrial spp./Bio-oracle for marine ones.

		10th percentile			**50th percentile**			**90th percentile**			
Group	**Par.**	**Estimate**	**SE**	**P**	**Estimate**	**SE**	**P**	**Estimate**	**SE**	**P**	**N**
					Thermal limits (CTmax)						
Fish	Asy.	31.138	0.330	**<0.001**	31.420	0.307	**<0.001**	33.334	1.127	**<0.001**	184
Fish	Inf.	27.595	1.010	**<0.001**	22.753	1.703	**<0.001**	15.195	1.962	**<0.001**	184
Fish	Sca.	3.381	0.443	**<0.001**	3.588	0.923	**<0.001**	6.195	1.731	**<0.001**	184
arthropods	Slo.	0.347	0.143	**0.016**	0.494	0.140	**0.001**	0.697	0.136	**<0.001**	193
amphibians	Slo.	0.744	0.227	**0.001**	0.868	0.234	**<0.001**	1.094	0.234	**<0.001**	220
Reptiles	Slo.	<0.001	0.248	0.999	0.229	0.240	0.342	0.385	0.253	0.130	298
					Thermal limits for optimal performance (UTNZ for birds and mammals; Topt for lizards)						
birds	Slo.	0.474	0.153	**0.002**	0.697	0.151	**<0.001**	0.930	0.150	**<0.001**	98
mammals	Slo.	0.111	0.158	0.482	0.282	0.155	0.071	0.514	0.156	**0.001**	231
lizards	Slo.	0.406	0.347	0.244	0.624	0.362	0.086	0.821	0.381	**0.032**	84
					Indexes of behavioral thermal tolerance (lizards)						
Panting T	Slo.	-0.139	0.507	0.784	0.164	0.590	0.781	0.372	0.628	0.555	48
VTM	Slo.	0.693	0.175	**<0.001**	0.833	0.187	**<0.001**	0.970	0.195	**<0.001**	51
Field max	Slo.	0.297	0.173	0.087	0.460	0.208	**0.029**	0.657	0.223	**0.004**	179
PBT max	Slo.	0.472	0.639	0.461	0.727	0.574	0.207	1.059	0.576	0.067	63
USP	Slo.	-1.872	0.481	**<0.001**	-1.406	0.440	**0.002**	-1.260	0.423	**0.003**	54
Mean T	Slo.	0.069	0.095	0.467	0.261	0.089	**0.004**	0.526	0.099	**<0.001**	657

4. Discussion

Our results raise significant concerns about assuming that heat tolerance constrains Tmax across animals of varied ecology and distribution. First, the assumption seems taxon-dependent. For example, while reptiles have become a flagship group to represent thermal vulnerability (Ex., Huey et al., 2009; Sinervo et al., 2010), CTmax hardly restricted Tmax across reptiles' warm edges. Reptiles' heat tolerance also seems less related to the temperatures of the sites of experimental measurement (Araújo et al., 2013; Hoffmann et al., 2013). Nonetheless, we detected strong correlations of CTmax-Tmax exp. for arthropods and amphibians which challenge the general view that these groups are more protected by small crevices, nocturnal habits, or capacity for evaporative cooling compared to reptiles (Sunday et al., 2014). Although tadpoles' CTmax limit the pond temperature at which they can live (Duarte et al., 2012; Gutiérrez-Pesquera et al., 2016; Pintanel et al., 2022), a previous study (Gouveia et al., 2014) did not find significant correlations between the CTmax of anuran larvae and atmospheric Tmax estimates at warm edges. At this respect, our results suggest that warm edges for anurans might be more frequently constrained by the effects of heat stress on metamorphosed individuals, specifically after ponds have dried up, rather than on tadpoles.

We also discovered that the shape of the relationship between maximum critical temperature (CTmax) and maximum temperature (Tmax) varies between marine and terrestrial species. This suggests that different processes establish warm geographical boundaries in these two realms. In the ocean, cold-adapted fish (Fig. 1 A, left side) showed two different types of CTmax-Tmax relationships, depending on their quantile. Concretely, higher heat tolerance only helps increasing Tmax for species at the highest quantile (90th). In turn, the CTmax of heat-adapted species often exceeded the highest Tmax registered in databases (34 °C), flattening the relationship. This suggests that heat-adapted fish may become free from heat-induced constraints on distribution. Such CTmax levels are observable for species inhabiting hot

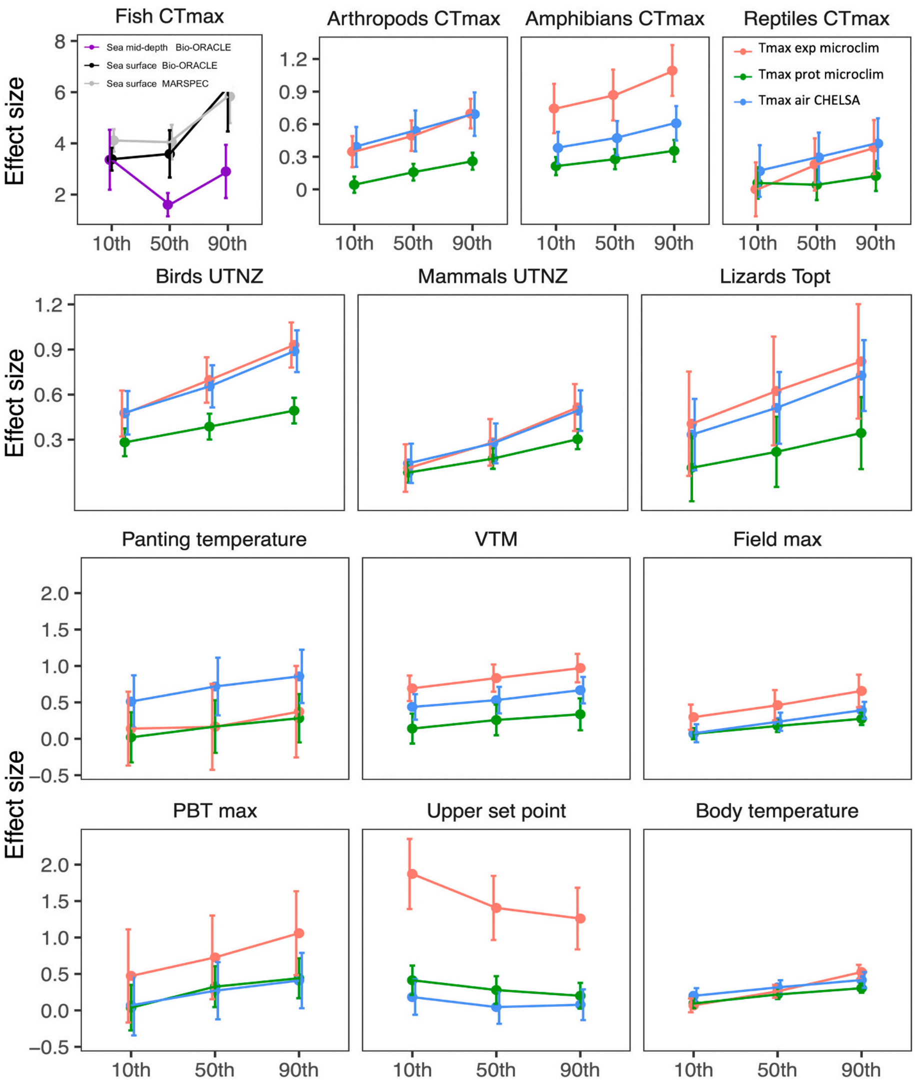

Fig. 2. Variation in the effect size of taxonomically detrended heat tolerance-Tmax quantile correlations between measures across the used quantiles. The quantiles represent how much species' heat tolerance is challenged by temperatures at their ranges' warm edges, being highest at the 90th. Each dot represents the effect size for one correlation between heat tolerance and one Tmax estimate for each taxon/heat tolerance index subset. Colors indicate the database source used for estimating Tmax.

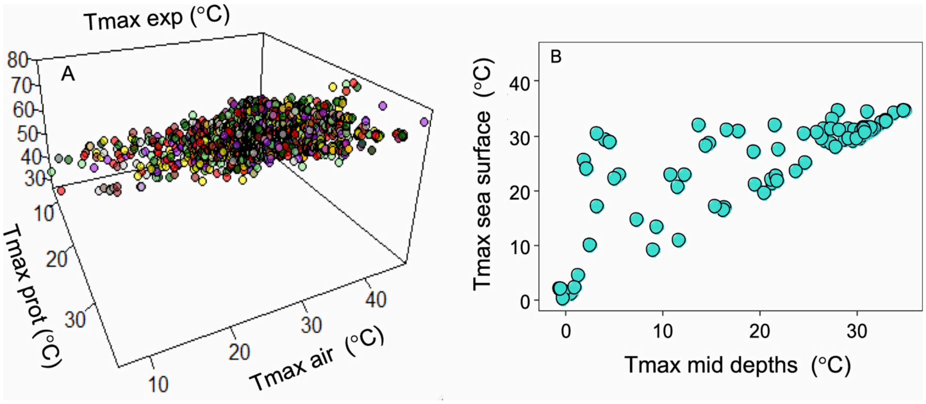

Fig. 3. Relationships among Tmax estimates measured at different microhabitats of species' geographic warm edges. A panel shows relationships across all terrestrial taxa studied herein. Colors represent data for 13 taxa subsets (marine fish, terrestrial arthropods, amphibians, different subsets of nonavian reptiles, birds, and mammals). B panel shows relationships for marine fish. While relations for terrestrial species are strongly linear, differences between mid and surface Tmax change across increasingly hot geographic thermal limits in the sea.

microhabitats, like tropical coastal pools or lagoons that may exceed 41 °C and reach deficient oxygen levels (Pörtner and Knust, 2007; Vinagre et al., 2019). Interestingly, equatorial fish species reach more extensive geographic ranges (Pie et al., 2021; Stuart-Smith et al., 2017), so this thermal release might contribute to that pattern.

On land, instead, maximal environmental temperatures always overcome the CTmax of the most heat-challenged species (90th percentile). This situation linearizes the relationship by always rewarding higher heat-tolerance with further expansion toward hotter regions. For some terrestrial taxa (Ex., birds, arthropods, amphibians), this relationship is evident even for species at lower quantiles, suggesting higher heat tolerance may help extend toward hotter regions before high temperatures impose strong constraints, perhaps by aiding competition (Amundrud and Srivastava, 2020).

Further, limits for optimal temperatures can also restrict the geography of endotherms and ectotherms, particularly among birds. Our results agree with a previous phylogenetic study on endotherms and Tmax air (Khaliq et al., 2017), further evidencing relationships with Tmax exp. and Tmax prot. Endotherms' high metabolic scope and thermal insulation may make them more powerful dispersers (Boratyński, 2020). Still, temperatures over their thermal optima seem to increase maintenance costs over prohibitive levels, blocking their dispersal/establishment beyond their warm edges when Tmax becomes too challenging.

Our results on behavioral indexes in lizards highlight the need to evaluate them before using them to infer thermal restrictions on animals' ecology and biogeography. Widely used indexes (e.g., the panting temperatures in birds and lizards (e.g., Conradie et al., 2019; Parmenter and Heatwole, 1975, respectively) may not identify thermal restrictions on species' geography. Accordingly, panting temperatures and maximal preferred temperatures in thermal gradients (PBT max) poorly constrained Tmax. Panting requires costly body water and may worsen the body's condition over time (Parmenter and Heatwole, 1975), and many reptiles do not pant (Camacho and Rusch, 2017). Thus, this behavior might only help momentarily to avoid an eventual heat shock during an activity or to achieve comfort at high temperatures rather than to survive long, hot, and often dry periods at warm edges. Further, maximal preferred temperatures measured in the laboratory traditionally carry over many methodological pitfalls that prevent their utility (Camacho and Rusch, 2017).

Surprisingly, a leading index to study thermal ecology and climatic vulnerability of reptiles (e.g., Hertz et al., 1993; Sinervo et al., 2010), the upper set point (USP), showed negative correlations with Tmax, which also undermines its use to estimate vulnerability to hot temperatures. We argue that a higher USP may represent adjustments for relatively cold environments instead of heat tolerance. By allowing their body temperatures to depart more over mean preferred levels, lizards living at cold geographic ranges for their heat tolerance (e.g., many *Liolaemus* in our sample) may attain higher sprint speeds (Bonino et al., 2011) or accelerate physiological rates (e.g., growth, Autumn and De Nardo, 1995). Further supporting this interpretation, this was the only tolerance index that showed stronger correlations for species at colder sites for their heat tolerance (i.e., species at lower quantiles). These results highlight the need to evaluate heat tolerance indexes before estimating thermal risk at species' warm edges with them.

In contrast, the VTmax and maximum field body temperatures restricted Tmax robustly across datasets and testing methods, except for Tmax measured at deep humid refuges (Tmax prot) which generally did not correlate with heat tolerance for any taxa. Particularly, there is a clear need for a higher VTmax to reach range edges with warmer Tmax air measured in the shade (Appendix C: S2C). In agreement with a couple of taxonomically restricted studies (Ex., Diaz-Ricaurte et al., 2020; Camacho et al., 2023), these results support the interpretation that when temperatures in the shade exceed behavioral tolerance at any given site, the site becomes thermally deleterious for populations of ectothermic vertebrates, imposing hot limits to their distribution.

Our most robust observed trend is the larger effect size for correlations among species of the higher quantile, present at all taxa. This new rule shows that higher heat tolerance is not universally important for warm edge expansion but mainly for species facing more thermally challenging situations at these edges. In contrast, previous interspecific patterns in heat tolerance (mostly represented by CTmax) have considered heat tolerance as mainly insensitive to geographic thermal gradients (Araújo et al., 2013; Bennett et al., 2021; Sunday et al., 2012). Besides, the different strengths of the relationships between animals' heat tolerance and Tmax, as revealed in this study, support the predictions made by Catullo et al. (2015). All this implies that animal species should not retrocede homogeneously against rises in environmental temperature, as many species seem unchallenged by high temperatures in the shade at their warm edges. The different strengths of heat tolerance-Tmax relationships also undermine widespread practices for estimating shifts in species' ranges (e.g., Cunningham et al., 2016; Lenoir et al., 2020; Moullec et al., 2022) or climatic vulnerability (e.g., Ponce-Reyes et al., 2012) based on location data only. Finally, since heat tolerance restricts Tmax with a range of different strengths, both on land and in the ocean, our results do not support statements of general differences in climatic vulnerability across these two realms (e.g., Sea vs. land, Pinsky et al., 2019; Sunday et al., 2019). Climatic variability strongly differs between air and water, and its impact on species resilience might also differ. Yet, both environments harbor species with distributions that are either highly limited by heat tolerance or largely unaffected by it. Finally, the discovered inter-quantile change in heat challenges could also have implications for studies at ranges' warm edges (AKA., rear-edge studies; Ex. Hampe and Petit, 2005; Fredston-Hermann et al., 2020; Moore et al., 2023). For taxa at quantiles exhibiting weaker correlations, populations at the trailing edges of their ranges may not need to adapt their thermal physiology to climate changes as intensively, compared to species at strongly correlated quantiles.

Our correlations among Tmax estimates across species show for first time patterns in the distribution of thermal challenges across animals' warm range edges. On land, the tight correlations among different Tmax indexes suggest that thermal challenges not only arise from too high Tmax exp., as proposed by Sunday's et al. (2014). In turn, concomitant thermal challenges seem to accumulate at warm range edges, limiting the dispersal of individuals or growth of populations toward hotter sites. First, the super high Tmax exp. often present at warm edges may dangerously raise body heating rates (Bakken, 1992). This situation increases the risks of heat shock for animals crossing exposed surfaces and those insufficiently sheltered in open habitats (Sunday et al., 2014; Camacho et al., 2015). In parallel, air temperatures often attained lethal and sublethal levels in the shade of warm range edges (i.e., close to the identity line; see Appendix C: Fig. S2B). This situation hinders options for behavioral thermoregulation at warm range edges and likely promotes the coevolution of CTmax and resistance time to sublethal temperatures, which in turn, strongly decrease as body temperatures rise (Terblanche et al., 2008; Rezende et al., 2014). In fact, some studies show that sublethal temperatures may impose stronger constraints on species' geographic distribution and thermal vulnerability than thermal limits alone (Ex., Rezende et al., 2020; Van Heerwaarden and Sgrò, 2021; Camacho et al., 2023). The coevolution of such traits might explain the recent unification of CTmax and resistance times (Jørgensen et al., 2021). In contrast, and although correlated with Tmax exp. and Tmax air, Tmax prot values lay well below the thermal tolerance of most terrestrial animals and were also uncorrelated to animals' heat tolerance. This suggests that animals are not often killed by exceedingly hot temperatures at well-sheltered microsites of ranges' warm edges. In turn, we argue that deep shelters are either generally unavailable or somehow insufficient for aiding animals to extend their warm range edges.

Correlations among Tmax indexes showed a different panorama of thermal challenges and scope for behavioral thermoregulation in the ocean. The narrower thermoclines were at the hottest and coldest warm edges (found in tropical and polar regions). This might make heat tolerance imperative to reach warmer range edges at these zones. At sites with steeper thermoclines, heat adaptation might be skipped to extend to warmer edges if fish could use deeper layers and avoid hot surface temperatures as some do (e.g., Cod, Claireaux et al., 1995; Stensholt, 2001). However, CTmax-Tmax relationships were stronger precisely for species of neither too cold nor too hot warm edges (i.e., the central region of scatter in Fig. 1). Thus, we hypothesize that deeper and cooler layers could be difficult to access for many fish.

In line with most studies, some factors could not be included in our quantile models. One was phylogenetic relatedness. We did taxonomic detrending similarly to Sunday et al. (2014; see appendix B) and used these results. Besides, we performed phylogenetic correlations for smaller subsets of species with available phylogenetic information. The obtained results were notably labile for taxons/indexes that already showed weak quantile correlations (mostly reptiles or mammals), but also for amphibians. These results underscore the importance of information on species' phylogenetic relations and of developing more flexible comparative methods to reach conclusions for some groups. Another important factor is exposure time to stressful temperatures, for example, derived from different experimental settings of heating rates and start temperatures. These factors have taxon-specific effect sizes (Ex. for Amphibians, Arthropods, or Lizards; Guevara-Molina et al., 2020; Lima et al., 2021; Camacho et al., 2023). Accounting for them can uncover relationships between heat tolerance and measurement site temperatures or geographical patterns of thermal vulnerability unseen when the time was not regarded (Rezende et al., 2014, 2020; Camacho et al., 2023). Yet, our Tmax estimates (bioclim 5, See methods) represent maximum temperatures of the hottest month averaged across 20 years. Thus, the closer Tmax reaches to, or the further it exceeds heat tolerance, the more accumulation of both short and long term exposures to stressfully hot temperatures. Therefore, the constraints that heat tolerance poses on Tmax on our graphs may derive from populational losses due to exposures to heat stress of different durations. We also recognize that intraspecific variability and plasticity are important for species' evolution and persistence (Terblanche et al., 2008; Clusella-Trullas and Chown, 2014; Morley et al., 2019) and must be better described. However, these factors did not erase interspecific patterns in Heat tolerance-Tmax, except for mammals or reptiles.

Biotic interactions may limit geographic ranges more strongly at species ranges' warm edges than at cold edges (Paquette and Hargreaves, 2021). Biotic interactions have recently been hypothesized as responsible for higher thermal niche underfilling at equatorward range limits (Moore et al., 2023). Based on our results and these ones, we propose new testable predictions arise to further understand the role of biotic interactions at ranges' warm edges: 1) for species reaching thermally challenging warm edges, biotic interactions should intensify the need for higher, constitutive, and less geographically variable heat tolerance. 2) Biotic interactions constrain ranges more strongly at equatorward sites, not due to happening at more challenging temperatures, but due to a higher local richness of competing species that lead to stronger underfilling of thermal niche. 3) Biotic interactions have a greater impact than thermal restrictions for survival/dispersal at less thermally challenging warm edges. 4) Biotic interactions do not systematically affect heat tolerance-Tmax relationships.

5. Conclusion

This meta-analysis extends the understanding of the Heat-tolerance Tmax relationship in several ways. 1) Showcasing the taxon and index dependency of heat tolerance-tmax relationships at species ranges' warm edges. 2) Indicating multiple sources of thermal challenges for animals at these sites. 3) Proposing new and testable hypotheses that relate range edges, heat tolerance, behavior, and biotic interactions. 4) Separating heat tolerance measures that help identify hot limits to animal species ranges from those that are unlikely to do it.

Credit authorship contribution statement

Agustín Camacho: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Miguel Trefaut Rodrigues:** Funding acquisition. **Refat Jayyusi:** Data curation. **Mohamed Harun:** Funding acquisition. **Marco Geraci:** Formal analysis. **Miguel A. Carretero:** Writing – review & editing. **Catarina Vinagre:** Writing – review & editing. **Miguel Tejedo:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

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Data availability

Data are provided in the Appendix A

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Appendices. Supplementary data

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