1 **TITLE**

2 Does heat tolerance actually predict animals' geographic thermal limits?

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26 **ABSTRACT**

27 The "climate extremes hypothesis" is a major assumption of geographic studies of

28 thermal tolerance and climatic vulnerability. However, this assumption remains vastly

29 untested for the warm edges of animals' geographic ranges, and multiple factors may

30 contribute to uncoupling heat tolerance and geographic limits. Herein, we compiled and

31 analyzed multiple types of heat tolerance indexes and of maximum temperatures for

each species' known distribution (hereafter, Tmax). The dataset includes over 1000

entries of heat tolerance and Tmax data distributed across marine fish, terrestrial

arthropods, amphibians, non-avian reptiles, birds, and mammals. With it, 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 to heat tolerance. Thirdly, we correlated the different estimates of Tmax among

them and across species. Restrictions are strong for amphibians, arthropods, and birds;

and inconsistent among reptiles and mammals. For marine fish, they describe a non-

linear relationship that contrasted 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 results

underline the importance of reliable species' heat tolerance indexes to identify their

thermal vulnerability at their range's warm 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.

Differently, the heterogeneous correlation of Tmax estimates in the Ocean supports the

view that fish thermoregulation is more limited at coastal zones. Our results undermine

arguments proposing that species of any realm (terrestrial or marine) are at

systematically higher thermal risk and that heat tolerance is insensitive to geographic

thermal gradients. 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 & Olden, 2017; Deutsch et al., 2008; Gaston et al., 2009; Khaliq et al., 2014; Kingsolver et al., 2013; Sinervo et al., 2010; Sunday et al., 2014; Terblanche et al., 2008). This research 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 & Olden, 2017; Khaliq et al., 2017; Pinsky et al., 2019; Pither, 2003; Rezende et al., 2020; Sunday et al., 2014, 2019. 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 Díaz-Ricaurte et al., 2020; Gouveia et al., 2014; although Khaliq et al., 2017 explored this for Endotherms). In contrast, many heat tolerance measures have been proposed for evaluating thermal restrictions on animals' distributions (e.g., Hertz, Huey & Stevenson, 1993; Huey et al., 2009; Sinervo et al., 2010; Camacho et al., 2018; Van Heerwaarden & Sgrò, 2021). Evaluating the restrictive capacity of different heat tolerance parameters seems particularly important at the warm edges of species ranges. 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 emerges to justify the worldwide utilization of heat tolerance metrics in studies of thermal vulnerability. This assumption posits that, insofar as it is

3

82   measured, heat tolerance generally constrains the highest environmental temperatures

83   that populations can withstand at species' warm range edges (Tmax).

84   Many factors, ranging from biological to purely methodological, could blur the

85   restrictions of heat tolerance on Tmax across species. Biological factors, such as local

86   adaptation (Geerts et al., 2015) and plasticity (i.e., acclimation, Morley et al., 2019),

87   may lead to intraspecific geographic variation in heat tolerance (e.g., Herrando-Pérez et

88   al., 2020) and in thermal risk (Bennet et al., 2019). This means that heat tolerance at

89   warm edges might be different than at the sites of experimental measurement.

90   Thermoregulatory behavior can also decouple individuals' body temperatures from too

91   high environmental temperatures (Buckley et al., 2013; Meiri et al., 2013; Sunday et

92   al., 2014) and even prevent the evolution of heat tolerance itself (Huey et al., 2003;

93   Muñoz & Bodensteiner, 2019). In parallel, species interactions might restrict

94   geographic ranges before the heat does so (e.g., Amundrud & Srivastava, 2020). Apart

95   from biological factors, methodological ones could also blur heat tolerance-Tmax

96   relationships by leading to inaccurate estimates of both variables. To cite some

97   examples: the incorrect estimation of heat tolerance (e.g., Camacho & Rusch, 2017;

98   Wolf et al., 2017), the scale-dependent variability in estimates of environmental

99   temperatures (Garcia et al., 2019), the duration of stressful heat exposures (Rezende et

100   al., 2014), or the lack of knowledge on species' distributions (Hortal et al., 2015).

101   Such an extensive list of species-specific problems might overcome a potential

102   restrictive effect of heat tolerance on Tmax (see above). If this is the case, heat

103   tolerance, or at least some of the ways in which it is represented, should be less

104   generally helpful in identifying limits to species' geographic distribution and

105   populations' thermal vulnerability. Alternatively, if robust relationships emerge

106 within/across major taxa, they should justify using heat tolerance parameters for

107 identifying heat-defined limits to species distributions.

108   The generality and sensitivity of the heat tolerance-Tmax assumption can be

109 observed by testing it across several major sources of variation in both measures.

110 Firstly, across multiple types of heat tolerance indexes, which can be sorted into three

111 main groups, ranging from higher/acute to lower/chronic stress indexes (Hochachka &

112 Somero, 2002). In this sense, we herein sorted them into thermal limits, upper limits to

113 optimal physiological temperatures, and indexes of behavioral tolerance (See methods).

114 Secondly, these heat tolerance indexes have been applied across large taxa, such as

115 marine fish, arthropods, amphibians, non-avian reptiles, birds, and mammals (Bennet et

116 al., 2021). Therefore, we can observe the taxon-dependency of the heat tolerance-Tmax

117 assumption. Thirdly, since the environmental history of animal lineages influences their

118 current heat tolerance (Bennet et al., 2021), extant species could be more or less

119 challenged by heat stress at their current warm edges. In this context, separating species

120 depending on how their heat tolerance relates to the current Tmax should help

121 characterize the potential restrictions that Tmax may impose on the distribution of

122 animals. Still, this procedure has not been done in studies relating heat tolerance and

123 environmental temperatures.

124   Finally, maximum temperatures measured at exposed sites (i.e., exposed soils,

125 water surface) often exceed animals' heat tolerance across their geographic ranges, so

126 they have been proposed to be used when representing thermal risk (Sunday et al.,

127 2014). However, thermoregulating animals can shelter from these temperatures in

128 thermal refuges like shaded or underground microhabitats. Thus, their heat tolerance

129 could be more related to Tmax measured in the shade than at exposed sites. Therefore,

130 correlating different Tmax estimates with heat tolerance seems necessary to evaluate

131 the robustness of the heat tolerance-Tmax assumption. Besides, Tmax estimates from

132 different microhabitats may exhibit complex relationships across latitudes (Sunday et

133 al., 2014). Given that, correlating Tmax estimates among them and across species

134 ranges' warm edges could inform on the thermal challenges experienced by animal

135 populations at these sites.

136   In this meta-analysis, we accounted for multiple sources of variation in testing

137 the heat tolerance-Tmax assumption. Specifically, we tested: a) whether species' heat

138 tolerance restricts Tmax estimated in different microhabitats; b) whether heat tolerance-

139 Tmax correlations are stronger for species whose heat tolerance is more challenged by

140 Tmax; and c) whether Tmax estimates correlate across animal ranges' warm edges.

141 **2. METHODS**

142 *2.1. Estimation of Tmax for each species*

143   Herein, Tmax represents the species' geographic thermal limit. It is calculated

144 as the maximum environmental temperatures registered at each species' hottest known

145 location. The location where it was registered is the species' warm edge (i.e., its trailing

146 edge under a climatic warming scenario, Donelson et al., 2019; Pinsky et al., 2019;

147 Stuart-Smith et al., 2017). Tmax is calculated as the mean of maximum temperatures

148 registered during each year's hottest month, also averaged across 20 recently past

149 years. This method for summarizing extreme temperatures is known as bioclim 5 (Fick

150 & Hijmans, 2017). We used the highest spatial resolution available for each Tmax

151 estimate.

152   For on-land species, Tmax exp (temperatures measured at sun-exposed soil) and

153 Tmax prot (measured at 20cm under shaded soil) were extracted from the microclim

154 dataset (5 min resolution, Kearney, Isaac, & Porter, 2014). Additionally, we obtained

155 Tmax air (measured in shaded air at around 1.5m high) from the CHELSA dataset (30-

156 sec resolution).

157   For marine fish, we obtained Tmax surf, representing sea surface temperatures

158 from the MARSPEC database (30-sec resolution). We also obtained Tmax surf and

159 Tmax mid-depth from the Bioracle database (5 min resolution; Assis et al., 2018).

160 Tmax mid-depth represents temperatures at the middle of the water column and thus

161 varies depending on the ocean depth, from a couple of meters at the coasts to hundreds

162 of meters in the open sea. Although datasets with different scales may lead to different

163 Tmax estimates (Garcia et al., 2019), we found that Tmax estimates from different

164 scales led to similar patterns (see discussion).

165   To find each species' Tmax and their warm edge, we extracted bioclim5 values

166 for every species' known location, obtained from the Global Biodiversity Information

167 Facility (GIBF). We only used locations associated with specimens deposited in

168 scientific collections to ensure their safe identification. All locations were cleaned for

169 likely captivity sites (e.g., zoos), long/lat zeroed records, mirrored records, records in

170 the sea for terrestrial species, and vice versa. Outliers were identified by the

171 interquartile range method and manually deleted. We followed suggestions by Sunday

172 et al. (2014) and show results for Tmax exp and Tmax surf (temperatures for exposed

173 soil and sea surface) in the main text and Figure 1. Results for other Tmax estimates

174 can be found in Appendix A and C.

175   Previous studies relating heat tolerance with the local thermal environment have

176 relied on either one measure of environmental temperature (e.g., air temperatures

177 measured in the shade, Huey et al., 2009; Khaliq et al., 2014) or estimates of body

178 temperatures (e.g., operative temperatures for an individual of 5g with idealized shape

179 for all species., Sunday et al., 2014). Ideally, to account for variation in body size and

180   thermoregulation options studies should somehow represent the distribution of

181   operative temperatures for every species at the hottest time of the year, and also the

182   time they are exposed to stressful temperatures for each individual. Yet, this is not

183   practical for a large diversity of body sizes, shapes, and habits. Thus, following Bakken

184   & Angilletta (2014), we represented thermal heterogeneity at each species' warm edge

185   by bracketing the range of environmental temperatures available at warm edges (i.e.,

186   from Tmax exp to Tmax prot). We discussed the robustness of our findings using

187   different Tmax indexes.

188

189   *2.2 Indexes of thermal tolerance*

190   Our heat tolerance indices represent a continuous gradient of heat stress

191   intensity (Hochachka & Somero, 2002, pp: 331), namely, from acute and extreme stress

192   (i.e., kills in minutes to hours) to chronic heat stress (i.e., kills or hampers reproduction

193   after hours to days of exposure). Accordingly, we grouped heat tolerance indexes into

194   three groups.

195   Our first group represents upper physiological thermal limits. These represent

196   temperatures that block individuals' locomotion and can kill during short exposures

197   (i.e., minutes). They are often termed CTmax, from Critical Thermal Maximum

198   (Lutterschmidt & Hutchison, 1997), and have been extensively measured in

199   ectothermic animals. We obtained them for 193 terrestrial arthropods, 220 adult

200   amphibians, and 298 non-avian reptiles (squamates and tortoises, simplified as reptiles

201   in the main text). We also obtained CTmax data for marine fish, usually estimated by

202   measuring the temperature that causes loss of equilibrium (LOE, 121 species) or the

203   lethal limit (63 species). This latter measure represents the mean of the first

204   temperature treatment that causes death in a fish during experimental heating (Comte &

205   Olden, 2017).

206   Our second group of indexes represents the upper thermal limits for optimal

207   physiological performance. Among endotherms, these limits are represented by the

208   Upper Thermoneutral Zone limits (UTNZ), an environmental temperature over which

209   metabolic and water loss costs sharply increase (McNab & Morrison, 1963). We used

210   measures for 98 birds and 231 mammals (Khaliq et al., 2014). Across lizards, upper

211   limits to optimal performance (Martin & Huey, 2008) have most often been measured

212   as the body temperature that maximizes sprint speed (T_{opt}, Huey et al., 2009, 84

213   species in our dataset).

214   Our third group of indices comprehends several measures of body temperatures

215   voluntarily tolerated by lizards, a widely studied taxon in thermal physiology. In this

216   group, heat tolerance has been represented in multiple ways. We obtained data for

217   panting temperatures (i.e., temperatures that induce panting to reduce head temperature,

218   Heatwole, Firth, & Webb, 1973). We also compiled the maximum body temperatures

219   measured in active lizards, which can be measured in several ways affecting their

220   values (Camacho & Rusch 2017). We separated data obtained in the field (Field max

221   temperatures, 179 species, Brattstrom, 1965; Cowles & Bogert, 1944), in laboratory

222   thermal gradients (PBT max, for maximum preferred body temperatures, 63 species)

223   and heating chambers (Voluntary Thermal Maximum or VTMax, 51 species, 23 from

224   the literature and 28 new data from a field trip to Mozambique, see methodological

225   details in Appendix B). Other studies have used either the 75th percentile (54 species,

226   Hertz et al., 1993; Sinervo et al., 2010) or the mean of body temperatures measured on

227   active lizards (657 species, Meiri et al., 2013). To avoid misrepresenting voluntary

228   limits in field maximum temperatures, we excerpted maximum field temperatures

229   measured in less than ten individuals per species.

230   Most of these datasets come from previous compilations made for adult animals

231   (Brattstrom, 1965; Bennett et al., 2021; Comte & Olden, 2017; Curry-Lindahl, 1979;

232   Diele-Viegas et al., 2018; Heatwole et al., 1973; Huey et al., 2009; Khaliq et al., 2014;

233   Meiri et al., 2013; Sinervo et al., 2010; Sunday et al., 2014). We also added new data

234   (e.g., Fangue et al., 2011; Garcia-Robledo et al., 2018; Vinagre et al., 2019; more on

235   Appendix A: Data). We used the highest value whenever several tolerance values were

236   available for any given heat tolerance index, measured with the same method within a

237   given species. Creating a fully comprehensive dataset on thermal tolerance is not the

238   aim of this study; interested users may find other large data compilations in the

239   literature (e.g., GlobTherm, Bennett, et al., 2018). While we provide data on heat

240   tolerance for more species and parameters, they bring up more data on experimental

241   contexts. Appendix A contains all the data and sources used herein.

242

243   *2.3.   Quantile correlations between Tmax and heat tolerance indexes*

244   We applied quantile mixed models to test whether heat tolerance measures may

245   limit Tmax values. For that, we obtained correlation parameters for the 10th, 50th, and

246   90th percentiles of Tmax conditional on thermal tolerance. In this way, we separated

247   species from less (10th percentile) to more (90th percentile) physiologically challenged

248   by maximal temperatures at their ranges' warm edges.

249   We first selected between linear and non-linear models to represent heat

250   tolerance-Tmax relationships. For this, we fitted both linear (LQMM, Geraci & Bottai,

251   2014) and logistic nonlinear quantile mixed models (NLQMM, Geraci, 2019b).

252   The random effects specifications for LQMM and NLQMM were at the genus

253   level, as this produced a better fit than correcting by family level. Standard errors and

254   95% confidence intervals were obtained via Bootstrap with 199 iterations. The analysis

255   was conducted in R version 4.0.0 (R Core Team, 2013) using the "lqmm" (Geraci,

256   2014), "nlqmm" (Geraci, 2019ab), and "aqmm" (Geraci, 2019c) packages.

257   Random effects have already been successfully used to control for taxonomic

258   relatedness (e.g., Sunday et al., 2014). Nonetheless, `we also used standard

259   phylogenetic correlations on subsets of species with available phylogenetic data (see

260   Appendix B).

261   We could not add more factors to these correlations (i.e., effects of acclimation

262   temperature, ramping rates, or exposure duration). Including additional factors may

263   improve the fit of correlations, but they did not change geographical patterns in thermal

264   tolerance in a previous study (Sunday et al., 2019). Besides, estimates for these factors'

265   effects are rare, species-specific (Camacho & Rusch, 2017; Clusella-Trullas & Chown,

266   2014). Further, various acclimation and exposure times to deleterious temperatures are

267   possible in natural conditions, depending on the local thermal conditions and

268   thermoregulatory behavior (see discussion). Thus, as typical in correlative studies, non-

269   included factors make part of the random error term in the model. We nonetheless

270   discuss the impact of lacking factors in our models.

271   By repeating the above-explained correlations for each Tmax estimate (i.e.,

272   Tmax exp, Tmax air, and Tmax prot) we accounted for the possibility that either

273   significant correlations or a lack of them for any group studied would derive from

274   species generally using or avoiding one of these microhabitats.

275   *2.4.   Test of differences in effect sizes across quantile correlations of Tmax-Heat tolerance.*

276   We also tested if heat tolerance is more important to reaching higher Tmax for species'

277   whose tolerance is more heat-challenged at their ranges' warm edges. In statistical

278   terms, we tested if the effect size of correlations varied systematically across the three

279   observed quantiles, accounting for our multiple estimates of Tmax (our response

280 variable). Specifically, we used a three-level meta-analysis of multiple outcomes (Van

281 den Noortgate et al., 2015) that compares slopes and their associated standard error

282 using linear mixed models. Here, the response variable was the regression slope of the

283 tests described in 2.3, and the fixed factor was the quantile of each regression. For the

284 case of non-linear correlations across fish species, we compared the scale across

285 quantiles, instead of the slope. The two grouping variables were: 1) "Tmax dataset",

286 which allowed to compare effect sizes within the same Tmax estimate. For terrestrial

287 groups, the levels were Tmax exp, Tmax air, and Tmax prot. For marine fish, we used

288 two estimates of Tmax surf (MARSPEC and BIORACLE) and one of Tmax mid-depth

289 (BIORACLE). 2) The grouping variable "Group" allowed us to compare size effects

290 within each of the thirteen groups of taxa and their associated heat tolerance indexes.

291 We performed this test using the rma. mv function from the metafor package

292 (Vietchbauer et al., 2010). Statistical significance for the fixed effect was calculated

293 through a Wald test with Knapp & Hartung's (2003) adjustment.

294   *2.5.   Correlations among Tmax indices*

295   We correlated the different Tmax indices among them and across species. We

296 used the same model as for correlating Tmax with heat tolerance, described in 2.3. For

297 terrestrial species, we correlated Tmax exp with Tmax prot, Tmax exp with Tmax air,

298 Tmax prot with Tmax air. For marine fish, we correlated Tmax surf with Tmax mid-

299 depth from the Bio-Oracle dataset. Results are shown in Figure 3 and Appendix E.

300 **3.   RESULTS**

301   *3.1. Quantile correlations between Tmax and heat tolerance indexes.*

302   Physiological thermal limits (hereafter CTmax) restrict Tmax (i.e., significantly

303 predicts its 90th percentile) across marine and terrestrial ectotherms, except reptiles

304 (Figure1; Appendix C, Figures S2: A, B, C; Table 1). While CTmax-Tmax

305 relationships were robust to changes in Tmax indexes for Marine fish, for terrestrial

306 taxa, CTmax was often not significantly related to Tmax prot (Appendix D: S2A, B,

307 and C; Appendix C S2 A, B, C, See methods). Unlike for terrestrial taxa, the heat

308 tolerance-Tmax relationship is better described by a non-linear trend for Marine fish

309 (AIC difference over 23 units, Table S4 D, Appendix F). Thus, we described the

310 relationships using the best-fitting model for each taxon. Phylogenetic analyses relating

311 CTmax and Tmax but without estimating quantiles rendered similar results. The

312 exception was the amphibians, for which a phylogenetic relationship was undetected

313 (Appendix F: S4).

314   Upper limits for optimal body temperatures predicted Tmax for endotherms

315 robustly across Tmax indexes. In contrast, squamates again showed weak to no

316 correlations between their optimal temperatures and Tmax (see Figure 1, Table 1,

317 Appendix C: Figures S2 A, B, C, and Appendix D: Tables S2, A, B, and C). When

318 applying phylogenetic correlations without quantiles, relationships for endotherms

319 remained, but significant correlations were obtained for lizards (Appendix F).

320   Only some behavioral traits robustly predicted Tmax for reptiles across heat

321 tolerance indexes and Tmax estimates (Figure 1 and Appendix C S2 A, B, C; Table 1

322 and Appendix D: S2 A, B, C). The weakest predictors were panting temperatures and

323 the maximum preferred temperatures measured in laboratory gradients. In contrast, the

324 strongest predictors of Tmax were the voluntary thermal maximum, the maximum field

325 body temperatures, and the mean preferred body temperatures. Yet, the last shows

326 visibly weaker relationships with Tmax, and smaller slopes (Figure 1, Table 1,

327 Appendix C S2 A, B, C; Tables Set 2: S2, A, B, C). Strikingly, the upper set point of

328 preferred temperatures correlated strongly but negatively with Tmax (Figure 1I, Table

329   1, and Appendix D: S2, A, B, C). Phylogenetic correlations led to different results,

330   depending on the estimate of Tmax and behavioral index of heat tolerance. Yet, they

331   remained significant for the VTmax and mean body temperatures (Appendix F).

3.2. Comparison of correlations' effect sizes across quantiles

333   Correlations' effects sizes were larger for higher quantiles across all the

334   taxa/heat tolerance index groups (three-level meta-analysis: df=115, z=8.247, p <.0001,

335   Figure 2, Appendix D: S2 D. This demonstrates that across animal species, the higher

336   Tmax is with respect to heat tolerance, the more important a higher heat tolerance

337   becomes to reach sites with even higher Tmax.

338   The patterns found were robust to changes in the scale of climatic datasets. For

339   instance, among Fish, CTmax x Tmax surf correlations led to similar results using 30 s

340   and 5 min databases (Figure 2). Likewise, CTmax x Tmax air (30 s) rendered similar

341   patterns and intermediate effect sizes when compared to Tmax exp and Tmax prot (5

342   min), just as expected if they came from the same scale.

3.3.   Correlations among Tmax estimates across species

344   On land, Tmax estimates from different microhabitats (i.e., at exposed soil,

345   shaded air, and under moist, shaded soil) were strongly correlated across species' warm

346   edges (Figures 3A. Appendix E: S3 A, B, C and Set 4: S4E). In turn, in the sea, Tmax

347   surf and Tmax mid-depth correlate with large heteroscedasticity (Figure 3B). In

348   concrete, the scatter indicates smaller differences among Tmax estimates at the hottest

349   and the coldest warm edges in the ocean. These are tropical and polar coasts, as known

350   from geographic occurrences (Appendix A). Phylogenetic correlations led to similar

351   results (Appendix F).

4. DISCUSSION

Our results raise significant concerns about assuming that heat-tolerance limits 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 compared to arthropods and amphibians. Reptiles' heat tolerance also seems less related to the temperatures of the sites of experimental measurement (Araújo et al., 2013; Hoffmann et al., 2013). The strong correlations of CTmax-Tmax exp for arthropods and amphibians also 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 often constrained by the effect of heat stress on metamorphosized individuals (i.e., after ponds have dried up) than on tadpoles.

The different ways in which CTmax related to Tmax in marine and terrestrial taxa call for different processes establishing geographic warm edges at both realms. In the Ocean, cold-adapted fish (Fig 1 A, left side) showed two different types of CTmax-Tmax relationship, depending on their quantile. Higher heat tolerance leads to increase Tmax only for species at the highest quantile (90th). In turn, the CTmax of heat-adapted species often overcame the highest Tmax registered in databases (34°C). This liberates their dispersal from heat restrictions and flats the hot side curve. Such CTmax levels

377 are observable for species inhabiting hot microhabitats, like tropical coastal pools or

378 lagoons that may exceed 41 °C and reach deficient oxygen levels (Pörtner & Knust,

379 2007; Vinagre et al., 2019). Interestingly, equatorial fish species reach more extensive

380 geographic ranges (Pie et al., 2021; Stuart-Smith et al., 2017), so this thermal release

381 might contribute to that pattern.

382   On land, instead, maximal environmental temperatures always overcome the

383 CTmax of the most heat-challenged species (90th percentile). This situation straightens

384 the relationship by always rewarding more heat-tolerant species with more dispersal

385 capabilities across geographic thermal gradients. For some terrestrial taxa (Ex., birds,

386 arthropods, amphibians), this relationship is evident even for species from lower

387 quantiles. All these findings suggest that the benefits of heat tolerance for expanding

388 the warm edges of groups strongly depend on the species' biology and thermal context.

389   Further, limits for optimal temperatures can also restrict the geography of

390 endotherms and ectotherms, particularly among birds. Our results agree with a previous

391 phylogenetic study on endotherms and Tmax air (Khaliq et al., 2017), further

392 evidencing relationships with Tmax exp and Tmax prot. Endotherms' high metabolic

393 scope and thermal insulation may make them more powerful dispersers (Boratyński,

394 2020). Still, temperatures over their thermal optima seem to increase maintenance costs

395 over prohibitive levels, blocking their dispersal/establishment beyond their warm edges

396 when Tmax becomes too challenging.

397   Our results on behavioral indexes in lizards highlight the need to evaluate them

398 before using them to infer thermal restrictions on animals' ecology and biogeography.

399 Widely used indexes (e.g., the panting temperatures in birds and lizards (e.g., Conradie

400 et al., 2019; Parmenter & Heatwole, 1975, respectively) may not identify thermal

401 restrictions on species' geography. Accordingly, panting temperatures and maximal

preferred temperatures in thermal gradients (PBT max) poorly restricted Tmax. Panting

requires costly body water and may worsen the body's condition over time (Parmenter

& Heatwole, 1975), and many reptiles do not pant (Camacho & 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 & 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, being stronger for species at lower quantiles.

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 & 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. 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., Ricaurte et al., 2019; Camacho et al., 2023), these

428   results support the interpretation that when temperatures in the shade exceed behavioral

429   tolerance at any given site, the site becomes thermally deleterious for populations of

430   ectothermic vertebrates, imposing hot limits to their distribution.

431   Our most robust observed trend is the larger effect size for correlations among

432   species of the higher quantile, present at all taxa. This shows that higher heat tolerance

433   is not universally important for warm edge expansion, but mainly for species facing

434   more thermally challenging situations at these edges. In contrast, previous interspecific

435   patterns in heat tolerance (mostly represented by CTmax) have considered heat

436   tolerance as mainly insensitive to geographic thermal gradients (Araújo et al., 2013;

437   Bennett et al., 2021; Sunday et al., 2012). The heterogeneous relationships found herein

438   between animals' heat tolerance and Tmax provide empirical support to Catullo et al.,

439   (2015) predictions. This implies that animal species will not retrocede homogeneously

440   against rises in environmental temperature, as many species seem unchallenged by high

441   temperatures in the shade at their warm edges. This finding also undermines

442   widespread practices for estimating shifts in species' ranges (e.g., Cunningham et al.,

443   2016; Lenoir et al., 2020; Moullec et al., 2022), climatic vulnerability (e.g., Ponce-

444   Reyes et al., 2012), based only on location-climate data. Finally, the strong context

445   dependence of heat tolerance restrictions on geography found both on land and in the

446   Ocean do not support statements of general differences in climatic vulnerability across

447   these two realms (e.g., Sea vs. land, Pinsky et al., 2019; Sunday et al., 2019). Climatic

448   variability varies significantly between air and water, and its impact on species

449   resilience may still differ. Yet, both environments harbor species with distributions that

450   are either highly limited by heat tolerance or largely unaffected by it.

451   The correlations among Tmax estimates across species inform on the

452   distribution of thermal challenges at species' warm edges. On land, the tight

453   correlations among different Tmax indexes suggest concomitant thermal challenges for

454   animals. On one hand, the super high Tmax exp existing at warm edges dangerously

455   raises body heating rates (Bakken, 1992). This situation increases the risks of heat

456   shock for animals crossing exposed surfaces and those insufficiently sheltered in open

457   habitats (Camacho et al., 2015; Sunday et al., 2014). In parallel, air temperatures often

458   attained lethal and sublethal levels in the shade (i.e., close to the identity line, see

459   Appendix C: Figure S2B). This situation hinders options for behavioral

460   thermoregulation and likely promotes the coevolution of CTmax and resistance time to

461   sublethal temperatures. Survival at sublethal temperatures strongly decreases as

462   temperatures rise (Terblanche et al., 2008; Rezende et al., 2014) and it can shape

463   geographic distribution Rezende et al., 2020) and vulnerability (Camacho et al., 2023).

464   The coevolution of such traits might explain the recent unification of CTmax and

465   resistance times (Jørgensen et al., 2021). Although they might evolve separately in

466   some cases, too (Camacho et al., 2023). In contrast, although correlated with Tmax exp

467   and Tmax air, Tmax prot values lay well below the thermal tolerance of most terrestrial

468   animals. They were also uncorrelated to animals' heat tolerance. Thus, we argue that

469   deep shelters are somehow inefficient for extending animals' warm edges.

470   Correlations among Tmax indexes showed a different panorama of thermal

471   challenges at the sea. The narrower thermoclines were at the hottest and coldest warm

472   edges (found in tropical and polar regions). This might make heat tolerance imperative

473   to reach warmer range edges. At sites with steeper thermoclines, heat adaptation might

474   be skipped to extend to warmer edges if fish can use deeper layers and avoid hot

475   surface temperatures (e.g. Cod, Claireaux et al., 1995; Stensholt et al., 2001).

476   As in most studies, some factors could not be included in our quantile models,

477   and thus, they could blur the relationships observed, particularly for reptiles or

mammals. For example, considering exposure time to stressful temperatures can uncover relationships between heat tolerance and measurement site temperatures, unseen when the time was not regarded (Rezende et al., 2014; 2020). Yet, our Tmax estimates (bioclim 5, see methods) include short and long-term hot periods. Thus, the restrictions of heat tolerance on Tmax detected by us should integrate populational losses due to exposure to different periods of heat stress. We also recognize that intraspecific variability and plasticity are important for species' evolution and persistence (Terblanche et al., 2008; Herrando-Perez et al., 2020; 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.

Behavior is another widely regarded confounding factor for global studies. Thermoregulatory behavior may buffer the selective pressure of high temperatures on heat tolerance, relying on thermal gradients to avoid harmful temperatures (i.e., using thermal refugia, Huey et al., 2003; Muñoz & Bodensteiner, 2019; Sunday et al., 2014). However, in the marine realm, CTmax-Tmax relationships became stronger precisely for species of neither too cold nor too hot warm edges (Fig 1), and these species had the highest thermoclines at their warm edges (Figure 3B). Similarly, on land, we found widespread and strong correlations of heat tolerance with Tmax exp and Tmax air, but not with Tmax prot. Besides, the last was systematically colder than heat tolerance across groups (Appendix C S2 A-C). These results suggest that behavioral thermoregulation (i.e, the use of deep shaded shelters) is of limited use in extending species ranges' warm edges.

Biotic interactions may limit geographic ranges more strongly at species ranges' warm edges than at cold edges (Paquette & Hargreaves, 2021). Since we found heat tolerance to be more restrictive on Tmax for species of higher quantiles, new testable

503 predictions arise to understand the role of biotic interactions at geographic warm edges:

504 1) At more thermally challenging warm edges, biotic interactions should intensify the

505 need for higher, constitutive, and less geographically variable heat tolerance. 2) Biotic

506 interactions have a greater impact than thermal restrictions for survival/dispersal at less

507 thermally challenging warm edges. 3) Biotic interactions do not systematically affect

508 heat tolerance-Tmax relationships.

509 **5.   CONCLUSION**

510   This meta-analysis extends the understanding of the Heat-tolerance Tmax

511 relationship in several ways. 1) Showcasing the taxon and index dependency of heat

512 tolerance-tmax relationships at species warm range edges. 2) Indicating multiple

513 sources of thermal challenges for animals at their warm range edges. 3) Proposing new

514 and testable hypotheses that relate range edges, heat tolerance, behavior, and biotic

515 interactions. 4) Separating heat tolerance measures that help identify hot limits to

516 animal species ranges from others that are very unlikely to do it.

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Tables

Group	Par.	10th percentile			50th percentile			90th percentile			N
		Estimate	SE	P	Estimate	SE	P	Estimate	SE	P	
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

862

863 **TABLE 1** Relationships between Tmax exp and Heat tolerance across animals.

864 Describes parameters, standard errors (SE), and P-values from nonlinear (marine fish)

865 and linear (other animal groups). Quantile mixed models for the 10th, 50th, and 90th

866 percentiles of Tmax exp conditional on indices of thermal tolerance. CTmax, critical

867   thermal maximum; UTNZ: upper thermoneutral zone limit; Topt: optimal temperature

868   for sprint speed; Panting T: body temperature that induces panting; VTM: voluntary

869   thermal maximum, body temperature that induces retreat; Field max: maximum

870   temperature observed in the field; PBT max: maximum preferred body temperature

871   measured in a laboratory thermal gradient; USP: Upper Set Point 75th percentile of

872   preferred temperatures; Mean T: mean body temperature of active individuals;

873   Par.=Parameter, Asy.=Asymptote, Inf.=Inflection point, Sca.=Scale, Slo.=Slope,

874   N=species number per analysis. See methods for definitions of tolerance indexes.

875   Correlations' intercepts can be observed in Table S1. Colours relate to quantiles shown

876   in Figure 1—Tmax exp sources: Microclim for terrestrial spp/Bio-oracle for marine

877   ones.

878

Figure legends and embedded Figures

FIGURE 1. Upper thermal tolerance indexes significantly associated with Tmax

(Maximum temperature available at exposed sites of animal species' warm edges. A-

C). Thermal limits as measured in marine fish, terrestrial arthropods, amphibians, and

terrestrial reptiles. 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
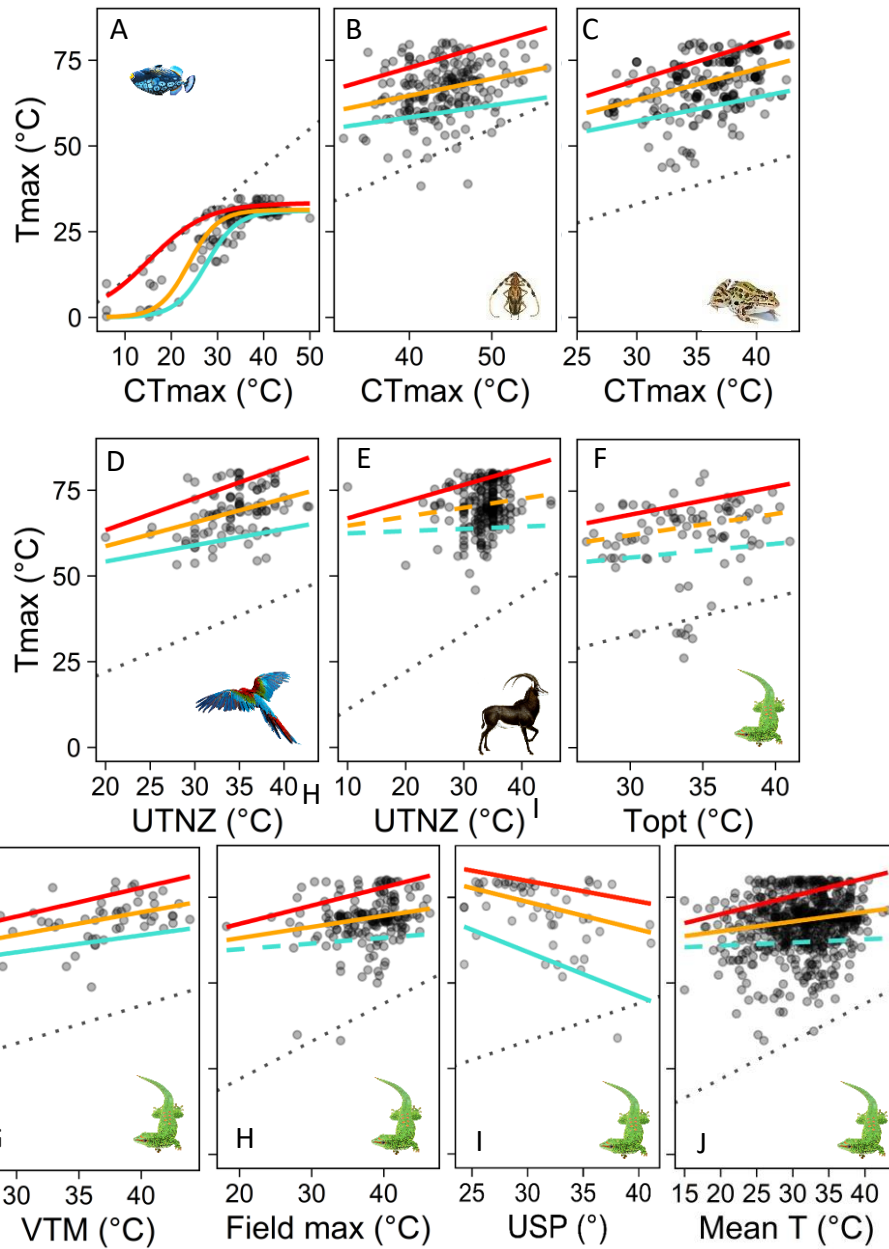
910   limit. Solid lines represent the slopes of taxonomically detrended predictions of Tmax

911   based on thermal physiology. Red, orange, and blue lines represent predicted 90th,

912   50th, and 10th conditional percentiles of Tmax on thermal tolerance, respectively.

913   Slashed lines represent non-significant associations. Error ribbons are not included due

914   to the small size of SE (see Table 2). relative to the axis scale. Supporting Figs. S2 A,

915   B, and C contain graphs for all relationships between heat tolerance and Tmax indexes.
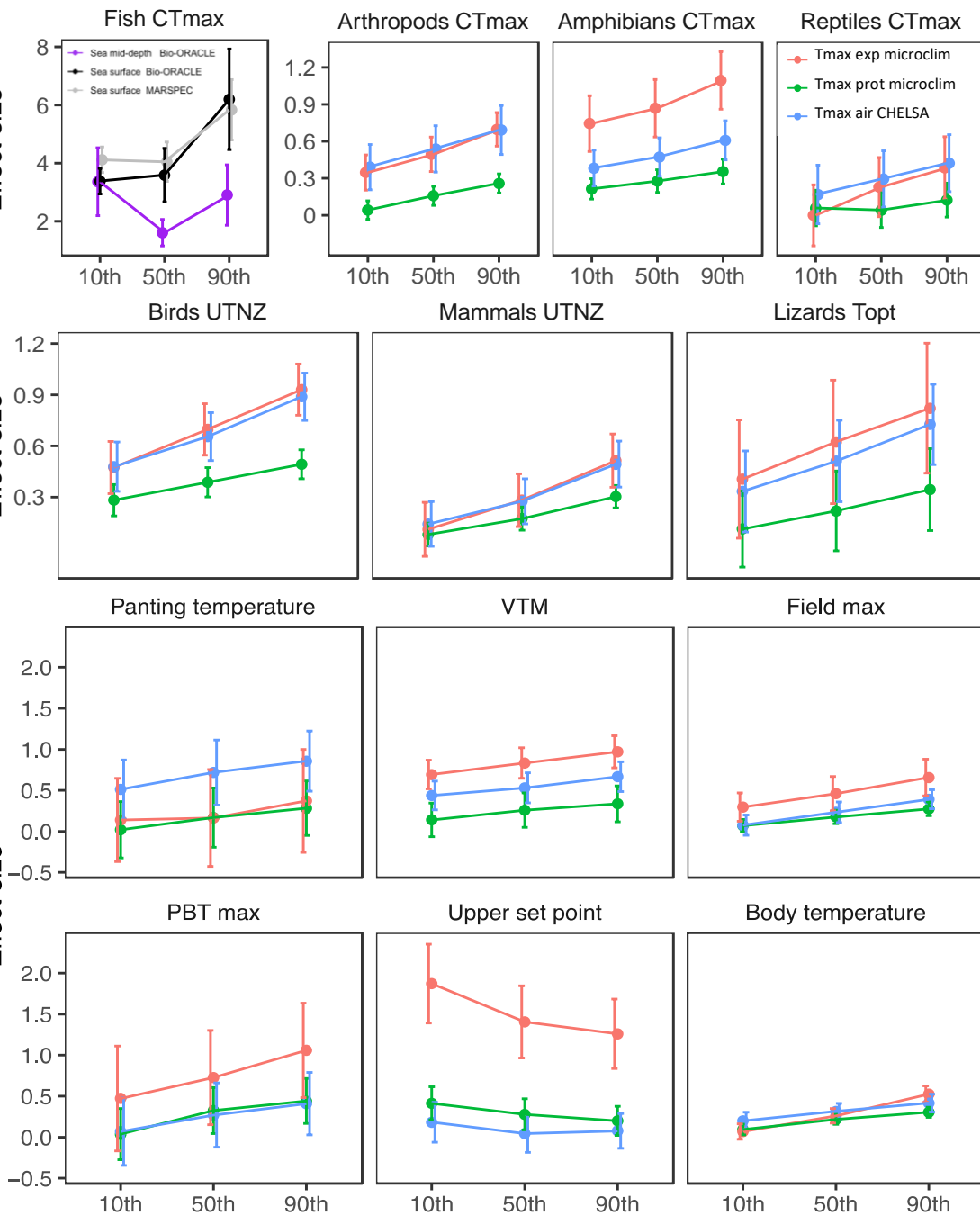
916

FIGURE 2. Variation in the effect size of heat tolerance-Tmax quantile correlations

between measures across the used quantiles. The quantiles represent how much

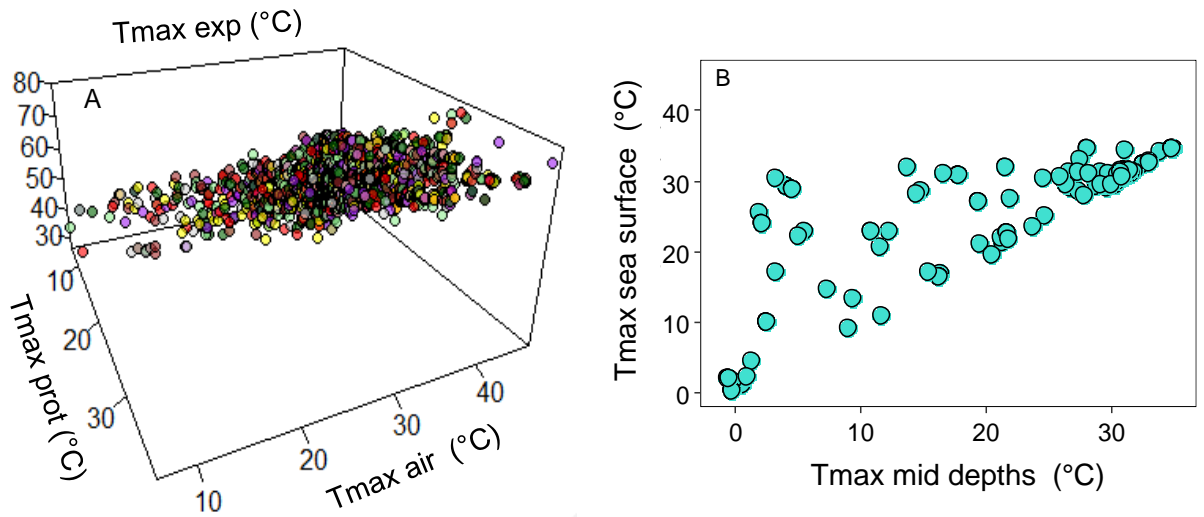species' heat tolerance is challenged by temperatures at their ranges' warm edges,

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.

FIGURE 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.