Title: An alternative explanation for global trends in thermal tolerance

Short title: Explaining thermal tolerance trends

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Abstract

Ectotherms from higher latitudes can generally perform over broader temperature ranges than tropical ectotherms. This pattern is thought to reflect trends in temperature variability: tropical ectotherms evolve to be ‘thermal specialists’ because their environment is thermally stable. However, the tropics are also hotter, and most physiological rates increase exponentially with temperature. Using a dataset spanning diverse ectotherms, we show that the temperature ranges ectotherms tolerate (the difference between lower and upper critical temperatures, and between optimum and upper critical temperatures) generally represents the same range of equivalent biological rates (e.g. metabolism) for cool and warm adapted species, and regardless of latitude or elevation. This suggests geographical trends in temperature variability may not be the ultimate mechanism underlying latitudinal and elevational trends in thermal tolerance. Rather, we propose that tropical ectotherms can perform over a narrower range of temperatures than species from higher latitudes because the tropics are hotter.

Introduction: The temperature-dependence of organism performance (e.g. growth rate, maximum running or swimming speed, or the scope for aerobic metabolism) is often described by a thermal performance curve, where performance rises from a lower critical temperature ($T_{\text{crit}}$) to an optimum ($T_{\text{opt}}$), and subsequently declines to an upper $T_{\text{crit}}$. The temperature range between lower and upper $T_{\text{crit}}$ is the thermal tolerance breadth (TTB), and it is a cornerstone of macroecology that TTB increases with latitude and elevation. Since the influential work of Janzen (1967), the global trends in TTB (e.g. Addo-Bediako et al. 2000; Sunday et al. 2011) are almost universally explained as adaptive responses of organism physiology to the greater temperature variability at higher latitudes and elevations (the ‘temperature variability hypothesis’). That is, animals that regularly experience a wide range of temperatures ought to evolve physiologies that tolerate a wide range of temperatures.
When reported in degrees Kelvin or Celsius, temperature measures the average kinetic energy of a substance. Because temperature is directly proportional to average kinetic energy, a given change in temperature at either low (e.g. 5 to 10°C) or high (e.g. 30 to 35°C) temperatures corresponds to the same change in kinetic energy. In contrast, almost all biological rates (e.g. metabolism and biochemical reactive rates) increase exponentially with temperature, according to

$$R_0 e^{-E/kT}$$

where $E$ is activation energy, $k$ is Boltzmann’s constant, $T$ is absolute temperature in Kelvin, and $R_0$ is an organism- and state-dependent scaling coefficient (Brown et al. 2004; Dell et al. 2011). This is because as temperature increases, an increasingly larger proportion of particles exceed the minimum $E$ required to take part in a reaction. The temperature-dependence of whole-animal performance (thermal performance curves) is governed by the effect of temperature on these lower-level processes (e.g. cellular metabolism and reactive rates) that increase exponentially with temperature; at least over the normal range of activity (0-40°C for most organisms; Brown et al. 2004). For example, the temperature-dependence of whole-animal performance in fishes is often measured in terms of the scope for aerobic metabolism, which is the difference between resting and maximum aerobic metabolic rate (Fig. 1). Because the biological rate processes that determine the shape of performance curves proceed more rapidly at higher temperatures, it could be expected that performance will decline more-rapidly on either side of $T_{opt}$ for higher values of $T_{opt}$ (Fig. 1). This effect would result in smaller differences between $T_{opt}$ and $T_{crit}$ for warm-adapted species, and therefore a narrowing of TTB with increasing $T_{opt}$. Thermal performance curves would also tend to be left-skewed, and they invariably are (Martin & Huey 2008; Angilletta 2009).

If biological rate processes that increase exponentially with temperature largely determine the slopes of the rise and fall in performance on either side of $T_{opt}$ (e.g. Fig. 1), then plotting
thermal performance curves on empirical temperature scales (e.g. in degrees Celsius or Kelvin) should tend to generate narrower TTBs for warm-adapted species than for cool-adapted ones (Fig. 2a), even if the difference in equivalent biological rates at lower and upper $T_{\text{crit}}$ (e.g. the resting metabolic rate at upper $T_{\text{crit}}$ minus that at lower $T_{\text{crit}}$) is the same (Fig. 2b). Because minimum, mean and maximum temperatures generally increase with decreasing latitude and elevation, it is therefore possible that the difference in kinetic energy (i.e. temperature in degrees Celsius or Kelvin) between lower and upper $T_{\text{crit}}$ decreases toward the equator and sea-level because the equivalent difference in biological rates (which underpins thermal performance curves) does not (Fig. 2b). Whether cool and warm adapted species generally maintain the same temperature-dependence of physiological processes (the ‘metabolic cold adaptation’ hypothesis) is a controversial topic (Holeton 1974; Clarke & Johnston 1999; Addo-Bediako et al. 2002; White et al. 2012), so whether tropical, temperate and polar ectotherms maintain a similar range of biological rates (e.g. resting metabolism) between lower and upper $T_{\text{crit}}$ is uncertain. While the temperature variability hypothesis is almost universally accepted as the explanation for many geographical trends in thermal tolerance, the potential role of temperature per se – and its exponential relationship with biological rate processes – is largely unexplored.

In this study, we analysed several datasets on $T_{\text{opt}}$ and $T_{\text{crit}}$ of diverse ectotherms to explore whether the commonly-observed global trends in thermal tolerance (e.g. Addo-Bediako et al. 2000; Sunday et al. 2011) could be explained by temperature’s exponential influence on biological rate processes rather than by adaptation of ectotherm physiology to temperature variability. We first examined data from fishes and terrestrial lizards to test whether the difference between $T_{\text{opt}}$ and $T_{\text{crit}}$ varies in a way that is consistent with our prediction about temperature’s exponential influence on biological rate processes. Our specific hypothesis was that the difference between $T_{\text{opt}}$ and $T_{\text{crit}}$ in degrees Celsius would be smaller for warm-adapted species than for cool-adapted ones, but will be the same for warm- and cool-adapted species.
when $T_{\text{opt}}$ and $T_{\text{crit}}$ are expressed as equivalent biological rates via the Boltzmann-Arrhenius relationship (equation 1). Next, we analysed an updated, comprehensive global dataset on lower and upper $T_{\text{crit}}$ of terrestrial and aquatic ectotherms (Sunday et al. 2011) to examine latitudinal and elevational trends in TTB when $T_{\text{crit}}$ is expressed as equivalent biological rates instead of in degrees Celsius. In doing so, our general aim was to explore whether global trends in ectotherm thermal tolerance could ultimately be caused by the temperature-dependence of biological rates rather than by adaptation of species to global trends in environmental temperature variability. We tested our hypotheses with data from studies that measured acute, short-term tolerance limits, which do not necessarily represent long-term survival limits of species (Peck et al. 2009; Peck et al. 2014) because the realised thermal niche of a species is generally narrower than temperatures bounded by lower and upper $T_{\text{crit}}$ (Sunday et al. 2012; Peck et al. 2014). As such, we seek to provide an alternative explanation of trends reported for acute, laboratory-derived thermal tolerance measurements rather than global trends in the temperature ranges that species tolerate over extended periods in the wild.

**Materials & Methods:**

Two recent comparative papers (Huey et al. 2009; Payne et al. 2016) reported optimal and critical temperatures in fishes and lizards, and found that $T_{\text{opt}}$ is strongly correlated with upper $T_{\text{crit}}$ for both groups. However, lower $T_{\text{crit}}$ could not be estimated with any degree of certainty for the fish dataset (Payne et al. 2016), and $T_{\text{opt}}$ was not correlated with lower $T_{\text{crit}}$ for terrestrial lizards (Huey et al. 2009). Given this, we only explored the relationship between $T_{\text{opt}}$ and the upper $T_{\text{crit}}$ (the difference between $T_{\text{opt}}$ and $T_{\text{crit}}$ we call the ‘heating tolerance’) for those data, and did not examine cooling tolerance. For the fish dataset, upper $T_{\text{crit}}$ was estimated by fitting a two-part performance curve to aerobic scope data and extrapolating to zero scope above $T_{\text{opt}}$ (see Payne et al. 2016 for data inclusion protocols, procedure for fitting of performance curves, and
95% confidence intervals for $T_{opt}$ and $T_{crit}$ estimates), and for lizards, upper $T_{crit}$ was identified as
the point where animals lost the righting response (Huey et al. 2009). For data on TTB, we
reanalysed upper and lower $T_{crit}$ of the diverse ectotherms presented in Sunday et al (Sunday et al.
2011), and updated this dataset by conducting a literature search of ectotherm critical
temperatures published since 2011. Like Sunday et al., we excluded data from our TTB analyses
that were derived from latitudes above 60°, because their lower $T_{crit}$ estimates are potentially
confounded by the freezing point of water.

We converted each value of $T_{opt}$ and $T_{crit}$ to an equivalent biological rate, $r$, via the
Boltzmann-Arrhenius relationship (equation 1). Activation energies, $E$, and scaling coefficients,
$R_0$, are known to vary across taxa, so we used different values of $E$ and $R_0$ to convert
temperatures to $r$ for different animal groups. Gillooly et al. (2001) derived separate relationships
between temperature and mass-normalised resting metabolic rates (in W g$^{-1}$) for multicellular
invertebrates, fish, amphibians and reptiles, so we adopted their relevant values of $E$ (0.788,
0.433, 0.496 and 0.757, respectively) and $R_0$ ($e^{23.53}$, $e^{10.38}$, $e^{12.59}$ and $e^{22.76}$, respectively) for those
four major animal divisions to transform our empirical temperature data (note: we divided all $r$
values from the Gillooly paper by 60 to correctly report units of W g$^{-1}$).

Phylogenetically-informed least squares regression was used to test relationships between $T_{opt}$
and heating tolerance for fish and lizards both in degrees Celsius and $r$. Although the need to
account for phylogeny in comparative analyses has been questioned (e.g. Westoby et al. 1995),
methods that incorporate phylogenetic information into analyses of data derived from multiple
species are often considered necessary to account for data non-independence (i.e. closely related
species tend to resemble each other; Felsenstein 1985). We were interested in the relationship
between $T_{opt}$ and heating tolerance because, under our hypothesis, performance should decline
more rapidly above $T_{opt}$ for higher values of $T_{opt}$, so considered this the most direct test of our
hypothesis. We chose not to compare heating tolerance to environmental temperature variability.
(i.e. the competing traditional hypothesis), because the range of temperatures experienced by a
species will vary not only by latitude and elevation, but also by microhabitat, season, through
ontogeny, and will be heavily influenced by thermoregulatory behaviour. Given these
complexities, we considered such an approach prone to error due to the uncertainty in measuring
temperature variation for each species. We built phylogenetic trees for lizards using the PDDIST
output published as online material in Huey et al. (Huey et al. 2009), and for fishes using
Betancur-R et al. (Betancur-R et al. 2013) (trees are presented in S1). Using the arbitrary branch
length method of Pagel (Pagel 1992), we conducted phylogenetically independent contrasts using
the PDAP package with the software Mesquite (Maddison & Maddison 2011), treating the five
sockeye salmon populations as polytomies. Because \( r \) was computed using different values of \( E \)
and \( R_0 \) for different animal groups, we did not use phylogenetically informed statistics for the
TTB data, and instead used linear models and generalised additive models (GAMs) to examine
relationships between latitude and TTB in degrees Celsius and \( r \). GAMs using penalized thin
plate regression splines were only fitted to biological rate-equivalent TTBs if AICs were
improved over a linear model. GAMs used a basis dimension \( k = 6 \) to avoid unrealistic smoothers,
and were fitted using the ‘mgcv’ package in R (R Core Team 2015). Like Sunday et al. and
others (e.g. Addo-Bediako et al. 2000), we compared TTB to elevation-corrected latitudes. To
further examine the influence of elevation on TTB, we ran additional linear models on the
terrestrial ectotherm data for which both latitude and elevation were reported. For these models,
we used the uncorrected latitudes from Sunday, and included the interaction term between
latitude and elevation to test whether TTB variation across latitude varied by elevation.

**Results**

As reported in the earlier papers (Huey et al. 2009; Payne et al. 2016), heating tolerance
decreases as \( T_{\text{opt}} \) increases, and this happens at a similar rate for both fishes and lizards (for fishes
[\text{n} = 14]: \text{slope} = -0.24, \text{intercept} = 10.93, \text{phylogenetically-informed least squares} \ t = -2.19, \text{R}^2 = 0.29, P < 0.05; \text{for lizards} [\text{n} = 70]: \text{slope} = -0.27, \text{intercept} = 17.12, \text{phylogenetically-informed least squares} \ t = -5.93, \text{R}^2 = 0.34, P < 0.001; \text{Fig. 3a}). However, when temperatures are expressed as equivalent biological rates, heating tolerance does not vary for different values of \text{T}_{\text{opt}} \text{for either fishes or lizards (phylogenetically-informed least squares for fishes}: \ t = -0.23, \text{R}^2 = 0.004, P = 0.82; \text{for lizards}: \ t = -1.38, \text{R}^2 = 0.03, P = 0.17; \text{Fig. 3b}). Results were qualitatively the same for fishes when analyses were rerun to exclude those data where extrapolated estimates of \text{CT}_{\text{max}} \text{were relatively uncertain (i.e. when we excluded the five fish datasets from Payne et al. 2016 where 95\% \text{CIs for} \text{CT}_{\text{max}} \text{encompassed} \geq 3\text{^\circ C} \text{range}; \text{for degrees Celsius}: \text{n} = 9: \text{slope} = -0.20, \text{intercept} = 9.13, \text{phylogenetically-informed least squares} \ t = -2.68, \text{R}^2 = 0.51, P < 0.05; \text{for equivalent biological rates}: \ t = -0.51, \text{R}^2 = 0.04, P = 0.63) \text{Thus, the difference between} \text{T}_{\text{opt}} \text{and upper} \text{T}_{\text{crit}} \text{in} \text{r} \text{does not vary between cool and warm adapted (i.e. for different} \text{T}_{\text{opt}) fishes or lizards.}

Our search of recent literature returned TTB measurements from an additional 54 species and this updated dataset of TTBs across latitude for terrestrial and aquatic ectotherms is shown in Fig. 4a and 4b, respectively. For empirical temperature, TTB increases linearly with latitude and with comparable slope and intercept estimates for terrestrial (\text{n} = 241; \text{slope} = 0.292, \text{intercept} = 25.77, \ t = 11.62, P < 0.001) and aquatic (\text{n} = 115, \text{slope} = 0.183, \text{intercept} = 28.66, \ t = 5.81, P < 0.001) ectotherms. In contrast, TTB in terms of equivalent biological rates does not vary with latitude for terrestrial ectotherms (Fig. 4c; \text{GAM edf} = 2.48, P = 0.09; \text{LM slope} = -7.09 \times 10^{-6}, \text{intercept} = 0.005, \ t = -0.57, P = 0.57) \text{and for aquatic ectotherms, biological rate-equivalent TTB is highest from the equator to} \text{~} 40-50^\circ \text{of latitude, and subsequently declines (Fig. 4d; \text{GAM edf} = 2.66, P < 0.001; \text{LM slope} = -2.18 \times 10^{-5}, \text{intercept} = 0.003, \ t = -6.53, P < 0.001). For aquatic ectotherms, rate-equivalent TTB does not decline with latitude when points above} 50^\circ \text{latitude are excluded} \text{(GAM edf} = 2.21, P = 0.07; \text{LM slope} = -4.18 \times 10^{-6}, \text{intercept} = 0.003, \ t = -1.02, P = 0.31). For
the reduced dataset that included elevation information, empirical TTB generally increased with
latitude and elevation, and the effect of elevation on empirical TTB was greater at lower latitudes
(significant negative interaction term, $n = 148$, $t = -6.172$, $P < 0.001$; Table S1), but neither
latitude, elevation nor their interaction significantly influenced TTB in terms of equivalent
biological rates (Table S1). Thus, the average range of equivalent biological rates between lower
and upper $T_{\text{crit}}$ is maintained across latitude and elevation for terrestrial animals, and across low
to mid latitudes for aquatic ectotherms, and declines thereafter. Latitudinal TTB results are
qualitatively the same if temperatures for all species are transformed with a single mean $R_0$ and $E$,
rather than using different $R_0$ and $E$ for the different major animal divisions.

Discussion:
These results support our hypothesis that the higher heating tolerance of cool adapted species
arises from maintenance of the same range of equivalent biological rates between $T_{\text{opt}}$ and upper
$T_{\text{crit}}$ among cool and warm adapted species. Similarly, terrestrial ectotherms across all latitudes
and elevations maintain the same average range of equivalent biological rates between lower and
upper $T_{\text{crit}}$ (Fig. 4c; Table S1). In contrast to the case for terrestrial ectotherms, aquatic
ectotherms actually exhibit higher rate-equivalent TTBs near the equator than the poles. However,
lower $T_{\text{crit}}$ of aquatic ectotherms are potentially influenced by the freezing point of water, with
tolerance measurements taken on marine ectotherms either limited to temperatures greater than ~
-2.0°C, or conducted on animals frozen in ice (as were most of the higher latitude aquatic data in
Fig. 4). An inability to move and extract oxygen from their habitat would undoubtedly confer
less plasticity of lower $T_{\text{crit}}$ near freezing temperatures for aquatic ectotherms, and indeed, the
downward inflection of biological rate-equivalent TTB for aquatic ectotherms occurs at the same
latitudes at which lower $T_{\text{crit}}$ of those species approaches the freezing point of seawater (~40-60°C;
Fig. 4d, S2). In other words, the poleward decline in biological rate-equivalent TTB from mid-
latitudes for aquatic ectotherms may be an artefact of their habitat freezing at low temperatures. In general, aquatic ectotherms also tolerate a smaller range of equivalent biological rates than terrestrial ectotherms (both for heating tolerances and TTBs; Fig. 3b, Fig. 4 c-d), and this is unsurprising given oxygen is far less available and more costly to acquire in water than in air (Pörtner 2001; Verberk et al. 2011). That is, the demand for oxygen increases with temperature in a similar way for terrestrial and aquatic ectotherms (i.e. via the Boltzmann-Arrhenius relationship), but the challenge of supplying these demands is far greater for aquatic animals. Differential oxygen availability is thought to explain why warming-induced reductions in body size are stronger for aquatic animals than for terrestrial ones (Verberk et al. 2011; Forster et al. 2012), and could also explain why aquatic animals tolerate smaller changes in their temperature-equivalent biological rates. Notwithstanding complexities associated with lower $T\text{crit}$ of aquatic ectotherms, heating tolerance and TTB data generally support our alternative hypothesis for explaining latitudinal and elevational trends in ectotherm thermal tolerance. However, support for our hypothesis does not necessarily imply rejection of the traditional temperature variability hypothesis, because both hypotheses predict lower empirical TTBs toward lower latitudes and elevations. One way of discriminating between these two potential explanations is provided by heating tolerance data from polar marine ectotherms, because while average temperatures are vastly different between equatorial and polar oceans, temperature fluctuations are similarly small (~ 2°C annual range). Under the temperature variability hypothesis, heating tolerance should be highest for species adapted to intermediate temperatures (i.e. mid-latitudes) and smallest for those adapted to low (i.e. polar) and high (i.e. equatorial) temperatures (conceptualised by the dashed black line in Fig. 5). Conversely, if heating tolerance represents a fixed difference in equivalent biological rates regardless of temperature (as indicated by Fig. 3b), then the relationship between $T\text{opt}$ and heating tolerance (Fig. 3a) would actually be curved rather than linear; this theoretical curve is fitted to
fish aerobic scope data in Fig. 5 and extrapolated to lower temperatures (blue circles and solid blue line; see S3 for derivation of the curve and model fitting). Estimates of $T_{opt}$ and upper $T_{crit}$ for aerobic scope in polar fishes are currently unavailable, so we cannot test whether heating tolerance for aerobic scope per se in such animals is low (as would be expected under the temperature variability hypothesis; dashed black line in Fig. 5) or high (as would be expected under our biological rate hypothesis; solid blue line in Fig. 5). However, there are data from several polar fishes where $T_{crit}$ was defined differently to our fish dataset (upper $T_{crit}$ data presented in Bilyk & DeVries 2011). Assuming $T_{opt}$ of polar fishes occurs somewhere within the range of environmental temperatures that they normally experience in their natural habitat (mean habitat temperatures are often lower than $T_{opt}$, but most similar to $T_{opt}$ for ectotherms from thermally stable habitats such as polar oceans; Martin & Huey 2008), and that $T_{crit}$ for aerobic scope approximates other $T_{crit}$ measures (Pörtner & Knust 2007; Pörtner 2010), then the heating tolerance of polar fishes can be estimated; these are shown in Fig. 5 (black data). Calculated in this way, the heating tolerance of those 11 fish species from thermally stable Antarctic waters match extrapolations from the temperate and tropical fish data under our hypothesis remarkably well (the blue curve in Fig. 5 is fitted to, and extrapolated from, blue fish aerobic scope data, not fitted to black polar data). While reliant on some assumptions about $T_{opt}$ and $T_{crit}$ of polar fishes (e.g. whether $T_{opt}$ for aerobic scope lies within the range of temperatures naturally encountered by polar fishes is uncertain; some lower-latitude species have $T_{opt}$ very close to modal habitat temperatures (Eliason et al. 2011), whereas others have $T_{opt}$ near the higher temperatures encountered within their range (e.g. Clark et al. 2011; Rummer et al. 2014)), this comparison is strong evidence that temperature’s exponential influence on biological rates (i.e. our new hypothesis) rather than temperature variability (i.e. the traditional explanation) determines the heating tolerance of marine ectotherms, because polar and tropical fishes encounter similarly-small environmental temperature fluctuations, but exhibit vastly different heating tolerance (i.e. ~
15°C versus ~ 3°C, respectively; Fig. 5). Consideration of temperature’s exponential influence on biological rates therefore seems to explain the apparent contradiction (Wilson et al. 2001; Seebacher et al. 2005) that polar marine fishes can tolerate acute exposure to temperatures far exceeding those they would ever experience in nature (sometimes by more than 15°C; Fig. 5; Peck et al. 2009), whereas tropical fishes live close to their upper thermal limits (Rummer et al. 2014). Still, heating tolerances presented in Fig. 5 were calculated differently for polar and other species, so a more definitive conclusion would come from examining fish aerobic scope data spanning the equator to the poles (should such data become available), and by accounting for the potentially (e.g. Clarke & Johnston 1999 versus White et al. 2012) elevated temperature-standardised metabolic rates of polar fishes (the metabolic cold adaptation hypothesis).

Interestingly, many polar invertebrates exhibit upper \( T_{\text{crit}} \) values similar to those of polar fishes (e.g. Peck et al. 2009), so exploring how temperature’s influence on biological rates affects heating tolerances of non-fish polar ectotherms could prove fruitful.

Importantly, the relatively high heating tolerance of polar fishes does not necessarily imply that these species ought to withstand significant long-term warming beyond current temperatures, because acutely-measured upper \( T_{\text{crit}} \) is often far higher than temperatures an ectotherm can tolerate for prolonged periods (Peck et al. 2009; Peck et al. 2014). For example, comparative analyses of Antarctic marine ectotherms indicates survival to temperatures of ~ 8-18°C under experimental warming of 1°C per day, but only 1-6°C under acclimations of several months (Peck et al. 2009; Richard et al. 2012); similar responses to experimental warming rates have been documented for temperate and tropical ectotherms (Nguyen et al. 2011; Morley et al. 2016).

There appears to be significant variation in the range of equivalent biological rates ectotherms tolerate at any given latitude or \( T_{\text{opt}} \) (residuals in Fig. 3b and 4c are large, particularly for terrestrial ectotherms), and it could prove fruitful to explore the relative importance of environmental heterogeneity (similar taxa from the same latitude can display very different
thermal tolerance limits depending on microhabitat differences; e.g. Kaspari et al. 2015) and methodological differences in driving this variation. For example, critical and lethal temperature limits are defined and measured in myriad ways, and are strongly influenced by experimental protocols such as warming rates (Nguyen et al. 2011), acclimation, and response measures (critical limits are variously defined as the onset of loss of the righting response: Huey et al. 2009; lack of response to tactile stimuli: Peck et al. 2009; or aerobic metabolic scope: Payne et al. 2016; limits that would often be defined as lethal limits given sufficient monitoring durations because life at temperatures that preclude movement, or where resting metabolism cannot be met aerobically, will be necessarily short), and these differences undoubtedly contribute to variation in the equivalent biological rates characterising different species’ TTBs (Fig. 4c) and heating tolerances (Fig. 3b). It is also important to note the compelling experimental evidence that ectotherms can adjust their thermal tolerance limits in response to environmental variability (Schaefer & Ryan 2006), and such plasticity might also contribute to the large differences in equivalent rates ectotherms can tolerate at any given latitude or $T_{opt}$. Nevertheless, the dominant geographical trends in environmental temperature variability do not translate into latitudinal or elevational trends in the range of equivalent biological rates species can tolerate.

Improving our understanding of how temperature regulates thermal tolerance is increasingly important given the rapidly changing climate and mounting evidence that species distributions are closely linked to thermal tolerance limits (Sunday et al. 2012; Sunday et al. 2014; Payne et al. 2016). That temperature variability drives thermal tolerance is a paradigm commonly invoked to explain a range of macroecological patterns such as latitudinal and elevational trends in species range size (Rapoport's rule; Stevens 1989; Chan et al. 2016), and to predict that tropical species will be most vulnerable to global warming (Ghalambor et al. 2006; Tewksbury et al. 2008). Although the temperature variability hypothesis for explaining global trends in thermal tolerance is intuitive, it does not satisfactorily explain several major patterns, such as the very different
heating tolerances between equatorial and polar oceans; both of which are thermally stable habitats. Our consideration of equivalent biological rates suggests the ultimate cause of some of the major global trends lie there instead. Maintenance of equivalent ranges of biological rates across TTBs and heating tolerance also raises interesting questions about thermal specialisation, as an increase in maximum performance for warmer-adapted species (“hotter is better”) is often seen to be traded-off for reduced performance breadth, with the total area under the curve kept relatively constant (Levins 1968; Gilchrist 1995). While we generally measure and report temperature in terms of kinetic energy (degrees C or K), few biological or ecological processes are directly proportional to kinetic energy, so it may be insightful (Buckley & Huey 2016; Payne et al. 2016) to also investigate temperature-dependent processes on more biologically-relevant scales such as in terms of equivalent biological rates.

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Figure legends:

Figure 1. Temperature’s influence on thermal tolerance breadth: an example for fishes. In fishes, thermal performance curves (blue lines) are often quantified as the temperature-dependence of ‘aerobic scope’ – the difference between resting (red line) and maximum (dashed lines) metabolic rates. Like most other biological rates, resting metabolic rate increases exponentially with temperature, so a given value of maximum performance (i.e. the aerobic scope at $T_{opt}$) will tend to decline more rapidly on either side of $T_{opt}$ for species that have higher
The difference between lower and upper $T_{crit}$ (the thermal tolerance breadth) will therefore be larger for cool-adapted species than for warm-adapted ones.

**Figure 2. Empirical versus “biological” temperature scales.** Because most biological rates, $r$, increase exponentially with temperature, the larger range of temperatures over which a cool-adapted species can perform (A) may correspond to the same range of equivalent $r$ for both cool- and warm-adapted species (B). In this figure, empirical temperatures on the x-axis in A have been converted to equivalent biological rates via the Boltzmann-Arrhenius relationship (equation 1 in main text). In reality, species with higher $T_{opt}$ may have higher maximum performance at $T_{opt}$ (the "hotter is better" hypothesis; Kingsolver & Huey 2008; Angilletta *et al.* 2010), and the position of performance curves for a species can shift due to acclimation or relative to $T_{crit}$, depending on how $T_{crit}$ is defined. While simplified, this figure serves to illustrate the concept of transforming empirical temperatures to equivalent biological rates.

**Figure 3. Empirical versus biological rate-equivalent heating tolerance.** Heating tolerance of terrestrial lizards ($n=70$; green data) and fishes ($n=14$; blue data), when $T_{opt}$ and $T_{crit}$ are presented in degrees Celsius (A) and as equivalent biological rates, $r$ (B). Both slopes are significant ($P<0.05$) in A; NS indicates neither is significant in B.

**Figure 4. Latitudinal trends in ectotherm thermal tolerance breadth, TTB.** In both A and B, TTBs (green and blue for terrestrial [$n=241$] and aquatic [$n=115$] ectotherms, respectively) are presented in degrees Celsius. In both C and D, temperatures have been converted to equivalent biological rates via the Boltzmann-Arrhenius relationship (equation 1 in main text). All curves are significant for A, B, and D ($P<0.001$), whereas neither a linear regression nor GAM was significant for TTB data in C ($P=0.57$ and 0.09, respectively).
Figure 5. Heating tolerance of polar fishes. Aerobic scope data for fishes from a range of latitudes (from Fig. 3A; \(n = 14\)) are represented by blue circles, and a non-linear model was fitted to these data (blue line; see S3 for derivation of the curve) and extrapolated to lower values of \(T_{\text{opt}}\), assuming heating tolerance represents the same average range of equivalent biological rates for any value of \(T_{\text{opt}}\). The black dashed line represents a conceptualisation of the temperature variability hypothesis as it relates to marine ectotherms. The estimated (see Discussion) heating tolerances of 11 species of polar fishes are overlaid (black diamonds), i.e. the blue curve was not fitted to the black data from polar fishes. Error bars represent the full range of environmental temperatures experienced in each polar species’ environment; ranges used to represent the uncertainty in estimates of \(T_{\text{opt}}\) and therefore heating tolerance.

References:


