

REVIEW AND SYNTHESIS

The complex drivers of thermal acclimation and breadth in ectotherms

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Abstract

Thermal acclimation capacity, the degree to which organisms can alter their optimal performance temperature and critical thermal limits with changing temperatures, reflects their ability to respond to temperature variability and thus might be important for coping with global climate change. Here, we combine simulation modelling with analysis of published data on thermal acclimation and breadth (range of temperatures over which organisms perform well) to develop a framework for predicting thermal plasticity across taxa, latitudes, body sizes, traits, habitats and methodological factors. Our synthesis includes > 2000 measures of acclimation capacities from > 500 species of ectotherms spanning fungi, invertebrates, and vertebrates from freshwater, marine and terrestrial habitats. We find that body size, latitude, and methodological factors often interact to shape acclimation responses and that acclimation rate scales negatively with body size, contributing to a general negative association between body size and thermal breadth across species. Additionally, we reveal that acclimation capacity increases with body size, increases with latitude (to mid-latitudinal zones) and seasonality for smaller but not larger organisms, decreases with thermal safety margin (upper lethal temperature minus maximum environmental temperatures), and is regularly underestimated because of experimental artefacts. We then demonstrate that our framework can predict the contribution of acclimation plasticity to the IUCN threat status of amphibians globally, suggesting that phenotypic plasticity is already buffering some species from climate change.

Keywords

Acclimation, critical thermal limits, global climate change, phenotypic plasticity, thermal biology, thermal performance curves.

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INTRODUCTION

Acclimation is a reversible and often beneficial change in a biological trait in response to environmental variation (Kingsolver & Huey 1998; Huey *et al.* 1999; Woods *et al.* 2002; Angilletta 2009; Reich *et al.* 2016). Acclimation is a type of phenotypic plasticity and thus occurs within a generation, in contrast to evolution, which is a change in a biological trait across generations. As an example, thermal acclimation can occur when extended exposure to a raise in temperature causes a physiological change in an organism that increases the critical thermal maximum (CT_{max} ; mean upper limit of performance) or optimal performance temperature (temperature at which performance is maximal; T_{opt}) of a biological trait (Sinclair *et al.* 2016), such as metabolism, behaviour, or immunity (Dietz & Somero 1992; Terblanche *et al.* 2005; Rafael *et al.* 2006, 2013). This, in turn, would enhance an organism's tolerance to higher temperatures, reducing opportunity

costs, such as lost foraging and mating opportunities (DeWitt *et al.* 1998; Sinervo *et al.* 2010). In addition to thermal optima and critical thermal limits, organisms can also acclimate their thermal breadths (Gabriel & Lynch 1992; Gabriel *et al.* 2005; Angilletta 2009) – the range of body temperatures over which they perform well (Feder 1982; Kolbe *et al.* 2014; Seebacher *et al.* 2015). Thus, acclimation capacity might allow ectothermic species to cope with increased temperature and climate variability (Somero 2010; Huey *et al.* 2012; Vasseur *et al.* 2014), two hallmarks of anthropogenic global climate change (GCC). Indeed, an inability to acclimate fast enough to track changing temperatures has been directly implicated to cause GCC-related population declines through mortality, and also indirectly by disrupting ecological interactions among organisms that differ in their abilities to thermally acclimate (Rohr & Raffel 2010; Rohr *et al.* 2011, 2013; Cohen *et al.* 2018).

Despite the potential importance of thermal plasticity for coping with an increased and more variable thermal regime,

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no general framework currently exists for predicting thermal acclimation and breadth across taxa, latitudes, thermal safety margins (TSM; CT_{\max} minus maximum environmental temperature), body sizes, traits, habitats, and methodological factors. In an effort to address this knowledge gap and resolve current controversies regarding thermal acclimation responses, we combine simulation modelling with a synthesis of the thermal acclimation and thermal breadth literature of ectotherms to develop this predictive framework. Given that ectotherms represent *c.* 99.9% of all known species (Daufresne *et al.* 2009), our analyses should be relevant to most of Earth's biodiversity (see Supporting Information Appendix for discussion on endotherms). We then evaluate whether this framework can predict the contribution of thermal acclimation plasticity to the IUCN (International Union for the Conservation of Nature) threat status of amphibians – the most threatened vertebrate taxon on the planet (Raffel *et al.* 2013). We hypothesize that (1) estimates of thermal plasticity will be affected by organismal traits, experimental methods, and interactions between traits and methods, (2) thermal variation, latitude, and body size will affect thermal tolerance responses in a manner consistent with current theory on thermal plasticity and physiological rates (detailed below), and (3) our thermal plasticity framework derived from our synthesis will be capable of predicting patterns of amphibian threat status, providing evidence consistent with the hypothesis (4) that phenotypic plasticity, in addition to natural selection, can help ameliorate the effects of GCC.

BACKGROUND, CONTROVERSIES, AND PREDICTIONS REGARDING THERMAL PLASTICITY

Phenotypic plasticity theory suggests that ectotherms from habitats with high temperature variability – such as temperate zones or terrestrial habitats – might experience selection for greater acclimation abilities (the degree to which CT_{\max} , CT_{\min} , or T_{opt} can be adjusted) than those inhabiting areas with low temperature variability (Gabriel *et al.* 2005; Angilletta 2009). Empiricists, on the other hand, have shown that the capacity for acclimation rarely correlates with the magnitude or predictability of thermal variability across latitudes (Angilletta 2009; Gunderson & Stillman 2015; Seebacher *et al.* 2015) and that acclimation of thermal optima rarely occurs in the laboratory (Angilletta 2009; but see Rummer *et al.* 2014). These findings have made hypotheses based on plasticity theory controversial (Brown & Feldmeth 1971; Feder 1982; Kolbe *et al.* 2014; Gunderson & Stillman 2015; Seebacher *et al.* 2015).

Current theory also implies that body mass should be an important driver of thermal acclimation (Brown *et al.* 2004; Kingsolver & Huey 2008; Pörtner *et al.* 2017) (Fig. 1). Theory based on first principles suggests that thermal acclimation capacities might be positively correlated with body size across species, and that acclimation rates (the speed at which thermal tolerances are adjusted) might be negatively correlated with size (Gabriel & Lynch 1992; Brown *et al.* 2004; Gabriel *et al.* 2005; Angilletta 2009) (Fig. 1a and b). This is because smaller-bodied organisms have higher mass-specific metabolic rates than larger organisms (Brown *et al.* 2004; Kingsolver & Huey 2008) (also see the Supplement 'Relation of results to

metabolic theory of ecology'), and they also heat and cool faster due to their lower thermal inertia. Relative to larger-bodied organisms, smaller-bodied organisms are also expected to have less mismatch between the demand for oxygen and the capacity of oxygen supply to tissues that can restrict whole-animal tolerance to thermal extremes (Pörtner *et al.* 2017), and can probably benefit more quickly from natural selection because of their typically shorter generation times. This faster acclimation of smaller organisms can also produce greater apparent thermal breadths than larger organisms, because smaller organisms can maintain higher observed performances over a larger range of temperatures (Fig. 2). Habitat temperature variation and body mass also likely interact, as both decrease towards the equator, especially for aquatic species (Blackburn *et al.* 1999; but see Makarieva *et al.* 2005; Horne *et al.* 2015), and body mass is generally positively correlated with lifespan (Brown *et al.* 2004). Consequently, relative to smaller, shorter-lived organisms, larger, longer-lived organisms are more likely to be exposed to extreme seasonal and interannual temperatures that likely select for the ability to acclimate (Fig. 1a and b).

In addition to organismal traits, acclimation responses can be affected by experimental methodologies (Terblanche *et al.* 2007; Chown *et al.* 2009; Rezende *et al.* 2011, 2014) (Fig. 1). As an example, although acclimation duration (how long experimenters hold organisms at an acclimation temperature before exposing them to the test temperature; Lutterschmidt & Hutchison 1997; Rezende *et al.* 2014) does not affect the true acclimation capacity of an organism, it is well documented to be positively associated with published estimates of acclimation capacities because acclimation takes time (Terblanche *et al.* 2007; Chown *et al.* 2009; Rezende *et al.* 2011, 2014). Thus, short acclimation durations can underestimate true acclimation capacities of organisms because they might not have had sufficient time to fully acclimate by the time performance is measured (Fig. 1a and b).

In addition to having independent effects, we hypothesize that the effects of experimental methods and organismal traits will depend on one another and that these statistical interactions will have several important consequences for accurately measuring thermal acclimation and breadth (Fig. 1). For example, if we assume that smaller organisms acclimate faster than larger organisms and the duration of time held at an acclimation temperature is short, then there might be sufficient time for smaller but not larger species to fully acclimate. Thus, the acclimation abilities of larger but not smaller species would be underestimated (Fig. 1a and b).

Given the well-documented correlations among body size, latitude, temperature variability, and habitat, and because experimental artefacts can arise because of interactions between experimental methodologies and body size, biologists might run the risk of drawing erroneous conclusions regarding the ability of ectotherms to acclimate, and thus cope with GCC. Hence, biologists should be including these factors and interactions in synthetic statistical models and choosing ecologically relevant temperatures and acclimation durations. After accounting for these factors and their interactions, we predict that larger organisms will have slower estimates of acclimation rates, greater estimates of acclimation abilities,

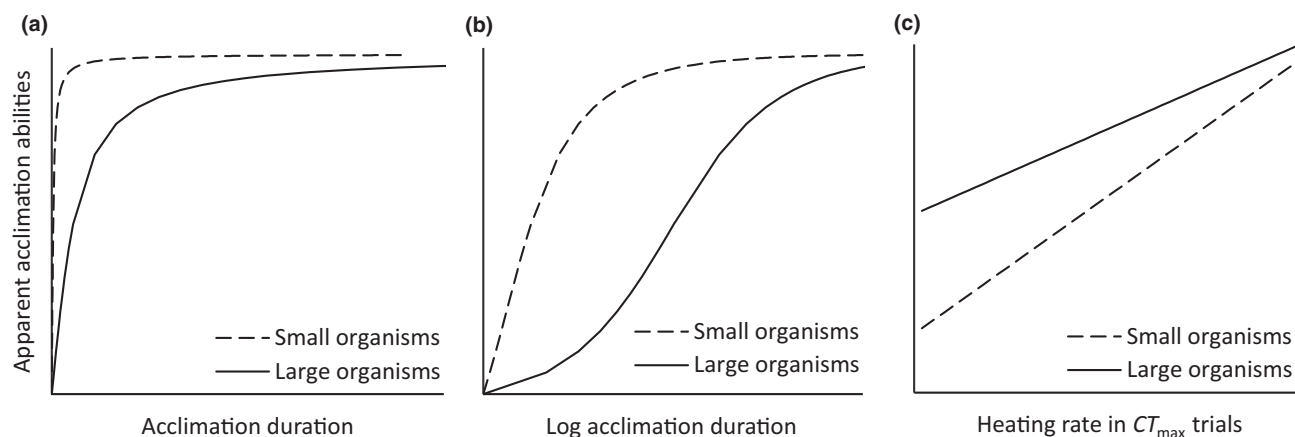


Figure 1 Hypothesised relationships, for both small and large organisms, between (a) apparent acclimation abilities and acclimation duration, (b) log acclimation duration, and (c) heating rate in critical thermal maximum (CT_{max}) trials. Consistent with panels (a) and (b), at short acclimation durations, only smaller organisms show a positive mean acclimation response ratio (across heating rates, Fig. 3a), whereas both small and large organisms show positive mean acclimation response ratios at long acclimation durations (Fig. 3c). Consistent with panel (c), at high acclimation durations (i.e. fully acclimated before the start of trials), smaller organisms show a greater increase in observed acclimation abilities across heating rates than larger organisms (Fig. 3c), perhaps because of faster acclimation abilities.

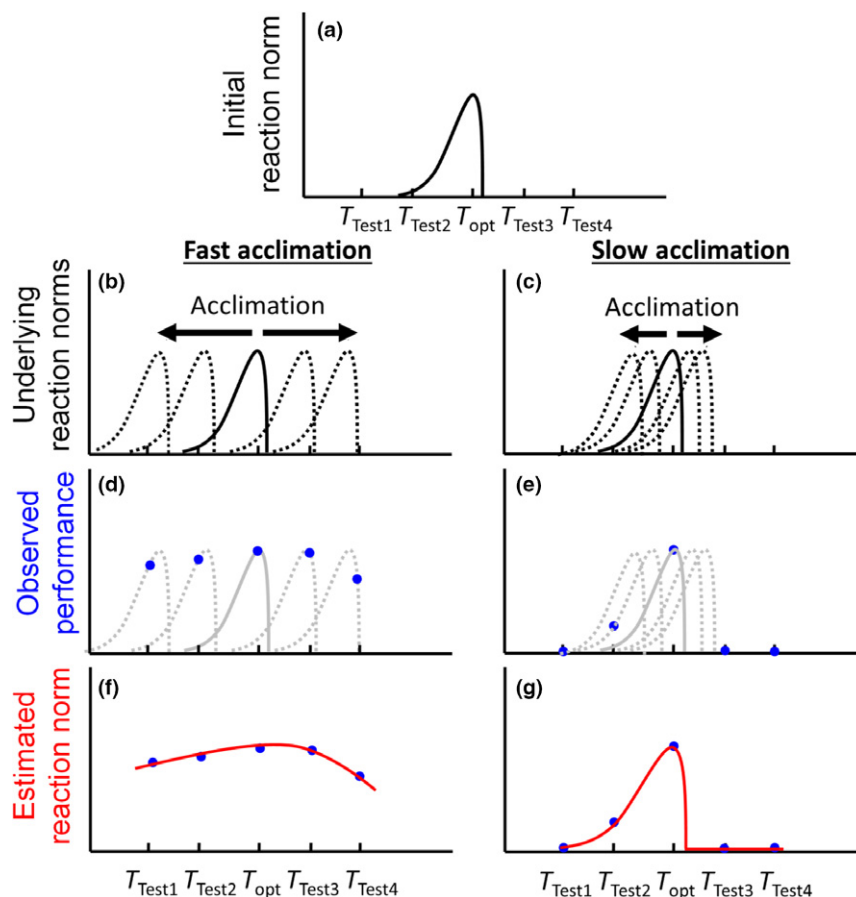


Figure 2 Conceptual framework connecting time to acclimate with thermal performance breadth. If organisms (a) have thermal response curves of fixed shapes with an optimal temperature (T_{opt}), but can acclimate either (b) rapidly or (c) slowly to different test temperatures ($T_{Test1} \dots T_{Test4}$) by sliding these reaction norms along the temperature axis during a finite acclimation time (dashed curves, one corresponding to each test temperature), then organisms that acclimate rapidly can (d) maintain high observed performance (blue points) over a larger temperature range than (e) those that acclimate slowly. When thermal performance curves (red lines) are fit to the resulting data, organisms that acclimate rapidly appear to have larger breadths than organisms that acclimate more slowly because they exhibit greater acclimation in the delay between when they first experience the test temperature and when researchers begin their performance measurements (f), (g).

and narrower acclimated thermal breadths than smaller organisms (Figs 1 and 2). Additionally, we predict that acclimation abilities will be greater for organisms from terrestrial than aquatic (marine, freshwater) habitats and from temperate than tropical zones (see Supporting Information Appendix for a discussion of how acclimation might also depend on trait identity). Finally, we hypothesize that acclimation should be affected by the TSM of a species, because this is expected to be a proxy for the strength of selection on thermal traits and because it has been hypothesised that species with small TSMs might appear less plastic than those with large TSMs, because of less room to increase their CT_{\max} relative to some hard limit (Stillman 2003; Stenseng *et al.* 2005). If most of these patterns emerge, it would represent the first synthesis of thermal tolerance responses that are consistent with theory on thermal plasticity and organismal metabolism (see Angilletta 2009; Gunderson & Stillman 2015; Seebacher *et al.* 2015 for extended discussions of the inconsistency between plasticity theory and empirical results on thermal acclimation). Hypotheses for how latitude, body size, and their interaction might affect the acclimation abilities and acclimated thermal breadth of organisms were too challenging to pose in the absence of a mathematical model, which we describe below.

METHODS

Data compilation

We analyse four empirical datasets that include latitude, body mass, habitat, acclimation duration, and indices of acclimation capacities of ectotherms (See Table S1–S5). The first dataset of Seebacher *et al.* (2015) provides 651 indices of acclimation strength, measured as the $\log(1 - \text{Post-acclimation thermal sensitivity} + 0.001) * -1$. Post-acclimation thermal sensitivity was quantified in Seebacher *et al.* (2015) as the Q_{10} of acclimation thermal sensitivity where 1 indicates that physiological rates do not change with a change in acclimation temperatures. Thus, according to Seebacher *et al.* (2015) ‘the closer Q_{10} is to 1, the less affected animal physiology will be to a change in environmental temperature, meaning that animals will be more resilient to climate change’. Hence, because the direction of the change in a physiological rate will depend on the trait (e.g. swimming speed vs. metabolic rate), we took the absolute value of the deviation from 1. The log transformation was used to normalize the variable and multiplying by -1 resulted in more positive values intuitively indicating stronger acclimation. The second dataset of Gunderson & Stillman (2015) provides 288 acclimation response ratios (ARR), which describe the change in CT_{\max} per unit change in acclimation temperature (i.e. a large ARR indicates a strong acclimation response). We added body size data to these first two datasets. These two datasets were reduced to 333 and 215 cases, respectively, with complete information and additional criteria applied (See Table S1), amounting to 191 and 231 species, respectively.

The third dataset of Dell *et al.* (2011, 2013) contains 2445 thermal response curves of a variety of performance traits of ectotherms, ranging from feeding rate to body velocity, spans three kingdoms of life (Animalia, Fungi, and Plantae), and is the only dataset to provide information on acclimated thermal breadth. Additionally, we added to this dataset acclimation

temperatures and times, and the duration of time between when organisms were placed at a test temperature and when a thermal trait was first measured (Table S1–S5; see Supporting Information Appendix for why this dataset does not conflate fixed and plastic responses). For some of our analyses, sample size was reduced to 128 of the 2445 thermal responses (reduced to 19 traits) for which there were non-monotonic performance curves (which are necessary to estimate optimal temperature, T_{opt}) and acclimation temperature, location, and mass data.

The fourth dataset is unpublished and consists of 1040 estimates of CT_{\max} of 251 amphibian species that we compiled from the literature. Given that amphibians can show considerable variation in body mass from water uptake or dehydration, we used snout-vent length as our body size estimate for this dataset. We use this dataset to evaluate whether our framework derived from syntheses of the first three datasets can predict the contribution of thermal acclimation plasticity to amphibian threat status associated with body size and latitudinal variation (See Tables S1–S5). Finally, for datasets with exclusively CT_{\max} , we added TSMs measured as the CT_{\max} – the mean of the annual maximum temperature of warmest month from 1970 to 2000 (i.e. BIOCLIM5 from WorldClim) for the collection location of each animal (Deutsch *et al.* 2008; Sunday *et al.* 2014). TSM was calculated using macroclimate estimates, but we encourage future studies to consider estimates of TSMs based on the operative temperatures experienced by species (e.g. Sunday *et al.* 2014).

Estimation of thermal response parameters

To calculate the parameters of each intraspecific thermal response in the Dell *et al.* dataset (i.e., T_{opt} , curve height, and breadth), we used the *bbmle* package in R to fit unimodal functions to all non-monotonic temperature performance curves (those where the minimum tested temperature $< T_{\text{opt}} <$ maximum tested temperature) with at least five points and assuming Gaussian distributed errors. We used Johnson-Lewin (Eq. S1) (Dell *et al.* 2011, 2013) and Weibull (Eq. S2) (Angilletta 2009) functions to fit the thermal performance curves because both can fit asymmetrical curves without falling below zero on the y-axis (see Supporting Information Appendix for additional details). We eliminated fits where T_{opt} was outside the range of temperatures tested. We calculated acclimated thermal breadths as the width of each thermal performance curve at 75% of the maximum height (T_{opt}). Because breadth measurements that exceed the range of tested temperatures are unreliable, we excluded 13 cases where this occurred, resulting in a final sample size of 107.

Overview of the mathematical model

We developed a mathematical model to generate hypotheses for how latitude, body size, and their interaction might affect the acclimation abilities and acclimated thermal breadths of organisms. This model of thermal reaction norms (Fig. 2) assumed the following: (1) all organisms possess a common (equally broad) Gaussian (symmetric) or Weibull (asymmetric) thermal performance curve with a T_{opt} that depends on their latitude of origin, (2) organisms acclimate to test temperatures

that differ from their thermal optimum by translating (i.e., sliding) their thermal performance curves along the temperature axis, (3) the magnitude of acclimation depends on the organism's acclimation rate and the acclimation duration up to some physiological limit of maximum acclimation (i.e., acclimation capacity), (4) acclimation rate scales allometrically with body mass and exponentially with test temperature, and (5) maximum acclimation depends linearly on absolute latitude. To generate predictions for the relationships among body size, latitude, acclimation, and performance breadth, we first simulated a pre-experiment laboratory acclimation period and then simulated an experiment in which 1,000 species were collected from various locations, acclimated to a given temperature in the laboratory for a fixed amount of time, and then performance was assessed across a temperature gradient. We assumed that organisms were allowed to acclimate to these experimental temperatures for a period of time that was shorter than the pre-experiment laboratory acclimation duration. Using the performance data simulated for each species at each temperature, we fit Gaussian and Weibull thermal performance curves for each species using the *nls* function in the *stats* package in R. We then extracted parameters for T_{opt} and breadth (as the parameter c) from the Gaussian fits, and numerically computed these quantities for the Weibull fits. We then analysed these data with models that paralleled those used for the real dataset. See Methods in the Supporting Information Appendix for additional details.

Statistical analyses

Overview

All analyses were conducted with R statistical software. Where possible, we employed a multimodel inference approach (*dredge* and *model.avg* functions in the *MuMIn* package of R) to ensure we were not drawing conclusions based solely on one model. Multimodel inference compares all possible models using the Akaike Information Criterion AIC and generates weighted coefficients and relative importance scores for predictors. We calculated conditional R^2 values (variance explained by both fixed and random effects) for the best model where possible (Nakagawa & Schielzeth 2013), otherwise R^2 was calculated for the correlation between fitted and observed values. Analyses on T_{opt} and acclimated thermal breadth were conducted on both Johnson-Lewin and Weibull estimates of these parameters. For all analyses, log-likelihood ratio tests using the *ANOVA* function in the *car* package of R statistical software were used to calculate the probability values for each effect of the best performing model (i.e., lowest AIC). To display results of our regression models, we generated partial residual plots from the best model based on AIC using the *visreg* function in the *visreg* package. In all partial residual plots, continuous predictors are discretised strictly for the purposes of visually displaying statistical interactions (see Supporting Information Appendix for additional details). To ensure transparency, all datasets and code to reproduce the statistical analyses and figures are provided in a supplemental file.

For all analyses, we chose not to include additional predictors that are included in some other acclimation studies, such as generation time and diel variation in temperature

(Angilletta *et al.* 2006; Angilletta 2009). Specifically, we did not include generation time or diel variation because the former is highly collinear with body size (Brown *et al.* 2004) and the latter is correlated with latitude and interacts with season. Due to this interaction, and that several studies did not provide the time of year of their collections, our sample sizes would have been further reduced if diel variation was included.

Does body size influence acclimation rate?

We first tested the hypothesis that time to acclimate is positively related to body size. The underlying assumption of these analyses is that once an organism is shifted to a new temperature, thermal tolerance will change asymptotically through time (Fig. 1a and b) and should scale with body size similarly to how metabolic rate scales with mass, which scales allometrically to the three-quarter power (Gillooly *et al.* 2001, 2002). Data limitations in all our datasets prohibited us from estimating acclimation rate directly and thus a mass-scaling exponent for acclimation rate (see Supporting Information Appendix for details). Instead, we indirectly tested our body-size hypothesis in two ways.

First, we rationalised that if acclimation rate is negatively correlated with size, then when acclimation duration is short, a signal of acclimation should be apparent for small but not large organisms (Fig. 1a and b). To test for this effect of duration of time held at an acclimation temperature, we used the *lme* function in the *nlme* package to conduct a weighted mixed effects analysis (weighting by sample size and treating the study and species combination as a random effect) with T_{opt} or CT_{max} as the Gaussian response variables, habitat (freshwater, marine, terrestrial), trophic assignment (T_{opt} only), and life stage (CT_{max} only) as categorical moderators, and acclimation temperature, log acclimation duration, absolute value of latitude, and log body size as crossed continuous predictors (two- and three-way interactions only). These analyses were conducted on all datasets except for the Seebacher *et al.* dataset because minimum acclimation duration in this dataset was 1 week (See Table S1), and thus it lacked the short acclimation periods necessary for testing effects of both short and long acclimation durations on acclimation responses. To evaluate whether acclimation durations in our datasets were sufficient to acclimate large organisms, we repeated the acclimation duration analyses except we treated log acclimation duration as a response variable and excluded interactions.

Second, if smaller organisms acclimate faster than larger organisms, if heating rates in CT_{max} or cooling rates in CT_{min} trials are slow, or if there is a delay between when organisms are placed at a test temperature and when trait performance is measured, then smaller organisms might be more likely to acclimate to these new temperatures during trials before the measurement of trait performance (see Terblanche *et al.* 2007; Chown *et al.* 2009; Rezende *et al.* 2011, 2014 for discussions on heating and cooling rates). This, in turn, will reduce their ARR, resulting in a greater underestimation of the acclimation of smaller than larger organisms (Fig. 1c, see Supplement for additional clarification of this hypothesis). To test this hypothesis, we included heating rate into our multiple

regression models on CT_{\max} from the Gunderson and Stillman dataset predicting an acclimation time-by-body mass-by-heating rate interaction.

What is the relationship between observed and predicted acclimation abilities?

To quantify relationships among acclimation capacities, body size, and latitude, we repeated the acclimation time analyses described above except we included all effect sizes for each dataset where acclimation temperature data were available (see Tables S8–12 for details). For the Seebacher *et al.* analyses, we used the Q_{10} of acclimation thermal sensitivity as the response. For this dataset, results did not differ if we conducted analyses on both *in situ* and *ex situ* measurements (See Table S9) or on *in situ* whole body measurements only (See Table S10). Thus, we focus on analyses conducted on both *in situ* and *ex situ* measurements because it provided the larger sample size. For the Gunderson and Stillman analyses, ARR was the response variable and seasonality (standard deviation of annual mean weekly air temperatures) replaced latitude as a predictor. We then qualitatively compared the output from these statistical models to that from our mathematical model. To explore for differences among taxonomic groups in their optimal temperatures and acclimation capacities, we reconducted the analyses above replacing habitat with taxonomic group, because so many taxa are only found in one habitat type (e.g. all reptiles in our database are terrestrial, all fish are aquatic). To quantify the relationship between log body size and the time organisms were held at a test temperature before trait measurements were taken, we conducted a simple regression analysis using 1480 of the 2445 thermal response curves that had these data available.

What is the relationship between acclimation abilities and thermal safety margin (TSM)?

To determine the relationship between TSM and thermal plasticity across multiple taxa and species, we conducted a simple linear regression analysis with CT_{\max} ARR from the Gunderson and Stillman dataset as the response variable and TSM as the predictor (using the same random effects and weights as in the previously described multiple regression analysis), and we also added TSM to our best fitting multiple regression model for this response variable (described in previous paragraph). This latter analysis reduces the likelihood of ‘third variable problems’ because it controls for several other factors likely to affect thermal plasticity.

What is the relationship between observed and predicted thermal breadth?

To quantify relationships among acclimated thermal breadth, body size, and latitude, we used the *lme* function in the *nlme* package to conduct a weighted mixed effects analysis (weighting by sample size and treating the study and species combination as a random effect) with breadth measurements from Dell *et al.*’s thermal performance curve dataset as the Gaussian response variables, habitat (freshwater, marine, terrestrial), trophic assignment (T_{opt} only), and life stage (CT_{\max} only) as categorical moderators, and acclimation temperature, log acclimation duration, absolute value of latitude, and log body size as crossed continuous predictors (two- and three-

way interactions only). We then qualitatively compared the output from this statistical model to that from our mathematical model.

Can our framework predict the contribution of acclimation plasticity to IUCN threat status?

To test whether our statistical model of thermal acclimation and breadth could predict the contribution of acclimation plasticity to amphibian threat status, we treated amphibian species as the replicate in the amphibian CT_{\max} dataset, IUCN threat status as a binomial response variable, TSM, log body size, absolute value of latitude, log elevation, and log range size as crossed predictors, and a local estimate of the magnitude of climate change as a covariate (slope of the previous 50 years of maximum temperatures). IUCN threat status assignments are supported by objective, data-driven criteria that have been validated across a broad range of species (Rodrigues *et al.* 2006). To evaluate the contribution of acclimation plasticity to amphibian threat status, we analysed the subset of amphibian CT_{\max} data for which we also had ARR measurements, treating log elevation as a covariate, and TSM, log body size, absolute value of latitude, and log ARR as crossed predictors.

RESULTS

Does body size influence acclimation rate?

We rationalised that if acclimation rate is negatively correlated with body size, then when acclimation duration is short, a signal of acclimation should be apparent for small but not large organisms (Fig. 1a and b). We found evidence consistent with this hypothesis on two fronts. First, in the Gunderson and Stillman dataset, short acclimation durations were sufficient to detect acclimation (a positive ARR) for small organisms but longer acclimation durations were necessary to detect a positive ARR for larger organisms (Three-way interaction Acc. time \times mass \times heat rate: $X^2 = 5.27$, $P = 0.022$; Fig. 3a and c). Additionally, body size and acclimation duration interacted similarly to affect acclimation signatures (i.e. a positive correlation between acclimation temperature and T_{opt} or CT_{\max}) in both the Dell *et al.* (Fig. 3b and d, See Table S6) and amphibian CT_{\max} (See Table S7, Fig. S1) datasets.

Second, the Gunderson and Stillman dataset also provided information on the heating rate of CT_{\max} trials, offering another means of testing our hypothesis that time to acclimate is positively related to body size. As a reminder, we hypothesised that, if smaller organisms acclimate faster than larger organisms, then when the heating rate is slow, smaller organisms should be more likely to partly or fully acclimate to the new warmer temperatures during trials. This would reduce their ARR, thus diminishing the signal of acclimation more for smaller than larger organisms (Fig. 1c). As predicted, analysis of the Gunderson and Stillman dataset revealed that when the heating rate in CT_{\max} trials was slow, smaller organisms failed to show positive ARRs (confidence interval overlaps with zero on left side of Fig. 3c); in contrast, larger organisms showed positive ARRs (confidence interval almost never overlaps with zero) at most heating rates (Acc. time \times mass \times heat rate: $X^2 = 5.27$, $P = 0.022$; Fig. 3c). Although

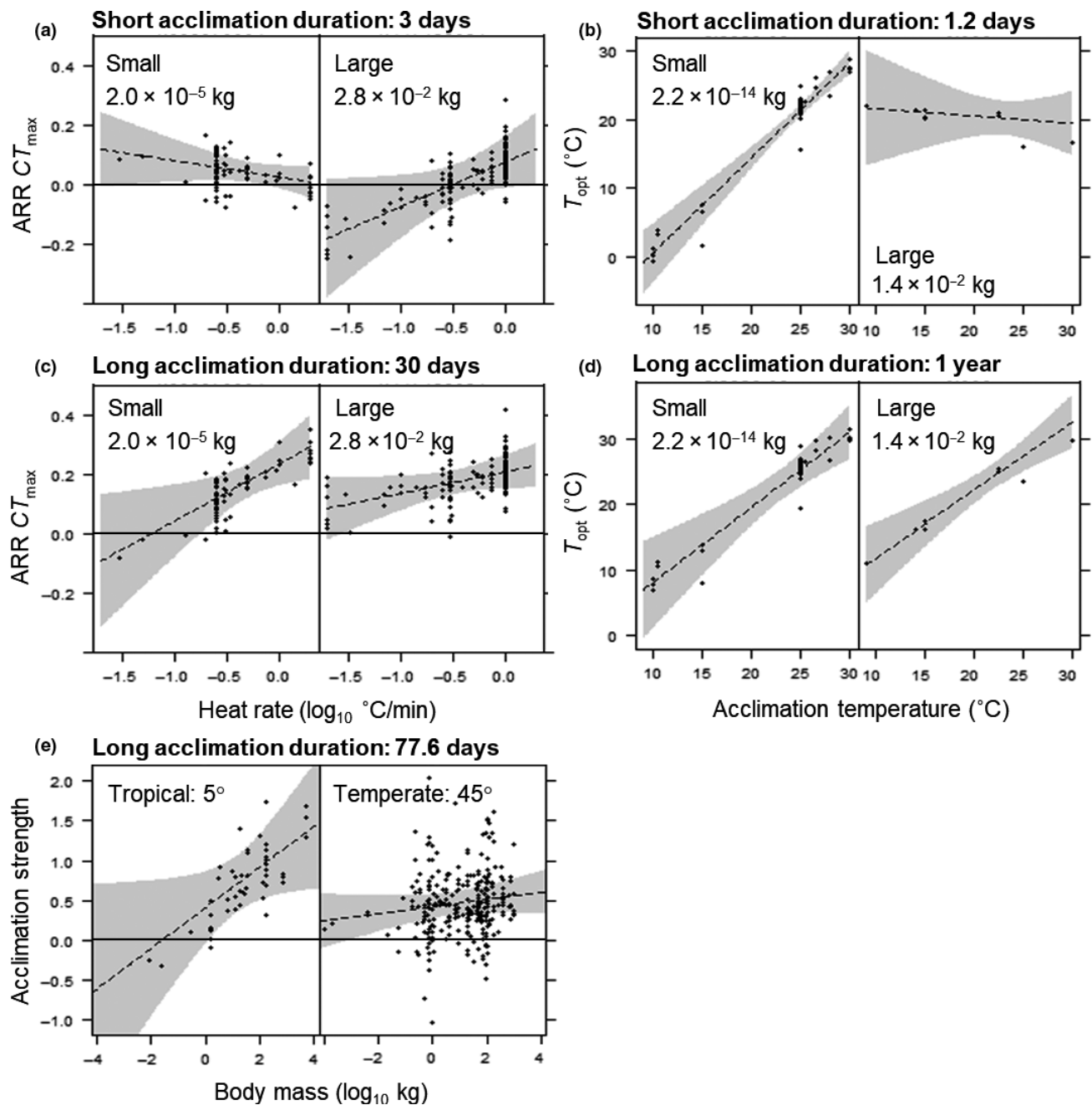


Figure 3 Partial residual plots showing that small organisms acclimate faster than larger organisms (a–d) and that acclimation abilities depend on an interaction between latitude and body size (e). Partial residual plots hold all factors in the statistical model that are not being displayed constant (see Supporting Information Appendix ‘Supplementary Discussion: Details on the *visreg* package’). Acclimation was measured as the acclimation response ratio (ARR) which is the correlation between acclimation temperature and critical thermal maximum (CT_{max} ; a & c) or optimal performance temperature (T_{opt} ; b & d). See ‘Methods: Statistical analyses’ for the measure of acclimation strength from Seebacher *et al.* (2) used in (e). When acclimation durations are short, only smaller organisms show a positive ARR (a; i.e., they acclimate) or positive slope (b) (see same result in Fig. S3), but when acclimation durations are long, both small and large organisms show acclimation responses (c & d; T_{opt} three-way interaction: $X^2 = 10.23$, $P = 0.001$, $n = 60$; range of absolute value of latitudes 25–57 °). Similarly, when acclimation durations are long, small organisms do not show positive ARRs when the heating rate in CT_{max} trials is low (presumably because they are at least partly acclimating to the new warmer temperatures during the trial), whereas large organisms show positive ARRs at most heating rates (c; heat rate \times size \times duration: $X^2 = 4.47$, $P = 0.0345$, $n = 262$). Subpanels represent different body size categories (breaks based on 50th and 90th percentiles and 20th and 80th for T_{opt} and CT_{max} , respectively; see Supporting Information Appendix ‘Supplementary Discussion: Details on the *visreg* package’) and short and long acclimation is represented by 20th and 80th percentiles. Despite smaller organisms acclimating faster than larger organisms, when acclimation durations were long (conditioned on 77.6 d, the 80th percentile), large organisms showed greater acclimation capacity in general, but especially in the tropics (e; Latitude \times mass: $z = 2.18$, $P = 0.029$). This result matches the findings from the two other datasets (see Fig. 2 and See Supporting Information Appendix, Figs S4–S5). Grey shading shows associated 95% confidence bands.

other mechanisms could produce these heating rate patterns (see Supplement for a discussion of them), these patterns are consistent with acclimation rate being negatively correlated with body size. Hence, across a diversity of taxa, habitats, and traits, our weight-of-evidence approach provides patterns consistent with the hypothesis that smaller organisms acclimate quicker than larger organisms.

Given that larger organisms appear to take longer to fully acclimate than smaller organisms, we also tested whether the mean acclimation duration imposed by experimenters (using the Dell *et al.* dataset because it had the most acclimation durations) was sufficient to fully acclimate large organisms (see Methods). In these analyses, acclimation duration was independent of body size ($X^2 = 0.27$, $P = 0.598$), and the grand mean acclimation duration was 85 h (or $5.49 \log_{10} + 1$ s; See Fig. S2), which is insufficient to detect significant acclimation for organisms exceeding 8.6 g (See Table S6, S8).

What is the relationship between observed and predicted acclimation abilities?

Four important predictions emerged from our mathematical model on the relationship between latitude and body size on acclimation abilities (Figs 4a and b, 5a): (1) small organisms should show weak if any acclimation in the tropics, (2) larger organisms should generally have greater acclimation abilities than smaller organisms across latitudes, (3) the difference in acclimation abilities between large and small organisms should be largest in the tropics and smallest in temperate zones, and (4) smaller organisms should exhibit a greater increase in acclimation abilities with increasing latitude than larger organisms. Statistical analyses of our empirical data provided evidence consistent with all of these hypotheses. In the Seebacher *et al.* dataset, significant acclimation was detected for both small and large organisms at mid-latitudes, but only for large organisms at low latitudes (Fig. 3e, 5b, See Table S9 and S10). Similar patterns were apparent in the Dell *et al.* dataset (Fig. 4d,e, 5c, See Table S8) and amphibian CT_{\max} (See Table S11, Fig. S4) dataset. The Gunderson and Stillman dataset also showed the same pattern, although latitude was replaced by seasonality (Fig. 5d; see Methods, correlation between seasonality and latitudes $<50^\circ$: $P = 3.1 \times 10^{-6}$, Table S12, Fig. S5), providing evidence consistent with the hypothesis that the greater capacity to acclimate at mid-latitudes might be a function of greater variability in environmental temperature. Additionally, despite smaller organisms apparently acclimating faster than larger organisms, when acclimation durations were sufficiently long in the Seebacher *et al.*, Dell *et al.*, and Gunderson and Stillman datasets, larger organisms generally had greater acclimation abilities across latitudes than smaller organisms (Fig. 5b–d). Also predicted by our model (Fig. 5a), across all three datasets, smaller organisms exhibited a greater increase in acclimation abilities with increasing latitude or seasonality than larger organisms (Fig. 5b–d). The model deviated from the empirical data for the acclimation abilities of large organisms. The model suggested that, like smaller organisms, larger organisms should exhibit an increase in acclimation abilities with increasing latitudes and seasonality (Fig. 5a), but all three datasets showed

that acclimation abilities of larger organisms actually declined with increasing latitudes or increasing seasonality (Fig. 5b–d).

After organismal traits and experimental methods were accounted for, taxonomic groups generally did not exhibit significant differences in thermal optima or acclimation abilities that were consistent across the datasets (Tables S13, S14, Fig. S6), indicating that phylogeny is unlikely to account for substantial residual variation. However, given that we did not explicitly control for phylogeny in our analyses, we cannot completely rule out that phylogeny accounts for some of this variation, especially for analyses on body size. Contrary to our hypothesis, there were no consistent effects of habitat (freshwater, marine, terrestrial) on acclimation responses across the datasets and habitat generally did not significantly interact with other predictors (See Tables S6–S12).

Our simulations suggest that the apparent weaker acclimation of smaller organisms relative to larger organisms is partly a product of them acclimating so fast that much of their acclimation occurs during the delay between when they first experience the test temperature and when researchers begin measuring performance (i.e., an experimental artefact; Figs 1 and 3). This was also supported by the experimental data. Based on the entire Dell *et al.* dataset (1480 curves with necessary data for analyses), body size was associated negatively with acclimation duration ($F_{1,1478} = 41.92$, $P < 0.001$, See Fig. S7), a methodological pattern that can exaggerate this artefact. For example, very small organisms were held at a test temperature for a mean of 8.82 h (the y-intercept) before a trait was first measured, which, according to our analyses on time to acclimate (see Fig. 3), is sufficient time for substantial if not full acclimation for such small organisms.

What is the relationship between acclimation abilities and thermal safety margin (TSM)?

TSM was a significant negative predictor of CT_{\max} ARR in both the simple regression (Coefficient \pm standard error: $-0.0041691 \pm 0.00109574$, $X^2 = 14.65$, $P = 0.0001$) and the multiple regression analyses (Coefficient \pm standard error: -0.002077 ± 0.000966 , $X^2 = 5.07$, $P = 0.024$). Thus, our results are consistent with the hypothesis that small TSMs select for thermal plasticity more so than they constrain it.

What is the relationship between observed and predicted thermal breadths?

Our mathematical model also provided hypotheses for how latitude and body size might interact to affect acclimated thermal breadth. Consistent with model predictions (Fig. 5c), species exhibited an increase in acclimated thermal breadth with increasing latitude (latitude \times body mass: $X^2 = 13.61$, $P < 0.001$; Fig. 5c and f, See Table S15) and decreasing body size (Fig. 5f; See Table S15). Our model suggests that smaller organisms could appear to have greater acclimated thermal breadths than larger organisms because they acclimate more rapidly, maintaining higher observed performances over a larger range of temperatures (Fig. 2).

Although the model and data were generally consistent, one of the hypotheses generated by the model was not supported by

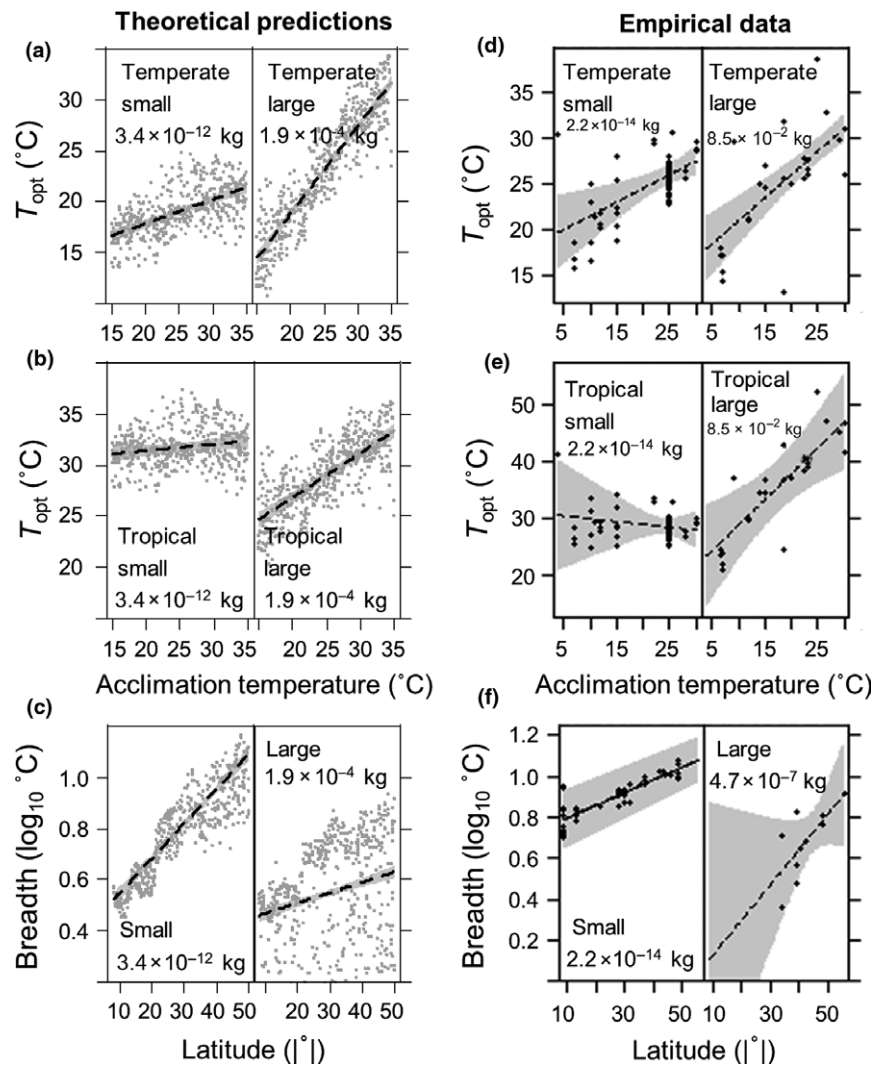


Figure 4 Partial residual plots showing the predicted and observed effects of acclimation temperature, body mass, and latitude on optimal performance temperature and acclimated thermal breadth for a diversity of taxa and habitats. (a), (b), and (c) show results from our mathematical model for optimal performance temperature (T_{opt}) at 45 and 5 degrees latitude and for acclimated thermal breadth, respectively (see Supporting Information Appendix for parameters). (d), (e), and (f) show the same plots, respectively, but for Johnson-Lewin model fits (see Supporting Information Appendix, Fig. S8 and S9 for similar results using Weibull fits) to empirical data obtained from Dell *et al.* dataset (three-way interaction for T_{opt} : $X^2 = 8.08$, $P = 0.0045$, $n = 105$; two-way interaction for breadth: $X^2 = 13.61$, $P < 0.001$, $n = 64$; log masses $< 10^{-5}$ kg). Subpanels represent different body size categories (breaks based on 20th and 80th percentiles). Grey shading shows associated 95% confidence bands. See Supporting Information Appendix, Fig. S11 for similar results from the model when no relationship between acclimation rate and temperature is assumed (assumption here is an exponential relationship).

the empirical data. In contrast to predictions of the model (Fig. 4c), the empirical data showed that smaller organisms had greater breadths than larger organisms in the tropics and that breadths tended to converge in temperate zones (Fig. 4f). Importantly, these acclimation and breadth results were robust to whether symmetric or asymmetric curves were used in the mathematical model (See Supporting Information Appendix) and whether Johnson-Lewin or Weibull models were fit to the thermal performance curve data (Fig. 2,3 vs Figs S8 and S9).

Can our framework predict the contribution of acclimation plasticity to IUCN threat status?

Surprisingly few studies have linked the degree of plasticity of species to their IUCN threat status. Owing to their much

narrower breadths and longer times to acclimate and evolve (Figs 3 and 4), our framework derived from our data analysis suggests that larger tropical ectotherms might experience greater lethal and sublethal effects from climate change than smaller temperate ectotherms because of restricted thermal plasticity. As predicted, large tropical amphibian species with small geographic ranges (species with large ranges were rarely threatened regardless of body size or latitude; See Fig. S10) had the strongest negative relationship between threat status and TSM and thus might be most threatened by recent GCC (Fig. 6a and b). In fact, in temperate zones, the relationship between threat status and TSM was positive for large amphibians suggesting that other factors correlated with TSMs might be more important drivers of threat status in these regions. Also, as predicted, this threat level decreased as latitude

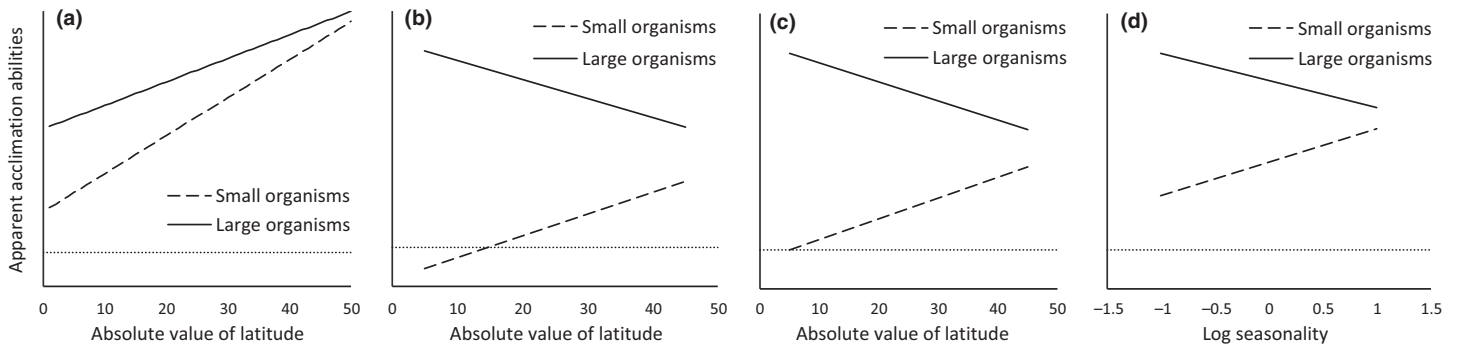


Figure 5 Predicted (a), from the mathematical model) and observed (b–d), from Seebacher *et al.*, Dell *et al.*, and Gunderson and Stillman datasets, respectively) relationships among acclimation abilities, latitude or seasonality, and body size (20 and 80% percentiles) when acclimation durations are long. In the model and across all datasets, large organisms generally show greater apparent acclimation abilities than small organisms across latitudes and seasonalities, small organisms show little apparent acclimation abilities in the tropics, and the difference in acclimation abilities between large and small organisms decreases with increasing latitude or seasonality because acclimation abilities increase more with increasing latitude for small than large organisms. The model deviates from the empirical data for the change in acclimation abilities of large organisms across latitudes. Apparent acclimation abilities were standardised so that all empirical datasets had the same estimated acclimation abilities for large organisms at 5 ° latitude or –1.0 log seasonality, which is why units have been removed. The dotted line is the zero acclimation line. The data used to generate (a–d) are shown in Figures 5a,b; 4e; 5d,e; and S5, respectively.

increased or body size decreased (interaction: $X^2 = 8.66$, $P = 0.0033$; Fig. 6a and b). Importantly, this relationship between threat status and TSM was detectable despite the many factors other than GCC contributing to amphibian declines (Rohr *et al.* 2008; Wake & Vredenburg 2008; Rohr & Raffel 2010; Li *et al.* 2013).

We had several hypotheses regarding the relationship between threat status and thermal acclimation plasticity. Given that the previous analyses suggested that TSMs were unlikely to be drivers of threat status at mid-latitudes (because the relationship were flat or positive; Fig. 6a and b), we did not expect thermal plasticity to be strongly related to threat status in temperate zones. In contrast, at low latitudes, we hypothesised that thermal plasticity would only reduce threat status when TSMs were small, because extreme temperatures should pose less of a threat to amphibians with large relative to small TSMs. Finally, because large tropical amphibians appeared to be more threatened by small TSMs than small tropical amphibians (Fig. 6a and b), we hypothesised that this might be because of more circumscribed, costly, or less effective thermal plasticity. To test these hypotheses, we added thermal acclimation plasticity (the ARR of CT_{max} ; 74 species with available data) to our threat status models (See Appendix, Table S16) with the expectation that there should be significant statistical interactions among TSM, ARR, body size, and latitude.

As predicted, thermal acclimation plasticity was generally unrelated to threat status at mid-latitudes (i.e., there is only a weak relationship with the exception of large amphibians at mid-latitudes experiencing a negative relationship between ARR and threat status; Fig. 7). Additionally, the independent variables were poorer fits (i.e., more spread around the best fit line and thus larger residuals) to the threat status data at mid- than low latitudes (Fig. 7). At low latitudes, acclimation plasticity was associated with greater reductions in threat status when the TSMs were small relative to large (Fig. 7), suggesting that plasticity can be protective against thermal variability

in tropical and subtropical regions. In fact, at low latitudes, the slope between ARR and threat status was never significantly negative at large TSMs (Fig. 7c and d, See Table S16). At low latitudes, increases in thermal plasticity were associated with sharp reductions in threat status for small amphibians (i.e., were protective), but moderate increases in threat status for large amphibians (see several two- and three-way interactions among ARR, TSM, SVL, and Latitude in Table S16, Fig. 7a and b). These results are consistent with larger, tropical amphibians having more restricted, less effective, or more costly thermal plasticity than smaller tropical amphibians, which might partially account for the global patterns in amphibian threat status (Fig. 6).

DISCUSSION

The results we present here demonstrate that methodological factors, body mass, latitude, and TSM interact to shape the actual and measured thermal acclimation responses of ectotherms. Our model and the empirical data suggest that the apparent shorter times to acclimate of smaller than larger organisms at least partially drive the generally observed wider acclimated thermal breadths of smaller organisms (Fig. 2), and our analyses of IUCN threat status are consistent with the hypothesis that thermal plasticity can protect species from climate variability (see also Urban *et al.* 2014). Despite each of the four diverse datasets we studied having various strengths and limitations, our findings were consistent across these datasets that spanned variation in acclimation duration, body mass, habitat, trait type, latitude, and > 500 species.

Analyses of these datasets were consistent with several of the body size and latitudinal hypotheses generated by our relatively simple mathematical model. These included (1) small organisms showing weak if any acclimation in the tropics, (2) larger organisms generally having greater acclimation abilities than smaller organisms across latitudes, (3) the difference in acclimation abilities between relatively large and small

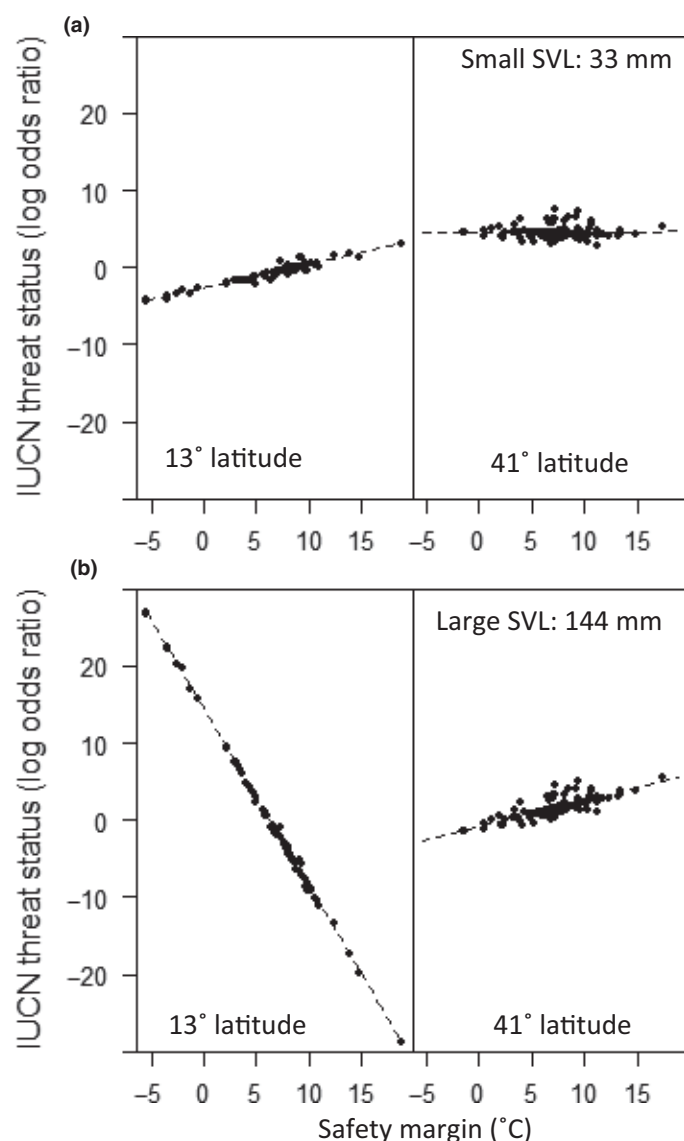


Figure 6 Partial residual plots showing that large tropical amphibians are most threatened by climatic variability, because as thermal safety margin increases, only large tropical amphibians show a sharp decline in threat status. (a) and (b) show the interaction ($X^2 = 8.66$, $P = 0.0033$) among thermal safety margin (critical thermal maximum – maximum temperature of warmest month), the absolute value of latitude, and log body size (a) small snout-vent lengths [SVL], (b) large SVL; 20th and 80th percentiles) on the odds that amphibian species with small geographic ranges (conditioned to the 20th percentile; $3.8 \log \text{ km}^2$) are categorised as threatened or not by the IUCN ($n = 186$; see Supporting Information Appendix, Fig. S10 for species with large geographic ranges). Subpanels represent different latitude categories (breaks at 10th and 90th percentiles).

organisms being greatest in the tropics and smallest in temperate zones, (4) smaller organisms exhibiting a greater increase in acclimation abilities with increasing latitude than larger organisms (Figs 4a–d, 5), and (5) acclimated thermal breadth increasing with latitude and decreasing with body size (Fig. 4c and f). Although we were unable to test the hypothesis that acclimation rate should scale with body size to the $\frac{3}{4}$ power, our model assumed this and its output was consistent with the

extensive experimental data, findings which are congruent with metabolic scaling theory (Gillooly *et al.* 2001, 2002; Brown *et al.* 2004). Additionally, we provide evidence consistent with the hypothesis that thermal optima regularly acclimate despite this being previously questioned (Angilletta 2009). Although other factors that we did not study, such as phylogenetic inertia or epistasis (Angilletta 2009), undoubtedly also affect thermal acclimation and breadth, our empirical results suggest we are capturing many of the principal mechanisms driving variation in thermal acclimation and breadth across the globe and species (but see caveats in Supporting Information Appendix). Additionally, given that body mass is strongly correlated with generation time and latitude is strongly correlated with diel variation in temperature, our findings have the potential to be extended to these other common predictors of thermal acclimation (Angilletta *et al.* 2006). An important caveat, however, is that all the trends we report based on absolute latitudes only span tropical to temperate regions and almost certainly would be nonlinear if polar regions were included, because polar ectotherms are extremely stenothermal and have very limited abilities to acclimate to higher temperatures (Pörtner 2002; Peck *et al.* 2004). Moreover, we acknowledge that there can also be important latitudinal and temperature variation within the geographic range of a species (Kuo & Sanford 2009) and even inter- (i.e. genetically based differences) and intraindividual (e.g. life-stage differences) variability in thermal responses that are unaccounted for in the current analyses (Dong *et al.* 2017).

Although our empirical analyses were consistent with most of the hypotheses derived from our mathematical model, there were also important areas where the model and empirical analyses deviated. For example, smaller organisms had greater breadths than larger organisms in the tropics and breadths tended to converge in temperate zones (Fig. 4f), findings that were opposite to the predictions of our model (Fig. 4c). The mechanism driving these observed patterns is equivocal. Another example where the model and empirical data conflicted was that the model suggested that both small and large organisms should increase in acclimation abilities with increasing latitudes and seasonality (Fig. 5a), but all three datasets revealed that acclimation abilities of larger organisms actually declined with increasing latitudes or seasonality (Fig. 5b–d). It is unclear why large organisms showed the opposite latitudinal acclimation pattern as small organisms. One untested hypothetical mechanism is that the higher temperatures in tropical than temperate zones might disproportionately place greater oxygen demands on large than small organisms (oxygen diffusion becomes less problematic for smaller organisms). To partially compensate for these oxygen limitations, this might impose greater selective pressures for acclimation on large tropical than large temperate organisms (Pörtner *et al.* 2017). Another possible hypothesis for why larger organisms show more plasticity in tropical than temperate zones is that larger organisms might be compensating for the fact that they exhibit much smaller acclimated thermal breadths in tropical than temperate zones compared to smaller organisms (Fig. 4f). Regardless of the mechanism, these opposing responses of relatively large and small organisms across latitudes are likely why previous researchers failed to detect latitudinal and seasonality gradients

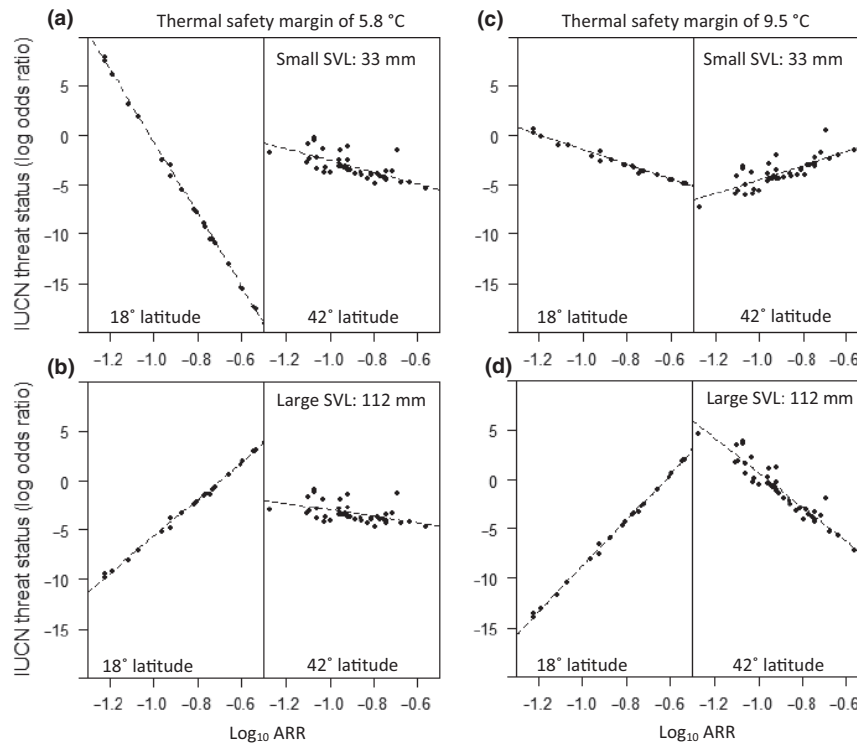


Figure 7 Partial residual plots suggesting that large tropical amphibians might be threatened at least partially because of limited acclimation abilities. The panels show the interaction ($X^2 = 8.66$, $P = 0.0033$) among acclimation response ratio (ARR, a measure of thermal acclimation plasticity), the absolute value of latitude, and log body size (a and c) small snout-vent lengths [SVL], 20th percentiles and (b and d) large SVL, 80th percentiles) on the odds that amphibian species with a small (a and b) 20th percentile; 5.8 °C) or large thermal safety margins (c and d) 80th percentile; 9.5 °C) are threatened ($P < 0.05$; $n = 74$; see Supporting Information Appendix, Table S16 for full statistical model). Subpanels represent different latitude categories (breaks at 10th and 90th percentiles). When the thermal safety margin is large, thermal plasticity is not associated with sharp reductions in threat status (c and d). When the thermal safety margin is small (a and b), thermal plasticity is significantly associated with reductions in the threat status of small but not large tropical amphibians, which might be why large amphibians are more threatened than small amphibians in the tropics.

in acclimation using these datasets (Gunderson & Stillman 2015; Seebacher *et al.* 2015) (see Supporting Information Appendix for additional details). Additionally, given that acclimation studies vary in the body sizes of their focal organisms, the interaction between latitude and body size we reveal here could account for variation among studies in the strength of reported latitudinal signals in acclimation abilities. A final noteworthy deviation between theory and empirical data was the lack of greater thermal acclimation abilities of terrestrial than aquatic organisms, despite terrestrial species experiencing greater temperature variability. One possible explanation for this deviation is that terrestrial species might be better able to regulate body temperature through behavioural means than aquatic species (Dong *et al.* 2017). Alternatively, given that oxygen availability is more circumscribed in aquatic than terrestrial environments, this deviation from theory might also be a product of limited oxygen availability restricting whole-animal tolerances to thermal extremes (Pörtner *et al.* 2017). A more thorough integration of oxygen, behavioural, and thermal constraints might address these apparent contradictions between theory and data (Pörtner *et al.* 2017).

Two contradictory but logical hypotheses have been proposed for how TSM should affect thermal plasticity. The first suggests that there should be selection for greater thermal plasticity as a means of coping with environmental temperatures

that are close to the upper lethal limit of species (Somero 2010; Huey *et al.* 2012; Vasseur *et al.* 2014). In support of this hypothesis, some researchers have presented evidence consistent with the hypothesis that thermal plasticity can reduce the threat from climate change (Urban *et al.* 2014; Reich *et al.* 2016). In contrast, it has also been hypothesised that species with small TSMs might appear less plastic than those with large TSMs because they have less room to increase their CT_{max} assuming there is some hard physiological limit (Stillman 2003; Stenseng *et al.* 2005). Indeed, studies of marine rocky intertidal invertebrates have shown that the most warm-adapted species have the least ability to further increase their tolerance of high temperatures (Stillman 2003; Stenseng *et al.* 2005). Our meta-analysis conducted across studies and species provides data consistent with the hypothesis that, on average, small TSMs seem to select for plasticity more so than they restrict it.

Our analyses suggest that large tropical amphibians are more threatened than any other tested amphibian group. Our assertion that tropical ectothermic species should be more sensitive to GCC than temperate species is consistent with previous studies (Deutsch *et al.* 2008). Additionally, our analyses suggest that large tropical amphibians might be experiencing considerable threat because of limited thermal plasticity. Indeed, the greatest difference between large and small amphibians in the protectiveness of thermal plasticity (i.e. slope between threat

status and ARR) occurred at low latitudes (Fig. 7a and b). This might be a product of most CT_{\max} studies ignoring time to acclimate. Because smaller organisms seem to acclimate sooner than larger organisms, even with the same ARRs, smaller organisms pay the costs of their physiology mismatching their environment for a shorter period of time. Alternatively, these patterns could be a result of the acclimated thermal breadths of large organisms being much smaller than small organisms in the tropics (Fig. 4f). Overall, these results suggest that variation in thermal acclimation abilities might partly account for why amphibians are more threatened as body size increases and latitude decreases (Urban *et al.* 2014).

If larger organisms are more sensitive to temperature changes than smaller organisms, as suggested by our amphibian IUCN analyses, then GCC might tip the balance towards smaller species. Examples that are consistent with this notion are GCC reducing the body sizes of aquatic organisms (Daufresne *et al.* 2009; Horne *et al.* 2015), temperature variability benefiting pathogens (small-bodied) more so than hosts (large-bodied), and GCC being associated with recent disease emergences (Rohr & Raffel 2010; Sinervo *et al.* 2010; Rohr *et al.* 2011; Raffel *et al.* 2013; Cohen *et al.* 2016). Moreover, our results suggest that global warming might generally give smaller species an edge in species interactions, resulting in asymmetries in species interactions (Dell *et al.* 2014; Cohen *et al.* 2017) that likely have significant consequences for community composition and ecosystem functions (Parmesan 2006; Reich *et al.* 2016).

Although previous research has often failed to detect acclimation in small organisms (Feder 1982; Kolbe *et al.* 2014; Seebacher *et al.* 2015) – suggesting that they might be at increased risk from GCC – our empirical and modelling results reveal that many small organisms (especially those at high latitudes) might indeed be capable of rapid acclimation, and because of this rapid acclimation, they have broad apparent thermal breadths. To date, much of this acclimation has apparently gone undetected because of slow heating rates in CT_{\max} studies and delays in performance measurements that typify most experiments, or has been underestimated because most thermal plasticity studies ignore acclimation rates, which appear to be shorter for smaller organisms. It remains unclear how much of the perceived lower acclimation abilities of smaller than larger organisms is a product of these experimental artefacts vs. a true biological phenomenon. Our results also suggest that researchers might be underestimating the plasticity of larger organisms because many experiments do not provide sufficient time for them to fully acclimate to new temperatures. These results, coupled with many forecasts of GCC-induced extinctions not including behavioural or physiological plasticity to temperature (Thomas *et al.* 2004; Urban 2015), suggest that some studies might have overestimated the risks of GCC to ectothermic animals. Recently, researchers came to similar conclusions for plants (Reich *et al.* 2016). Such conclusions should not be taken as evidence that effects of GCC will not be catastrophic; however, it is at least a rare, albeit thin, silver lining in research on the effects of GCC on biodiversity. In conclusion, by providing a mechanistic understanding of acclimation based on geographic and species traits that are easily measured or inferred (i.e. latitude, ecto- vs endotherm, body size), combined with an understanding of the role of methodological artefacts, we have helped move towards a

framework for quantitatively predicting which ectothermic species and locations on the planet are most vulnerable to GCC, which should facilitate targeting limited conservation resources.

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AUTHOR CONTRIBUTIONS

JRR developed the ideas, conducted the analyses, generated the figures and wrote the manuscript. AID and EAR developed the thermal performance curve and critical thermal maxima databases, respectively. DJC developed the mathematical model. JMC fit the Johnson-Lewin and Weibull curves to the thermal performance data. BS suggested the utility of critical thermal maximum studies in amphibians for acclimation analyses. All authors edited the manuscript.

DATA AND CODE ACCESSIBILITY STATEMENT

Data used for analyses in this manuscript can be found at <http://biotraits.ucla.edu/>, <http://www.esapubs.org/archive/ecol/E094/108/>, or in Database 1, which is an Excel file with 19 worksheets. One worksheet is the R code used to produce the Figures and Tables in this paper. Nine of the remaining 18 worksheets are the datasets used for specific analyses in the paper. The remaining nine worksheets are the metadata that accompany each of the nine datasets.

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SUPPORTING INFORMATION

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

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