

RESEARCH PAPER

Physiological acclimation and persistence of ectothermic species under extreme heat events

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Funding information

British Antarctic Survey; Canada Research Chairs

Editor: Adam Algar

Abstract

Aim: To test if physiological acclimation can buffer species against increasing extreme heat due to climate change.

Location: Global.

Time period: 1960 to 2015.

Major taxa studied: Amphibians, arthropods, brachiopods, cnidarians, echinoderms, fishes, molluscs, reptiles.

Methods: We draw together new and existing data quantifying the warm acclimation response in 319 species as the acclimation response ratio (ARR): the increase in upper thermal limit per degree increase in experimental temperature. We develop worst-case scenario climate projections to calculate the number of years and generations gained by ARR until loss of thermal safety. We further compute a vulnerability score that integrates across variables estimating exposure to climate change and species-specific tolerance through traits, including physiological plasticity, generation time and latitudinal range extent.

Results: ARR is highly variable, but with marked differences across taxa, habitats and latitude. Polar terrestrial arthropods show high ARR [95% upper confidence limit (UCL95%) = 0.68], as do some polar aquatic invertebrates that were acclimated for extended durations (ARR > 0.4). While this physiological plasticity buys 100s of years until thermal safety is lost, combination with long generation times leads to decreased potential for evolutionary adaptation. Additionally, 27% of marine polar invertebrates have no capacity for acclimation and reptiles and amphibians have minimal ARR (UCL95% = 0.16). Low physiological plasticity, long generations times and restricted latitudinal ranges combine to distinguish reptiles, amphibians and polar invertebrates as being highly vulnerable amongst ectotherms.

Main conclusions: In some taxa the combined effects of acclimation capacity and generation time can provide 100s of years and generations before thermal safety is lost. The accuracy of assessments of vulnerability to climate change will be improved by considering multiple aspects of species' biology that, in combination may increase persistence under extreme heat events, and increase the probability for evolutionary rescue.

*Morley and Bates are equal contributors.

KEYWORDS

acclimation, acclimation response ratio, extreme events, generations, geographic range, persistence, physiological plasticity

1 | INTRODUCTION

Accurate predictions of future patterns of biodiversity require the ability to identify which species possess mechanisms to persist in the face of rapid climate change. An increasing focus is on the importance of physiological tolerance, plasticity (acclimation capacity) and evolutionary adaptation (adaptive capacity) of physiological tolerance (Norberg, Urban, Vellend, Klausmeier, & Loeuille, 2012). An increase in exposure through the magnitude and frequency of extreme weather events is expected to challenge the ability of individuals and populations to cope with not only warming, but also extreme heat events that vary in duration, frequency and magnitude (Coumou & Rahmstorf, 2012; Lopez et al., 2018).

Striking patterns have emerged from species-specific data on physiological performance and tolerance to environmental temperature patterns (Araújo et al., 2013; Deutsch et al., 2008; Gaston et al., 2009; Sunday, Bates, & Dulvy, 2011; Tewksbury, Huey, & Deutsch, 2008), as well as organisms' capacities to alter short-term tolerance of high heat via acclimation across habitats and latitudes (Comte & Olden, 2017; Gunderson & Stillman, 2015). For example, tropical and polar fauna are expected to be relatively stenothermal, adapted to living in stable temperatures with relatively constrained thermal tolerance breadths (Clarke & Gaston, 2006; Sunday et al., 2011). Combined estimates of the present and future exposure to extreme heat, physiological tolerance and adaptive potentials of species are needed to increase the accuracy of species-specific vulnerability assessments (Williams, Shoo, Isaac, Hoffmann, & Langham, 2008), as well as a means for testing general patterns and evolutionary constraints across taxa and habitats.

Natural selection of more resistant physiological phenotypes within a population can lead to an overall increase in tolerance limits (Kellermann et al., 2012). For instance, some populations exposed to predictable seasonal variation in temperature may have evolved the plasticity to increase their thermal tolerance in the warmest season, protecting them during exposure to extreme heat events. This process of physiological adjustment is referred to as acclimation, which involves the flexible changes in the reaction norms of physiological pathways in response to warming or cooling (Fry, Brett, & Clawson, 1942; Prosser, 1973). Moreover, acclimation can lead to a reduction in the thermal sensitivity of physiological processes and increase tolerance thresholds (Seebacher, White, & Franklin, 2015). Thus, acclimation capacity allows organisms to adjust their physiology to tolerate greater extremes and the rapid changes in environmental temperatures that are increasingly being observed with rising global mean environmental temperatures (Coumou & Rahmstorf, 2012; Lopez et al., 2018). Thus, what may lead to strong shifts in where species are found is not slow gradual shifts in mean environmental

temperatures, but exposure to rapid changes in temperature that lead to strong sublethal and lethal effects.

The "acclimation response ratio" (ARR; Claussen, 1977) is the change in the upper thermal tolerance relative to change in mean temperature, quantified in experiments as the slope of the relationship between the upper thermal tolerance and acclimation temperature. Thus, ARR offers a metric of physiological plasticity capturing acclimation capacity (Figure 1) to rapid temperature change. However, ARR is typically far lower than 1, so that an increase of 1°C in environmental temperature does not lead to a corresponding increase in upper thermal tolerance of 1°C (Gunderson & Stillman, 2015). Hence, the extent to which acclimation can buffer an organism from increasing temperature extremes is limited, but it is possible that acclimation may afford a species added time, increasing the chances of population level adaptation through evolutionary rescue (Schaum & Collins, 2014).

Here we test the acclimation response of maximum acute tolerance to more extreme heat exposure in ectothermic vertebrates and invertebrates from terrestrial and aquatic (freshwater and marine) habitats. We calculate how much extra time physiological acclimation can lend before thermal safety is lost, and which geographic regions across latitude are likely to be most at risk from climate warming. To assess the potential for adaptation, and how adaptation may trade-off with exposure to climate change, we test if acclimation capacity (ARR) increases the potential for species' persistence. We calculate the benefit of acclimation as both a function of time (in years) and also a biologically meaningful unit (discrete generations). We thus indicate the potential for evolutionary rescue, that is, the chances of an advantageous phenotype, and therefore genotype, being fixed across generations (that will allow increased resistance to extreme warming events). We further test for relationships in exposure to environmental warming and multiple traits related to taxon-specific vulnerability including physiological tolerance, plasticity, geographic range and generation time. Compiling these multiple parameters into an exposure and vulnerability framework allows us to also identify groups of taxa that are more or less vulnerable.

2 | METHODS

We first conducted long-term experiments of thermal limit acclimation focused on marine polar invertebrates, and then combined these with an extensive range of empirical estimates of acclimation capacity in terrestrial, freshwater and marine ectotherms (Supporting Information Appendix S1, Figure S1). We use these data in combination with future climate projections (Representative Carbon Pathways RCP8.5 and 4.5) to quantify the added time that

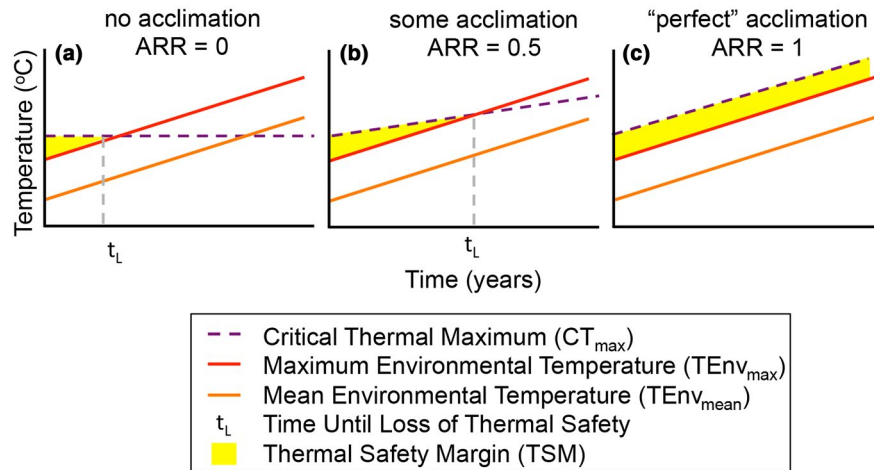


FIGURE 1 Conceptual figure depicting the time until thermal safety is lost: (a) number of years without acclimation [acclimation response ratio (ARR) = 0], (b) with some acclimation (ARR = 0.5) and (c) with perfect acclimation (ARR = 1). The predicted increases in mean environmental temperature (T_{env_mean} = solid lower line) and maximum environmental temperature (T_{env_max} = solid upper line) are shown for the RCP8.5 projected rates of environmental warming (the same plots for the RCP4.5 rates of warming are presented in Supporting Information Appendix S1, Figure S3). The difference between T_{env_max} and the critical thermal maximum (CT_{max}) (= dotted line) provides an estimate of warming tolerance, which we extend to predicted CT_{max} with acclimation, calculated using the acclimation capacity (ARR) [Colour figure can be viewed at wileyonlinelibrary.com]

acclimation can lend species, potentially improving the chances of evolutionary rescue under warming scenarios that will also bring greater exposure to extreme heat events (Bell, 2013). Given the rate of climate warming and the degree to which the species' heat tolerance adjusts to increasingly warmer acclimation temperatures (i.e., its ARR), we calculate how much time acclimation will provide each species ($N = 319$) in our dataset before extreme environmental temperatures exceed their adjusted, upper thermal tolerance (Figure 1). We project warming tolerance in units of years, as well as number of generations for the subset of species for which generation times were available ($n = 189$).

2.1 | Warm acclimation capacity (ARR)

Acclimation occurs over a fixed temperature range within which animals are able to adjust their physiological pathways. While we aimed to select acclimation values for critical thermal maxima (CT_{max}) that were as close to maximal as available data allowed (so that our estimates of ARR were conservative), we were restricted by the ranges in acclimation temperatures selected by the authors of the different studies. The acclimation capacities we used therefore represent a window within the upper half of the thermal niche across all species included, as reported in <https://doi.org/10.5285/20010bfb-c6d3-430f-b1f7-d16790ab8359>.

2.2 | Long-term experimental temperature incubations

Data for species from marine polar habitats were not available and thus we ran our own experiments. We held experimental animals in tanks for up to 9 months at both ambient (0°C) and at elevated temperatures (2.9 or 6°C). After this prolonged period of acclimation

we assessed their capacity to tolerate extreme heat, using CT_{max} as the ARR. Incubations were conducted for four Antarctic marine invertebrates, the gastropod mollusc *Nacella concinna*, the anemone *Urticinopsis antarctica*, the sea urchin *Sterechinus neumayeri* and the sea star *Odontaster validus*. Incubation temperatures were chosen that resulted in less than 5% mortality of each species and did therefore not conflate acclimation with the selection of more tolerant phenotypes.

Adults of each species were collected by SCUBA divers during the austral summers between 2006 and 2010 from 5–10 m depth at South Cove, Ryder Bay, Antarctic Peninsula ($67^{\circ}34' \text{ S}$, $68^{\circ}08' \text{ W}$). Animals were transported by boat and remained submerged until they were transferred to flow-through laboratory aquaria at 0°C . The animals were transported to the UK and then held in the British Antarctic Survey 0°C re-circulating aquarium in Cambridge for approximately 2 months before being introduced to the re-circulating experimental tanks. Seawater chemistry was monitored every 2–3 days using Nutrafin Aquarium test kits (Tropical marine centre Ltd., Chorleywood, Hertfordshire, UK). Ammonia, nitrite and nitrates were maintained well below 0.4, 0.2 and 5 mg/L, respectively, by a combination of biological filtration, protein skimming and partial seawater exchanges (approximately 5–15% every 2–3 days) to prevent toxicity from metabolic by-products. A 12:12 h light : dark cycle was maintained throughout. Twenty to thirty individuals of each species, for each treatment, were either transferred into the acclimation tanks or remained in the aquarium at 0°C as controls. The acclimation tanks were warmed to incubation temperature at a rate of $0.2 \pm 0.1^{\circ}\text{C}$ per day.

At the termination of each experiment, remaining individuals were transferred to a jacketed tank (Peck, Clark, Morley, Massey, & Rossetti, 2009). The internal volume of each tank was 75 L and temperature was controlled by a 20% ethanol/water mix being pumped

through the hollow walls of the jacketed tanks from a heater-cooler unit (LTD20G, Grant Instruments, Shepreth, Cambridgeshire, UK). Initial temperatures were either set at the respective acclimation temperatures, or 0°C (for the control group). These temperatures were held for 24 hr and then raised in 0.5°C steps every 12 hr.

Critical temperature limits were identified using behavioural stimuli specific to each species, which were assessed at least twice a day. The temperature at which there was a lack of response to tactile stimulus of the foot of *N. concinna*, the tentacles of *U. antarctica*, the spines of *S. neumayeri* and the ambulacral groove of *O. validus* was recorded as the CT_{max}.

2.3 | Data synthesis

To obtain global coverage across latitude, literature searches were conducted for studies that tested the upper temperature limits of marine (including estuarine and intertidal species), freshwater or terrestrial ectothermic animals at more than one acclimation temperature (up to December 2015; Supporting Information Appendix S1, Figure S1). Search terms “acclimate” or “acclimation” and “temperature” were used in Google, Google Scholar and the Web of Knowledge. The reference lists of selected papers were also searched to locate further studies. To ensure the surface climate data scenarios, described later, were applicable, terrestrial species from altitudes above 1,000 m, or when source populations were not attributed to a location of collection, were excluded. Data for acclimation responses for 319 different species (97 amphibians and reptiles, 40 terrestrial arthropods, 102 fishes and 80 aquatic invertebrates) were collated from 153 studies where temperature limits were assessed through an incremental increase in temperature (the dynamic method; Richard, Morley, Thorne, & Peck, 2012). A list of the data sources is found in the Appendix.

We further extracted parameters representing methodological protocols for experimental determination of thermal limits, study location and specimen origin. We were able to obtain complete information for the following parameters: thermal limit endpoint metric (critical or lethal); rate of temperature change (°C/day); acclimation temperature; life stage (adult or juvenile); source (wild, laboratory raised), latitude, longitude and hemisphere of collection. Inclusion of those parameters that were independent of ARR did not significantly improve the model fits <https://doi.org/10.5285/20010bfb-c6d3-430f-b1f7-d16790ab8359>.

Species' latitudinal range extents were extracted from online databases by searching for the most northerly and southerly record and used for estimating latitudinal range extent. Databases included general databases such as the Global Biodiversity Information Facility (www.gbif.org), World Register of Marine Species (www.marinespecies.org), the Encyclopedia of Life (www.eol.org), taxon specific databases and primary literature (sources for each generation time are reported in the accompanying data file). Generation time of each species was searched for using the terms, “generation time of ...”, “age at first maturity of...” and “age at first reproduction of ...” in Google and Google Scholar. A full citation list for generation time is presented in <https://doi.org/10.5285/20010bfb-c6d3-430f-b1f7-d16790ab8359>.

2.4 | Statistical modelling

Statistical modelling was conducted in R version 3.5.1 (R Core Team, 2018). Model structures and results summary tables are reported in Supporting Information Appendix S1, Tables S1–S4.

First, to test for patterns in acclimation capacity (ARR) across latitude (shown in Figure 2) we used mixed effects models fitted using restricted estimation likelihood (R package nlme; Pinheiro, Bates, DebRoy, & R Core Team, 2016). We included latitudinal bin as a factor with the following divisions: tropical (low: 0–25°), temperate (mid: > 25–55°) and polar latitudes (high: > 55°), fitted independently for (a) reptiles and amphibians, (b) terrestrial arthropods, (c) fish and (d) aquatic arthropods. To control for variation in thermal tolerance responses owing to different experimental designs and inclusion of multiple estimates for the same species within a study, we included study and species name as random effects on the intercept.

Second, to test for the responses of years and generations gained by ARR across latitude as a continuous variable (shown in Figure 3), we used a general linear mixed effects model implemented with the function glmmPQL in R package nlme (for the Poisson distribution). To test for a latitudinal response of percent increase in years gained due to ARR (which was best fit as a Gaussian distribution), we used the function lme. In all cases, latitude was included as a linear and polynomial term (and retained when significant) to allow curvature in the response variables. In addition, an interaction with taxonomic grouping was included across latitude to allow different responses for each taxon, and this interaction term was removed if it was not significant. We modelled spatial autocorrelation (using corSpher) based on the latitude and longitude of each study, and the random effects of species nested in genus nested in class. This controlled for non-random variation due to spatial structuring that relates to warming exposure and shared phylogenetic history, which can constrain species traits such as generation time.

2.5 | Projections

Our aim was to produce data-informed projections of the time (given estimates of warming rates) that species may have until their thermal safety margins are exceeded, and therefore how much of a temporal buffer acclimation might provide.

A challenge in extracting relevant global surface temperatures across terrestrial, marine and freshwater environments is that there is no one climatology dataset that is presently applicable across realms. For terrestrial habitats we selected microclim (Kearney, Isaac, & Porter, 2014) to provide estimates of current environmental temperatures (in the shade and with solar heating). Microclim represents global estimates of hourly microclimates based on long-term monthly averages, to provide relevant temperature for terrestrial ectotherms where mean environmental temperatures (soil in the shade, used to approximate Tenv_{mean}, Figure 1) and maximum environmental temperatures (rock in full sun, used to approximate Tenv_{max}, Figure 1) are down-scaled from weather stations above the ground (Kearney et al., 2014).

For marine systems we used Bio-oracle (Tyberghein et al., 2011) to provide estimates of mean and maximum temperatures from monthly climatologies in marine systems (<http://www.oracle.ugent.be>): mean (SST_{mean}) and maximum (SST_{max}) sea surface temperature at a spatial resolution of 5 arc minutes thus provided estimates of Tenv_{mean} and Tenv_{max}.

WorldClim (10 arc minute resolution) was selected for freshwater locations (<http://www.worldclim.org/>) where Tenv_{mean} was estimated by BIO10 ("Mean Temperature of Warmest Quarter") and Tenv_{max} by BIO5 ("Max Temperature of Warmest Month"). We expect that small bodies of water will warm in the summer, and that average near-surface air temperature across the summer months is a good estimate of the temperature of freshwater systems (generally) in the summer months. Animals at the surface of freshwater systems (air interface), or in very small bodies of water, might further be exposed to higher temperatures; we estimated this potential as the maximum air temperature (without solar heating). We compared estimates from WorldClim (which represent surface air temperatures) to *in situ* measurements and found that in many cases that *in situ* measures were not available at the relevant frequency or coverage to accurately reflect maximum exposures for freshwater fauna, which ultimately

shape acclimation physiology (i.e., lack of high *in situ* temperatures in Supporting Information Appendix S1, Figure S2). However, maximum temperatures of the warmest months do correspond with the maximum temperatures recorded in lakes (Supporting Information Appendix S1, Figure S2).

To calculate rates of warming for each grid square we used the CMIP5 ENSMIN RCP8.5 anomaly between 1956 and 2005 compared to between 2050 and 2099, provided by the National Oceanic and Atmospheric Administration (NOAA) Climate Change online portal: <http://www.esrl.noaa.gov/psd/ipcc/ocn/>. This was chosen as a worst-case scenario to highlight the value of acclimation, even under extreme warming projections. The analysis was also conducted with a more conservative warming scenario, RCP4.5 (Supporting Information Appendix S1, Figure S3).

To calculate the number of years until thermal safety is lost (i.e., tL, time until loss of thermal safety, Figure 1), we first calculated the thermal safety margin (TSM) as the difference between the current maximum environmental temperature (Tenv_{max}) and tolerance to extreme heat (CT_{max}) at the current mean environmental temperature (Tenv_{mean}).

$$TSM = CT_{max} \text{ at } Tenv_{mean} - Tenv_{max} \quad (1)$$

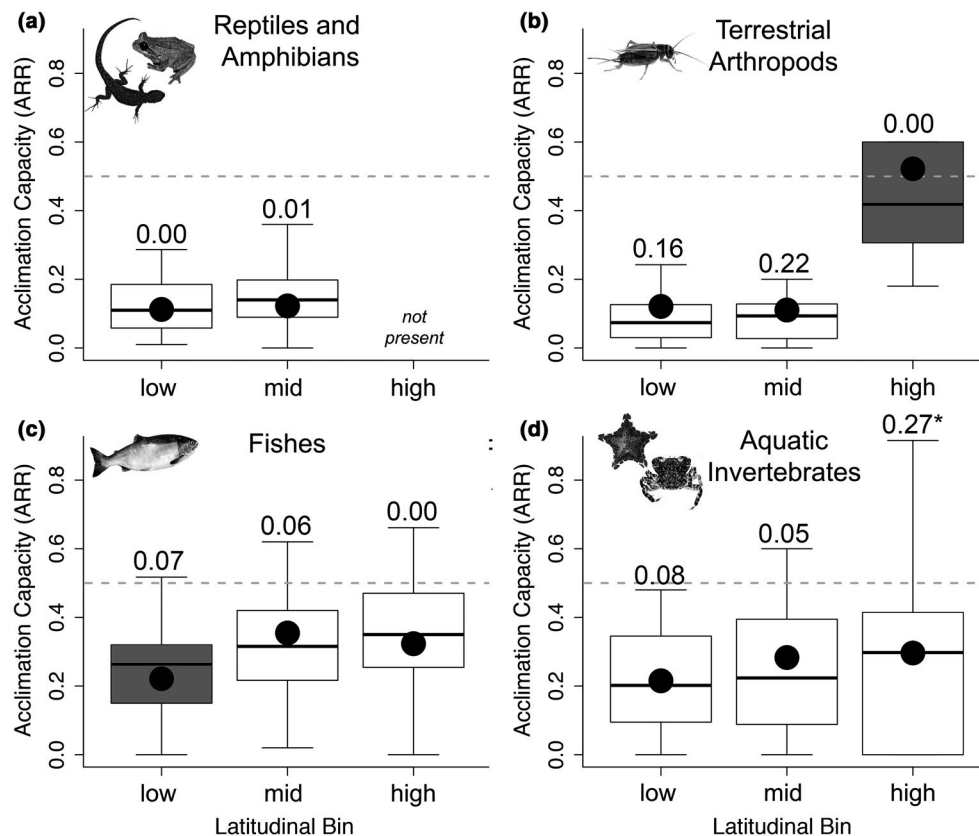


FIGURE 2 Warm acclimation capacity plotted against latitude for key taxa, habitats and regions. Species representing terrestrial and aquatic habitats are separated into three latitudinal bins, low latitude, 0 to 25°, mid latitude, > 25–55°, high latitude, > 55°. Data are shown for: (a) amphibians and reptiles ($n = 97$ species), (b) terrestrial arthropods ($n = 40$), (c) fish ($n = 102$) and (d) aquatic invertebrates ($n = 71$). Filled bars indicate a significant difference between latitudes (Supporting Information Appendix S1 Table S1). The numbers above the bars indicate the proportion of all species in each latitudinal band that have zero acclimation capacity [acclimation response ratio (ARR) = 0]. *indicates that the proportion of species with an ARR of 0 was significantly higher in high-latitude than mid- and low-latitude aquatic invertebrates ($\chi^2 = 12.3$, $p < 0.01$)

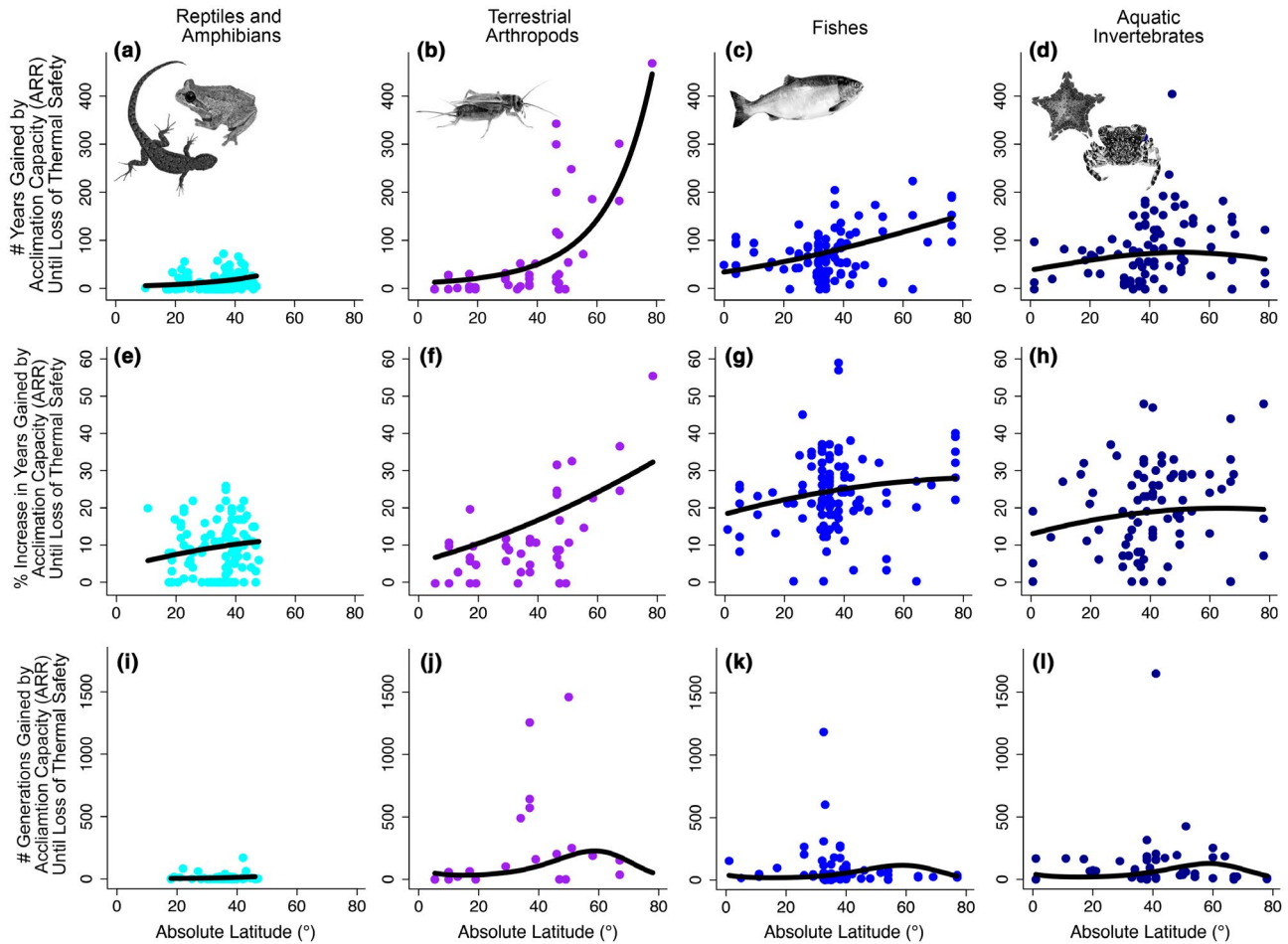


FIGURE 3 Loss of thermal safety across latitude and taxa calculated from the acclimation capacity and the projected rate of warming for the RCP8.5 pathway. (a–d) Number of years until loss of thermal safety provided by acclimation in four groups of ectotherms, T_{Lacc} (Equation 3). (e–h) Percent increase in years gained until loss of thermal safety provided by acclimation calculated as $(T_L/T_L + T_{Lacc}) \times 100\%$ where Equation 2 describes T_L . (i–l) Number of additional generations provided by acclimation, N_g in Equation 4. Black regression lines are predictions from mixed-effects statistical models (Supporting Information Appendix S1, Tables S2–S4). Results for the RCP4.5 pathway are in Supporting Information Appendix S1, Figure S3 [Colour figure can be viewed at wileyonlinelibrary.com]

We divided this value by the predicted rate of environmental warming (ΔT_{env}) (projected as the RCP8.5 or RCP4.5 pathway).

$$tL = \frac{TSM}{\Delta T_{env}} \quad (2)$$

The extra years added by the increase in CT_{max} through acclimation attributable to warm acclimation capacity for a particular time interval was then calculated by multiplying tL by ARR . $tLaccl$ is thus time until loss of the component of thermal safety added by acclimation (in years).

$$tLaccl = tL \times ARR \quad (3)$$

Generation time (GENTime) was then used to calculate the adaptive capacity, that is, the number of extra generations (N_g) that can be provided by warm acclimation capacity for those species where data were available (Figure 3b; 187 records listed in <https://doi.org/10.5285/20010bfb-c6d3-430f-b1f7-d16790ab8359>).

$$N_g = \frac{tLaccl}{GENTime} \quad (4)$$

We further tested for covariance across exposure rate of environmental warming and multiple traits related to taxon-specific sensitivity including physiological tolerance and plasticity, latitudinal range extent and generation time.

We computed an overall vulnerability (Vul) to warming as a function of exposure and vulnerability for each species. We added exposure to warming (ΔT_{env}), vulnerability to warming (TSM), adaptive capacity (acclimation response ratio, ARR), generation time (GENTime) and risk of extinction due to small population size (Runge, Tulloch, Hammill, Possingham, & Fuller, 2014) as latitudinal range extent (LATrange).

$$Vul = \Delta T_{env} + TSM + ARR + GENTime + LATrange \quad (5)$$

Average data for exposure and the vulnerability traits were scaled and centred prior to computing the vulnerability score,

with negative values indicating lower exposure and sensitivity. Thus, a negative value across all inputs indicates a species that on average is less vulnerable, and a positive value indicates the opposite.

3 | RESULTS

High variability is found in ARR across all latitudes (Figure 2), but when we account for variation due to methodology across studies there is a slight but significant decrease in central tendency in tropical fishes (Figure 2c). By including polar species, we further find that ARR is greatest at high latitudes in invertebrates (terrestrial arthropods and various aquatic invertebrate phyla, Figure 2b,d). In contrast to our expectation, we also find high variation in ARR in polar oceans (Figure 2c,d). To illustrate this variability, three of the species with the lowest acclimation capacity are the polar amphipod *Paracerodocus miersii*, the anemone *Urticinopsis antarctica* (ARR = 0) and the sea cucumber *Heterocucumis steineni* (ARR = 0), conforming to the expectation of low acclimation capacity in polar stenotherms. By contrast, some Antarctic marine invertebrates have surprisingly high potential to adjust to warming (Figure 2d), particularly when incubated at acclimation temperatures for long durations of up to 4 months. *Nacella concinna* elevated its CT_{max} from 6.9 to 8.1°C with a 3°C increase in incubation temperature (ARR = 0.4; Morley et al., 2011), *Odontaster validus* increased its CT_{max} from 12.7 to 15.2°C for a 3°C increase in incubation temperature (ARR = 0.4) and *Sterechinus neumayeri* increased its CT_{max} from 11.3 to 14.3°C for a 3°C increase in incubation temperature (ARR = 0.5). Yet despite the potential for some polar marine species to increase their heat tolerance, the mean ARR for the polar region was low, 0.28 ± 0.25 , and the highest proportion of species with no acclimation capacity was in the polar regions (35% of species with ARR = 0).

Our scenarios estimating the time for environmental warming to exceed the thermal tolerance thresholds of species reveal that warm acclimation capacity has the potential to offer between 0 and 1,000 years for evolutionary rescue under the RCP8.5 pathway (and, on average, an additional 40 years longer given the RCP4.5 pathway, Appendix, Supporting Information Figure S3). The time that warm acclimation adds until loss of thermal safety differed amongst vertebrate and invertebrate groups, between habitats on land and water, and across latitudes (Figure 3a–d, Supporting Information Appendix S1, Table S2).

In all groups, tropical species have the least time before loss of thermal safety (Figure 3a–d). Overall, reptiles and amphibians also stand out as having the lowest number of years until loss of thermal safety for the data range available (c. 10 for low and 15 for mid-latitudes, Figure 3a), due to low ARR (0.15 ± 0.1) and small thermal safety margins before acclimation. By contrast, the greatest number of years until loss of thermal safety was projected for the terrestrial arthropods at high latitudes (> 200 years), where high ARR

combined with low rates of warming (Figure 3b). Fishes and marine invertebrates experience intermediate time durations through physiological acclimation before thermal extremes exceed their thermal tolerances, with invertebrates peaking at mid-latitudes and fishes peaking at polar latitudes (c. 90 years, Figure 3c,d). Similar patterns are also observed when the percent increase in years gained by acclimation is calculated (Figure 3e–h; Appendix, Supporting Information Table S3), with an average increase across the different taxonomic groups falling between 10 and 20%.

Converting years until loss of thermal safety gained by acclimation to generation time indicates that physiological plasticity may increase the adaptive potential of aquatic invertebrates relative to fish (overall), based on more rapid generation times of invertebrates (Figure 3i–l). The median number of generations gained in the amphibians and reptiles was fewer than five, while fishes were around 30. By comparison, land (arthropods and aquatic invertebrates, which have faster generation times than vertebrates, gained c. 100 and 60 generations under the RCP8.5 pathway, respectively (the number of generations increases for the RCP4.5 pathway by 30–35%). In all groups, the number of generations achieved through acclimation declines towards the poles, because generation time is longer in cold environments.

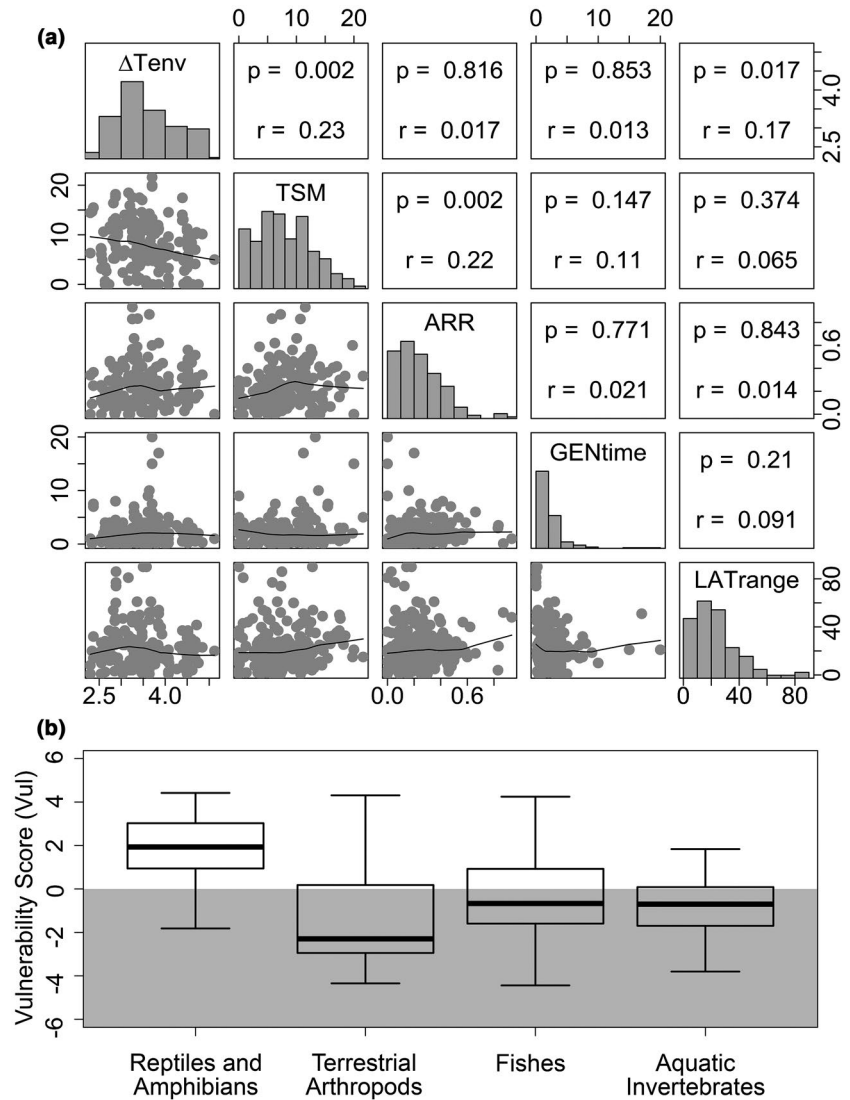
Considering exposure and generation time together identified several species, even in the tropics and at the poles, with greater than expected adaptive potential. For example, while the tropical barnacle *Amphibalanus amphitrite* has a low ARR, it has a rapid reproductive cycle and development time (leading to a fast generation time). Thus, some species from warmer environments (Moss et al., 2016) with faster generation times may gain many generations for evolutionary rescue due to acclimation before thermal safety limits are breached.

When comparing the relationship of exposure to warming and traits related to the sensitivity of each species, TSM, ARR, generation time and latitudinal range extent were not strongly correlated (Figure 4a). Overall, the correlation coefficient (possible range was 0 to 1) was low (typically less than 0.1 with the maximum at 0.23). However, warming rate was significantly related to TSM (negative relationship) and latitudinal range size (hump-shaped relationship). Species with wider TSMs also had slightly higher ARR (Figure 4a). Additive combination of these traits with indices of warming exposure into a vulnerability score reveals that reptiles and amphibians are relatively vulnerable (median of 1.9, $n = 49$ unique species, Figure 4b). Fast generation times of terrestrial arthropods (e.g., fruit flies, *Drosophila* spp.) promotes the potential for evolutionary rescue within the years afforded by acclimation. This group was scored as the least vulnerable of the taxa in our study (median of –2.3, $n = 19$ unique species, Figure 4b).

4 | DISCUSSION

We find patterns of thermal acclimation that largely conform to our predictions, with important exceptions. On land, the seasonality

FIGURE 4 Relationships amongst exposure to ocean warming and traits expected to relate to species-specific sensitivities. (a) Plot of relationships of all possible combinations of ΔT_{env} (Change in environmental temperature projected by the RCP8.5 pathway), thermal safety margin (TSM, Equation 1), acclimation capacity (acclimation response ratio, ARR), generation time (GENTime) and latitudinal range extent (LATrange) produced using the function “pairs” in the raster package. The numbers labelling the y axes are specific to the dataset falling in the respective row or column. The numbers on the upper diagonal are a correlation coefficient, r , and p indicates the level of significance. The black line is the weighted spline fit through the centre of the data. (b) Vulnerability (Vul, Equation 5) was quantified as an additive function of the exposure and sensitivity and plotted for the four taxonomic groupings (50 reptiles and amphibians, 20 terrestrial arthropods, 75 fishes and 45 aquatic invertebrates): negative or positive values indicate scores that lie below (less vulnerable, grey shading) or above (more vulnerable) the central tendency, respectively



hypothesis predicts ARR to be greatest at high latitudes, which was supported by our findings of latitudinal patterns in ARR. This result differs from those of a previous study (Gunderson & Stillman, 2015), which did not detect an increase in ARR in terrestrial ectotherms at high latitudes. This may be because we included species data for latitudes above 55°. Hence, we offer the novel insight that ARR is remarkably high in terrestrial arthropods that also survive the extreme terrestrial polar environment where long days can lead to high temperatures due to solar heating, but which are in contrast to cold night-time temperatures (Clarke & Gaston, 2006). High acclimation rates may allow these species to take advantage of windows of opportunity, such as times of the day and seasons when conditions are warm enough for liquid water to be present (Sinclair, Addo-Bediako, & Chown, 2003), without maintaining high heat tolerance (i.e., CT_{max}) year-round.

Without the polar species Gunderson, Dillon, and Stillman (2017) found that the acclimation capacity of arthropods was low, not greatly reducing the number of predicted future days of the

year that breach thermal safety margins. Gunderson et al. (2017) also found a difference between amphibians and reptiles, which was different to the current study. However, consistent with the current study reptiles gained the least benefit from acclimation capacity.

The vulnerability of terrestrial vertebrates in our dataset (amphibians and reptiles) suggests very limited physiological capacity to cope with increases in extreme heat events (Sunday et al., 2014). There are a number of potential phylogenetic constraints that can explain these differences between taxa. The greater vulnerability of reptiles and amphibians, compared to arthropods, is likely linked to differences in body size (Rohr et al., 2018). It is also possible that heat avoidance behaviours have offset evolution of physiological acclimation responses in ectotherms from land, simply because taking advantage of thermal microhabitats available across landscapes is possible (Gunderson & Stillman, 2015; Sunday et al., 2014). For these species to remain in their current distribution, other mechanisms, such as avoidance of extreme heat in the warmest parts of the

day or year, will be crucial (Gibbon et al., 2000; Sunday et al., 2014). Conservation strategies must therefore facilitate the mechanisms that will be most critical for particular taxa, such as maintaining existence and access to microhabitats (i.e., shade and freshwater pools) to promote the persistence of these fauna in a warmer climate.

Tropical species are predicted to be amongst the most vulnerable because they have narrow thermal safety margins, and small increases in temperatures result in large biological changes (because many biological rates are temperature-dependent, and faster at warmer temperatures). Thus, expectations from global trends of biological rates (Payne & Smith, 2017) and latitudinal differences in thermal sensitivity, the factorial change in biological rates for a 10°C increase in temperature (Q_{10}), after acclimation (Seebacher et al., 2015) implicate tropical faunas as being highly sensitive. Our findings do show some support for high climate change vulnerability in the tropics (across all taxa), although we have limited coverage of species sampled from tropical latitudes. However, we do find that fast generation times in warm-adapted species may provide greater potential for adaptation, compared to assessments where time is used as the unit for comparing species-specific vulnerability. Thus, we recommend projecting biological responses in a measure more relevant to species ontogeny, that is, generations instead of units of “time”.

We further find that longer-duration studies will be critical to quantify acclimation capacity, in particular in polar ecosystems where rate-dependent biological processes are limited by temperature. The pace of acclimation varies across latitude and it may take many months for acclimation to occur in polar marine ectotherms, whereas physiological adjustment can be complete within a matter of days in the tropics (Peck, Morley, Richard, & Clark, 2014). In fact, three of the four polar species that we incubated for longer than 90 days (starfish: *Odontaster validus*, urchin: *Sterechinus neumayeri*, limpet: *Nacella concinna*) returned warm acclimation capacities greater than 0.4. These species are amongst the highest ARR in the marine dataset, which further implicates the key role of experimental duration in climate change studies (Pinto, Schwarzkopf, & Krockenberger, 2016). Thus, more acclimation potential may lie hidden in existing data based on short acclimation durations (median and range of acclimation durations in the dataset) calling for longer experimental duration times (Munday, Warner, Monro, Pandolfi, & Marshall, 2013; Suckling et al., 2015) in assessments of species capacity to adjust.

Heat waves may be fundamental in determining the distribution of individuals living close to their population range limits (Wernberg et al., 2016). Even so, thermal regimes are multidimensional (Waldock, Dornelas, & Bates, 2018) and shifts in extremes may also be accompanied by increasing mean temperatures and higher short-term fluctuation. The various dimensions of temperature regimes have the potential to differentially affect the persistence of species through a combination of physiological processes that have different sensitivities over different time-scales (e.g., Hoefnagel & Verberk, 2015). Combining experimentally derived physiological

responses for different time periods and levels of biological organization is key to formulating accurate predictions for how individual responses will scale to the population and community level (Waldock et al., 2018). For instance, CT_{max} is a good assay for an organism's ability to survive extreme events, and therefore a good measure of resistance mechanisms under extreme heat exposure. However, CT_{max} will not reflect more subtle changes in fitness and energetics as processes that will be influenced by changes in the mean environmental temperature, such as oxygen supply and demand, which can have different temperature sensitivities (Hoefnagel & Verberk, 2015).

Given that an increase in temperature will also lead to increased energetic costs (due to metabolic rate increases) or extra costs associated with adjustment of physiological pathways—acclimation to high temperatures will demand higher energetic requirements. Increased energetic costs may in turn lead to shifts in species interactions (e.g., increased herbivory), or be tempered by species interactions such as reduced capacity to avoid predation, and therefore underpin biodiversity change (Bates, Stuart-Smith, Barrett, & Edgar, 2017). Linking energetic costs of physiological adjustment to populations and communities represents a gap in theoretical ecology (Waldock et al., 2018).

Our analyses demonstrate how physiological acclimation potentials assessed for species at a global scale may interact with generation time, to differentially extend the duration of persistence based on thermal tolerance alone. For example, despite their polar habitat, we find greatest potentials for species persistence in high-latitude terrestrial arthropods (Figure 3a), due to their greater physiological plasticity and relatively short generation times. We further highlight that combining multiple dimensions of exposure and sensitivity to environmental warming, including thermal physiology, reveal that reptiles and amphibians stand out in being both exposed and sensitive, and indeed population declines are severe for this group (Gibbon et al., 2000).

Thus, we challenge the capacity for climate change vulnerability assessments, based on short-term laboratory experiments of thermal tolerance limits alone, to make accurate predictions of future biodiversity patterns. We further suggest that acclimation potential should not be dismissed, but may result in ecological surprises as some species appear to have remarkable plasticity. This may be particularly true in polar habitats where the long duration of the experimental acclimation period prior to assays led to a much higher ARR than originally anticipated. Indeed, there is increasing awareness that adaptation can be rapid, including the evolution of higher thermal limits (e.g., Rezende, Tejedo, & Santos, 2011). Therefore, the degree to which physiological plasticity will increase the chances for evolutionary rescue is an exciting area of research (Bell, 2013). We advocate for the thoughtful execution of experiments and the inclusion of physiology into vulnerability assessments with traits related to different sensitivity components to improve accuracy in our capacity to identify species and taxa that will win and lose as the Earth warms.

ACKNOWLEDGMENTS

A.E.B. is grateful to the Canada Research Chairs program for salary support. S.A.M., L.S.P. and S.H. were funded by Natural Environment Council Funding to British Antarctic Survey.

DATA ACCESSIBILITY

All data are available from: Morley, S. A., Peck, L. S., Sunday, J., Heiser, S. and Bates, A. E. "Acclimation potential of global ectothermic species, collated from literature, 1960 to 2015" (2018) Polar Data Centre, Natural Environment Research Council, Cambridge, UK <https://doi.org/10.5285/20010bfb-c6d3-430f-b1f7-d16790ab8359>

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BIOSKETCH

The collective research of this team has a focus on understanding the mechanisms that determine species physiological tolerance and plasticity. This information is used to model the vulnerability of assemblages, species and populations to environmental variability, projecting future patterns of biodiversity. More detailed profiles can be found on the following individual web pages: <https://www.bas.ac.uk/profile/smor/>, <https://www.bas.ac.uk/profile/lspe/>, <http://www.zoology.ubc.ca/person/sunday>, <https://www.uab.edu/cas/biology/people/current-grad-students/sabrina-heiser>, <http://www.faculty.mun.ca/abates/index.php>

SUPPORTING INFORMATION

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

How to cite this article: Morley SA, Peck LS, Sunday JM, Heiser S, Bates AE. Physiological acclimation and persistence of ectothermic species under extreme heat events. *Global Ecol Biogeogr*. 2019;28:1018–1037. <https://doi.org/10.1111/geb.12911>

APPENDIX: ARR DATA SOURCES

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