For submission to …….

Title :a meta-analysis

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Abstract

Exposure to extreme temperatures can negatively affect the reproduction and longevity of animal species, damaging population growth and increasing extinction risk. Whilst the critical thermal limits of many species have been studied, there has been no large-scale study on how temperature affects reproduction. Here we synthesise X effect sizes from X studies which investigate effects of temperature on reproduction and longevity.

We found that ….

In conclusion, our study indicates that, on a global scale, reproductive success in species is notably more susceptible to thermal variations than longevity. As reproductive output is arguably the most important measure of population fitness, it is important that policies aimed at mitigating species loss in response to climate-induced temperature fluctuations consider adopting more conservative thermal thresholds where reproductive success is impaired, rather than focusing on survival limits at which species perish.

Keywords: thermal fertility, reproduction, meta-analysis,

Introduction

Climate change is driving unprecedented alterations to the environment on a global scale; we are currently experiencing the most accelerated change in temperature in the last 2,000 years (IPCC, 2023), and extreme weather events such as heatwaves are increasing in severity and frequency (Buckley and Huey, 2016). High temperatures can negatively affect the reproduction, survival and longevity of species, damaging population growth and increasing extinction risk.

Measuring survival of species under different temperatures is a common method to assess their thermal tolerance (e.g. (Bennett et al., 2021, Clarke, 2017)). However, it's equally crucial to consider sub-lethal consequences of temperature stress, with reproductive impairment being a key concern. High temperatures can disrupt both the ability of individuals to produce any viable eggs or sperm (fertility), and the number of eggs or offspring produced by fertile individuals (fecundity) (Walsh et al., 2019). At extreme temperatures this reproductive impairment is widespread across many taxa, including plants (Sage et al., 2015), corals (Paxton et al., 2016) , insects (David et al., 2005), fish (Breckels and Neff, 2013), livestock (De Rensis et al., 2017, Peña et al., 2019), and humans (Hajdu and Hajdu, 2022, Hoang-Thi et al., 2022).

Compromised reproduction in species has significant ecological consequences because it is arguably the ultimate determinant of population fitness. Even minor and persistent reductions in reproductive output can substantially lower population growth rates, hindering population health and elevating the risk of extinction (Savage, 2004).. Moreover, fertility loss affecting livestock and agricultural species can have huge economic repercussions (De Rensis et al., 2017, Peña et al., 2019).

Recent evidence suggests that reproductive impairment often occurs at less extreme temperatures than survival limits, emphasising the potential for warming to more severely impact population fitness through reduced reproductive capacity (Parratt et al., 2021). If this is a general trend, relying solely on survival limits to estimate species vulnerability to temperature extremes may overly underestimate the real risks.

We performed a systematic-review with meta-analysis on data from peer-reviewed journal publications to quantify, on a global-scale, estimates of the effect of temperature on reproduction. In total we analysed X effect sizes from X studies which reported reproduction and/or longevity in response to at least two temperature treatments. In addition, our novel analysis presents a comparison of thermal fertility and longevity limits.

Methods

**Data collection**

Literature search

We performed online literature searches as part of a broader project investigating how animal reproduction is affected by five abiotic factors affected by climate change: temperature, radiation, humidity, pH, and salinity (Doughterty et al 2023, in press). All searches were performed using the ISI Web of Science Core Collection (http://www.webofknowledge.com). Initial searches were performed between December 2020 and February 2021. Final searches were performed on the 24th August 2021. We considered literature from all available years. The search string specific to reproduction, the data used in this meta-analysis, was (AB=( fertilit\* OR infertilit\* OR fecund\* OR clutch OR sperm\* OR mating OR gamet\* ) OR TI=( fertilit\* OR infertilit\* OR fecund\* OR clutch OR sperm\* OR mating OR gamet\* )) AND (AB=( temperature OR thermal ) OR TI=( temperature OR thermal ) ) NOT (AB=( soil\* OR wom\*n OR cryo\* OR engineer\* OR polymer\* OR graphen\*) OR TI=( soil\* OR OR wom\*n OR cryo\* OR engineer\* OR polymer\* OR graphen\*)). The full search strings used for the broader project are presented in (Doughterty et al 2023, in press). The literature search was based on the procedure of PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) (Supplementary Fig. X).

Selection criteria

The set of studies selected for this meta-analysis are subsetted from the

Data extraction

For each study we extracted means, the number of replications, the number of individuals per replication and indicators of precision i.e. standard deviation or standard errors for a measure of reproduction at each temperature treatment. Where possible, data on longevity and/or survival was also extracted for these temperature treatments.. In cases where data was only presented as figures, the online tool WebPlotDigitizer v4 (Rohatgi 2019) to was used to extract raw data from scatter plots, and means and standard

deviations from bar plots.

Also mention that SE was converted to SD for each treatment

**Data analysis**

Effect size calculation

The standardised mean difference (SMD) (Hedges et al 1999) was calculated to measure the effect of temperature on reproduction and longevity. Usually there were more than two temperature treatments per study so SMD was calculated in a pairwise fashion between a reference treatment temperature, chosen to be the treatment closest to the rearing temperature of the study individuals. In the absence of a reported rearing temperature, the reference temperature was chosen to be the treatment temperature closest to 25℃, as 80% of the reported rearing temperatures were this value. Thus, there were often multiple effect sizes for each study due to multiple treatments or multiple traits being reported from the same study e.g. studies reporting both reproduction and longevity for multiple treatment temperatures. The potential non-independence of effect sizes occurring from the same study or sample of animals is discussed in the statistical analysis section. SMDs were calculated as Cohen’s d coefficients using the following formula.

(1)

(2)

Where and are the mean measures of a trait for individuals from the reference temperature and treatment temperatures respectively. are the pooled standard deviations whereby more weight is given to groups of individuals with a larger sample size. are the sample sizes and the standard deviations of the trait in individuals from the reference and treatment experiments respectively.

Effect size direction?

Phylogenetic trees

Phylogenetic history was incorporated in models to account for the potential non-independence of

effect sizes due to shared evolutionary history (Hadfield & Nakagawa 2010; Koricheva et al. 2013). As the number of species included in our sample was relatively large and spanned a wide range of phyla, there did not exist a single published phylogeny that included all species. Therefore, a bespoke phylogenetic tree was constructed using the Open Tree of Life (OTL) database (Hinchliff et al. 2015) and the rotl R package (Michonneau et al. 2016). Given the absence of accurate branch length data for these trees, all branch lengths were first set to one and then made ultrametric using Grafen’s method (Grafen 1989), using the R package ape v5.3 (Paradis et al. 2004). In cases

where the OTL database resulted in a polytomy, we manually searched for published phylogenies that could resolve them. The final ultrametric tree for the full dataset can be seen in Figure X.

Statistical analysis

All statistical analyses were performed using R v4.3.1 (R development Core Team 2019). Meta-analyses were performed using the package Metafor v2.1 (Viechtbauer 2010). For our preliminary analysis we separated our effect sizes by trait. In other words, we had three separate effect size datasets, one for each of reproduction, longevity and survival. We then performed a separate univariate meta-analysis for each dataset in order to quantify the mean effect sizes of temperature on each trait. Here, we explored various multilevel random-effects model with all combinations of study, species, observation ID and phylogeny as random factors (Nakagawa & Santos 2012). Phylogeny was incorporated into the model using a variance–covariance matrix, assuming that

traits evolve via Brownian motion.. The mean effect size was considered to be significantly different

from zero if the 95% confidence intervals did not overlap zero. The best fitting random-effects model, according to AIC, was selected as our base-level model for all following analyses.

Moderators

For each effect size there was additional recorded information relating to several potential moderators. The reference temperature used in the effect size calculation was recorded as well as three highly correlated variables related to the treatment namely, treattemp; the absolute treatment temperature, diff; the difference between the treatment and ctemp; a standardised

In addition, various taxonomic information was recorded including sex, species phylum, habitat type. For a full list of recorded information see Dougherty et al 2023, in press

Sensitivity analysis

We conducted sensitivity analyses in two ways. First, we removed effect sizes from our dataset which were most extreme in magnitude i.e. lying below/above the 2.5th/97.5th percentiles of effect size range. In another form of sensitivity analysis we used Geary’s test (Geary, 1930) to determine which effect sizes to remove. Specifically, effect sizes were deemed reliable and accurate if their standardised mean was greater than 3. Effect sizes that did not meet this threshold were removed. In both cases, we ran all our analyses again without these effect sizes to test whether their absence affected the results.

Publication bias

We examined the potential presence of publication bias by conducting a meta-regression in which we treated the study year as a fixed factor. This analysis helped us evaluate whether studies published earlier tend to report larger effect sizes compared to those published later. Such a pattern could suggest a bias against publishing studies with smaller effects, especially in emerging research areas (Koricheva et al. 2013).

Results

Conclusions

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