

Reproduction is more sensitive to warming than adult lifespan across invertebrates

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Abstract

Studies estimating the effect of temperature on wild animal populations typically focus on survival as a proxy for population health. However, high and low temperatures can also negatively influence animal reproduction, and recent work suggests that the thermal sensitivity of reproduction is more important for population persistence than the thermal sensitivity of survival in some species groups. If this is the case, studies focusing on survival may be underestimating the impacts of warming on population persistence. However, no study has yet compared the thermal sensitivity of reproduction and survival of the same species on a large taxonomic scale. We here take advantage of a systematic database of studies comparing the effect of temperature on the reproductive output (fecundity) and survival/lifespan of adults of 306 ectothermic invertebrate species. We used meta-analysis to quantify the thermal sensitivity of all three life history traits in relation to temperature conditions assumed to be optimal for population growth rate for each species ('reference temperatures'). We found that reproductive output and adult survival were maximised close to the reference temperatures, whereas adult lifespan was maximised 12 to 18°C below reference temperatures. All three life-history traits were negatively affected by warming, but a multivariate meta-analysis showed that reproductive output declined more than twice as steeply with warming than adult lifespan. We suggest that a reduction in reproductive capacity may be a key driver of wild population declines due to warming, and that studies focusing on survival are underestimating the impacts of warming on population persistence.

Introduction

Earth is currently experiencing the most rapid climate change seen in over 2,000 years, leading to higher global temperatures and more frequent and severe heat waves (Buckley & Huey 2016; IPCC 2023). These changes are already having significant effects on species distributions and phenology (Lawlor *et al.* 2024; Parmesan 2006; Sergio *et al.* 2018), leading to widespread local extinctions (Duffy *et al.* 2022; Román-Palacios & Wiens 2020). These shifts occur because species are limited in the temperature range they can tolerate; exposure to temperatures beyond this tolerable range causes the breakdown of metabolic function, ultimately leading to death (Bennett *et al.* 2021). Ectotherms are particularly vulnerable to temperature change because their body temperatures match that of the external environment (Angilletta *et al.* 2002). Temperature stress can also have important non-lethal effects on behaviour and life history. For example, reproductive output- the number of eggs or offspring produced after mating- typically peaks around 10-20°C in aquatic ectotherms, and 20-30°C in terrestrial ectotherms (Buckley *et al.* 2021; Pörtner *et al.* 2001; Shine 2005). Reproductive output depends on female resource acquisition, the production of viable eggs, and the donation of viable sperm by males (Pincheira-Donoso & Hunt 2017). In ectotherms, extreme low temperatures limit activity levels, making females unable to accrue resources to invest into reproduction (e.g. Pörtner *et al.* 2001; Shine 2005), and extreme high temperatures impair enzyme activity and the function of key metabolic processes (Fields 2001). Thus, at extreme high or low temperatures, individuals may become infertile, losing the ability to produce viable gametes (Berger *et al.* 2008; David *et al.* 2005; Snook *et al.* 2026; Walsh *et al.* 2019).

Estimates of the vulnerability of animal populations to future warming typically focus on the upper temperature that a species can survive (referred to as critical/lethal thermal limits) (Bennett *et al.* 2021; Kellermann *et al.* 2012). Yet these forecasts might need to also consider temperature effects on reproduction, for two reasons. First, the temperature range over which

the reproductive cycle can be completed is often narrower than the temperature range over which adults can survive (Buckley *et al.* 2021; Clarke 2014; Ørsted *et al.* 2022), meaning that reproductive impairment (fertility limits) often occurs at non-lethal temperatures (Walsh *et al.* 2019). For example, the temperature that causes male infertility is significantly lower than the lethal temperature for 19 of 43 fruit fly species tested, with an average difference of 1.15°C (Parratt *et al.* 2021). Second, reproduction is a key determinant of population growth rate (Reynolds 2003; Savage *et al.* 2004). Large populations that have a high growth rate are less vulnerable to extinction, because they are less sensitive to demographic stochasticity, and can recover more quickly from perturbation (Reynolds 2003). For populations at equilibrium, any reduction in reproductive output has the potential to increase the extinction risk, unless other demographic parameters (e.g. generation time) change to accommodate it (Hutchings *et al.* 2012; Reynolds 2003). Indeed, for many species, selection on reproductive output appears to be stronger than selection for adult survival (Siepielski *et al.* 2010). Moreover, while lethal temperatures are an important determinant of species distributions (Bennett *et al.* 2021; Rezende *et al.* 2020; Verberk *et al.* 2023), recent work shows that temperatures that render males infertile in laboratory conditions better match the observed natural species range than lethal temperatures (Parratt *et al.* 2021; van Heerwaarden & Sgrò 2021) and relate more strongly to extinction risk under laboratory conditions (van Heerwaarden & Sgrò 2021).

The thermal sensitivity of reproduction means that populations exposed to extreme temperatures could suffer a significant reduction in population viability without any observable reduction in survival. A key outstanding question then is the extent to which animal reproduction is more thermally sensitivity than survival. While this question has been tested in isolated taxa (van Heerwaarden & Sgrò 2021; Parratt *et al.* 2021; Parrett *et al.* 2024; Weaving *et al.* 2024), it has not yet been tested on a large scale. This is because, while there are published estimates of lethal thermal limits for more than a thousand animal species (Bennett *et al.* 2018), fewer studies have

used short-term temperature stress to assess fertility limits. Instead, studies often examine how reproductive output is affected by long-term temperature changes, exposing organisms throughout their entire lives (Dougherty *et al.* 2024). In such cases, changes in reproductive output better reflect changes in growth, resource acquisition, and resource allocation over a longer period, rather than the loss of key somatic or reproductive functions. Further, studies testing long-term temperature exposure (more than a few days) typically record lifespan (the average time until death) rather than survival (the number of individuals alive after some defined point). Like reproduction, survival and lifespan are reduced at high temperatures, either because key metabolic processes are impaired in adults, or because resource acquisition was impaired during development (Burraco *et al.* 2020). However, a slowing of metabolic rate has the effect of increasing lifespan and survival at lower temperatures, at the cost of reduced growth (Burraco *et al.* 2020; Stark *et al.* 2018). Ectotherm survival and lifespan are therefore expected to peak at a lower temperature than reproductive output (Keil *et al.* 2015; Pawar *et al.* 2024).

Despite the clear prediction that differences in the shape of the thermal performance curve for each life-history trait will lead to differing sensitivity at high and low temperatures, differences in the thermal sensitivity of reproduction, adult survival and adult lifespan have not been tested on a taxonomic scale. Further, quantifying the extent to which these traits are correlated in response to temperature, is critical for understanding how species will respond to future climate change. If responses are highly correlated, then measuring one allows predictions about the others, whereas a weak correlation requires estimating the temperature sensitivity of all traits separately. To test this, we need to compare the thermal sensitivity of all three life history traits within the same species. We carried out a meta-analysis of studies, focusing on ectothermic invertebrates, which report temperature effects on reproduction and survival or lifespan of sexually mature adults. Using this dataset, we answer three main questions. First, how does temperature influence the three life history traits in ectothermic invertebrates? Second, is reproduction more strongly

reduced than either adult survival or adult lifespan at extreme temperatures? Third, do the three life history traits show correlated responses to temperature across species?

Methods

Throughout we follow the extension to the PRISMA-EcoEvo reporting guidelines for ecology and evolutionary biology (O'Dea *et al.* 2021; see the Supplementary Material for a full reporting checklist).

Literature search and inclusion criteria

We focused our search on the database of studies reporting a link between temperature and animal reproduction produced by Dougherty *et al.* (2024; see the paper for full details on the systematic search methods used). The database contains 1,654 studies, of which 781 also recorded the effect of temperature on adult lifespan or survival. Each of these 781 studies were downloaded and read, and assessed against the study inclusion criteria listed below. Study screening and data extraction was performed by 27 co-authors (in order of paper number: FF, LRD, AC, BJC, PS, CS, MG, AB, JR, SL, ANDN, MS, GI, NP, HW, RRS, SG, CF, MK, ZVZ, AM, JE, EC, BCD, MR, IL, SAR), with data reporting issues checked by LRD and FF).

To be considered for inclusion in the meta-analysis, a study had to a) be a peer-reviewed scientific article presenting original data, b) focus on non-human animals, c) expose animals to two or more experimental treatments that differed in mean temperature, d) record some measure of reproduction AND adult lifespan or survival at more than one experimental temperature, and e) provide information (means, standard deviations/standard errors and sample sizes) so that a relevant effect size could be calculated. Additional study inclusion criteria are also presented in the supplementary methods.

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129 We considered three response traits: reproductive output, adult lifespan, and adult survival. For
130 reproductive output, we considered two metrics- fecundity (the number of fertilised eggs or
131 offspring produced by females after mating) and fertility (the proportion of females that
132 produced any fertilised eggs or offspring after mating). For sexually reproducing species, these
133 are shared fitness traits with both a male and a female component. We did not consider other
134 indirect reproductive traits (e.g. reproductive timing, mating behaviour, parental behaviour) or
135 traits that are restricted to one sex (e.g. gamete or gonad traits, male insemination success or
136 competitive fertilisation success). However, we considered any combination of male and female
137 temperature exposure, including sex-specific exposure and exposure of both sexes
138 simultaneously. We included both sexual (including hermaphroditic) and asexual
139 (parthenogenetic) reproduction, though these were rare.

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141 Adult lifespan is the time from adult eclosion (or some other time point in adulthood defined by
142 the study) until death. Adult survival is the proportion of sexually mature adults surviving after
143 some fixed time. We only included studies that recorded a measure of reproduction *and* adult
144 lifespan or survival at more than one experimental temperature. Importantly, studies did not
145 have to record reproduction and lifespan of the same individuals, though this was often the case,
146 and we accounted for this in the statistical analysis. When adult lifespan was presented for males
147 and females separately, we preferentially used data from females as they were tested most. In a
148 small number of studies, males and females were not measured separately; here we used the adult
149 lifespan data for both sexes combined. Most studies kept males and females together for the
150 duration of the experiment, therefore it is reasonable to assume that adult lifespan estimates are
151 for mated individuals. We did not include consider temperature effects on juvenile mortality,
152 because our focus throughout is the life history of those individuals that reach sexual maturity.

This ensures that we are comparing like with like: an individual that dies before reaching sexual maturity has no opportunity to reproduce.

Study screening and data extraction

We screened 781 studies in total. For each relevant temperature treatment and trait (reproduction or adult lifespan), we extracted means, sample sizes, and a measure of variance (standard deviation or standard error) from text, tables or figures (data extracted from figures using WebPlotDigitizer v4; Rohatgi 2019). We were able to extract data from 339 studies, of which 315 contributed data for reproduction and adult lifespan, and 27 studies contributed data for reproduction and survival (See Data sources). For a summary of the study screening process, including common reasons for excluding studies from the analysis, see **Figure S1**.

For each temperature treatment, we extracted additional information relating to two potential moderators. First, we recorded which life stage was exposed to the different test temperatures. Exposure to temperature stress during early development often leads to a larger life-history impact than adult exposure (e.g. McDermott Long *et al.* 2017; Sales *et al.* 2021). While early-life exposure may increase the potential for developmental plasticity or acclimation that could mitigate stress and reduce life-history changes, this effect appears to be minimal (Pottier *et al.* 2022; Weaving *et al.* 2022). However, in our dataset few studies exposed individuals only as juveniles. Therefore, we sorted effect sizes into two categories: those in which only sexually mature adults were exposed (after maturity category), or those in which individuals spent at least some time in the temperature treatments before they were sexually mature (before-and-after maturity category). If animals are more sensitive to temperature stress during development, we expected higher temperature sensitivity in the before-and-after maturity category compared to the after-maturity category. In contrast, if acclimation mitigates the effect of temperature stress,

we expected lower temperature sensitivity in the before-and-after maturity category compared to the after-maturity category.

The high prevalence of before-and-after maturity studies meant that the exact exposure duration was not controlled- it depends on how long each individual survives. We therefore could not quantify the effect of exposure duration in the analysis or restrict our analysis to paired reproduction and lifespan data that were assessed for the same duration. Instead, we classed treatments as 'long-term' when individuals were exposed to experimental temperatures for more than five days, and 'short-term' when exposed for five days or less, with almost 90% of effect sizes in the 'long-term' category (see results). While experimental temperatures for long-term exposures were relatively symmetrical, short-term exposures tended to use warmer experimental temperatures (**Figure S2**).

Second, we recorded which sex exposed was exposed to the different experimental temperatures, (reproduction dataset only). Previous work suggests that male reproduction may be more sensitive to extreme temperatures than that of females in invertebrates (e.g. David *et al.* 2005; Iossa 2019; Sales *et al.* 2018). However, very few studies in the dataset exposed males and females to experimental temperatures separately, and only 6 effect sizes came from a treatment in which only males were exposed. Therefore, we sorted reproduction effect sizes into two categories: those in which only females were exposed to experimental temperatures (females only category), or those in which both males and females were exposed to experimental temperatures (males and females category). We predicted that reproduction will be more sensitive to temperature when both males and females are exposed, because the combined effect of heat stress on both males and females will result in an additive reduction in reproductive fitness (e.g. Baur *et al.* 2022; Spinks *et al.* 2021).

Effect size calculations

Most studies were not designed to estimate thermal performance curves, and so tested a relatively narrow temperature range. We therefore did not directly compare the thermal performance curves of each species. Instead, we used a contrast-based approach, calculating the standardised mean difference (Hedges' g) in reproduction or adult lifespan between paired temperature treatments (**Figure 1A**). This approach is versatile, allowing us to include studies testing a broad temperature range alongside those which only test a few temperature treatments. Using this approach, X temperature treatments become $X-1$ effect sizes (**Figure 1A**). We calculated effect sizes in a pairwise fashion in relation to a single 'reference' treatment. We did this because both reproduction and adult lifespan are expected to show a univariate response curve with temperature, each with a single maximum (T_{OPT} ; **Figure 1A**). Assigning the reference treatment to this optimum will result in all contrasts producing negative effect sizes (**Figure 1B**) and allows us to compare the magnitude of performance change above and below the reference temperature. We assigned the reference treatment as the treatment closest to the rearing temperature used in each study, assuming that rearing conditions are often chosen because they maximise the population growth rate (or at least do not negatively affect it) and so should typically be close to T_{OPT} for this trait. When the rearing temperature was not provided, the reference treatment was assigned as the treatment with a temperature closest to 25°C. Here, 25°C was selected because the average rearing temperature of the 255 studies that did report a rearing temperature was $24.8 \pm 2.8^\circ\text{C}$. All remaining treatments, with temperatures above or below the reference treatment, were classed as 'experimental' treatments. Most studies reported reproduction or adult lifespan for more than two experimental treatments, resulting in two or more effect sizes per study. We controlled for the non-independence of effect sizes from the same study in all statistical models (see below).

Here, Hedges' g reflects the standardised change in a life history trait in the experimental treatment relative to the reference treatment. A negative Hedges' g value means that reproduction or adult lifespan decreases in the experimental treatment compared to the reference treatment. We expected reproduction to follow a unimodal relationship with temperature, with the reference temperature being close to optimal reproductive output. Therefore, we predicted that reproduction should decrease on either side of this optimum, resulting in an average negative mean effect. In contrast, adult lifespan shows a right-skewed unimodal relationship with temperature in ectotherms (Keil *et al.* 2015), with a lower T_{OPT} than for population growth rate. This mismatch between T_{OPT} for population growth rate (assumed to be close to the reference temperature) and adult lifespan means we predicted a positive mean effect size for adult lifespan below the reference temperature, and a negative mean effect size above it.

Univariate meta-analysis

All statistical analyses were performed using R v4.3.1 (R Development Core Team 2023) and the *metafor* v2.1 package (Viechtbauer 2010). We performed univariate meta-analyses separately for the reproduction and adult lifespan datasets. For each dataset, we fitted a multilevel meta-regression model with study and observation as random effects and deviation from the reference temperature as a (quadratic) fixed effect (Nakagawa & Santos 2012). Study was included to account for the fact that studies often included multiple effect sizes. We used an observation-level random effect (each row of data assigned a unique ID) to correctly partition residual variance. Given that multiple contrasts within a study might share a common reference treatment, we also included a sampling variance-covariance (VCV) matrix, assuming that effect sizes sharing a common reference were correlated by $r = 0.5$ (Noble *et al.* 2017). We also tested whether variation in effect sizes was explained by phylogenetic history (supplementary methods), but this moderator did not improve model fit for any life history trait, and so was not included in any models. We used the difference (in °C) between the experimental and reference temperature

as a fixed effect rather than the absolute experimental temperature. This is to account for the fact that species are adapted to different thermal environments and have different thermal optima. Therefore, an effect of temperature in this analysis refers to ‘normalised’ deviation from the (assumed) thermal optimum for each species, rather than absolute temperature. We fitted temperature difference as a quadratic effect, because we expected all three life history traits to show a typical inverted U-shape thermal response curve. We fitted a simple quadratic curve, rather than a more complex asymmetric curve (e.g. Kontopoulos *et al.* 2024) because we expect the averaging of many asymmetric curves arising from our inclusion of many different species and studies to result in a symmetric shape.

We quantified effect size heterogeneity in two ways. First, we calculated total I^2 as the proportion of effect size heterogeneity after accounting for total sampling variance (Higgins *et al.* 2003; Nakagawa & Santos 2012). We also estimated an I^2 for each random effect level (Nakagawa & Santos 2012) using the *orchaRd* v2.0 package (Nakagawa *et al.* 2023). I^2 itself does not provide a direct measure of heterogeneity, so we also visualised prediction intervals, which quantify the range of expected effect sizes expected from future studies (Borenstein *et al.* 2017).

Finally, we tested whether the relationship between effect size and temperature difference depended on two categorical moderators: life stage exposed and sex exposed. We did this by running the multilevel meta-regression model described above, but with the addition of a single moderator as a fixed factor (resulting in two meta-regression models per dataset). We then tested for an interaction between temperature difference and the included fixed factor. Unfortunately, we could not explore other moderator variables (such as habitat type, reproductive mode, fertilisation mode, or taxonomic group) due to unbalanced sample sizes. For all meta-regression models, we estimated marginal R^2 using the *orchaRd* v2.0 R package (Nakagawa *et al.* 2023).

Multivariate meta-analysis

We next used a multivariate approach to directly compare reproduction and adult lifespan responses to temperature for each study, and to estimate the within and between-study correlation between life-history responses. We did this for the subset of studies where both reproduction and adult lifespan data were measured using the same sample of individuals (N = 200 studies, 187 species). This dataset consisted of 792 trials, whereby a trial is defined as a temperature contrast consisting of the same experimental treatment, tested on the same sample of individuals), with each trial having one reproduction effect size and one adult lifespan effect size. This allows us to identify correlations at the observation level (same species, population, and experiment) rather than just at the species level (same species but different experiments). It also controls for differences in experimental methodology between the reproduction and adult lifespan datasets: here, each matched effect size has the same timing and duration of temperature exposure. Because we expect that lifespan is affected differently when exposed to cold vs warm temperatures, the between-study correlation estimate is expected to differ based on which side of the contrast from the reference temperature. We therefore split the dataset into a ‘warm’ subset (experimental treatments above the reference temperature, N = 174 studies, 167 species and 395 trials) and a ‘cool’ subset (experimental treatments below the reference temperature, N = 163 studies, 162 species and 397 trials). For each subset we then ran a multivariate multilevel meta-regression model, including reproduction and adult lifespan effect sizes from each study. We did not compare reproduction and adult survival using a multivariate model due to the small sample size for adult survival.

For each multivariate model, we accounted for the non-independence of effect sizes from the same trial or that share the same reference treatment using a VCV matrix with two levels, assuming that responses from the same trial and/or reference treatment were correlated by 0.5 (Noble *et al.* 2017). This matrix was not positive-definite, so it was coerced to be so using the

nearPD function in the *Matrix* v. 3.11 package. Each model included study and trial ID as random effects. Trial ID was a grouping variable used to identify the reproduction and adult lifespan effect sizes that were generated from the same experimental treatment, with each ID code relating to two effect sizes (one reproduction and one lifespan) from the same temperature contrast. Here, the random effect of trial ID is the equivalent to the observation-level random effect in the univariate models, except that each trial has both a reproduction and lifespan observation. To estimate the correlation between effect sizes at the between-study and within-study level we included ‘response trait’ as a random slope and estimated the correlation between the two traits assuming an unstructured VCV matrix (i.e., ‘UN’ in *metafor*). We included ‘response trait’ (reproduction or adult lifespan) as a fixed effect, which allowed us to estimate the mean effect size for each trait. We were also able to control for temperature effects by including an interaction between each response trait and temperature difference, with the latter included as a linear effect in the warm data subset model, and a quadratic effect in the cool data subset model, based on the shape of the data distribution above and below the reference temperature seen in Figure 3. Including temperature difference as a fixed effect in the warm data subset model also allowed us to test for a difference in the slope between the two life history traits.

Sensitivity tests

We ran sensitivity tests to determine the robustness of our results in relation to exposure duration (removing effect sizes for exposure less than 24 hours), the choice of reference temperature (removing effect sizes for which the rearing temperature was not reported), the presence of outliers (removing effect sizes with a value below -10 and above 10), and the effect of publication bias. We also repeated the univariate and multivariate models using a cluster-robust variance estimation approach to account for statistical dependence between effect sizes (Yang *et al.* 2024); this approach does not require that the correlation between dependent effect sizes in the VCV matrix be specified *a priori*. See supplementary material for details.

Results

The full dataset

Overall, we obtained 2,849 effect sizes from 339 studies, and 306 species. We obtained data from five animal phyla: insects (77% of species), arachnids (15%), crustaceans (15%), rotifers (1.6%), and annelids (0.3%) (**Figure 2**). All species are ectothermic invertebrates and mobile as adults. Most species are terrestrial (89.9%), reproduce sexually (86.7%), and are internal fertilisers (99.6%). Studies tested an average of 4.3 ± 1.7 temperature treatments, with most between 15°C and 35°C (**Figure S2**). The average minimum experimental temperature was $17.2 \pm 5.7^\circ\text{C}$, and the average maximum experimental temperature was $31.4 \pm 5.2^\circ\text{C}$. The average temperature range across all studies was $14.2 \pm 5.9^\circ\text{C}$. Almost all were laboratory experiments (98%), in which individuals were exposed to temperature treatments for more than 5 days (89.9%). Most experiments exposed individuals both as juveniles and as adults (53.2%), or as adults only (38.9%). The remaining experiments exposed only gametes or embryos (1.2%), or juveniles (6.7%).

Thermal sensitivity of reproduction

In total, 1,387 effect sizes (across 339 studies and 306 species) measured reproduction, with 99.3% estimating fecundity. Most reproduction effect sizes were generated when both sexes were exposed to experimental temperatures simultaneously (62.8%), followed by female-only exposure (36.6%). Very few effect sizes came from a treatment in which only males were exposed (six effect sizes, two studies). For most reproduction effect sizes (90.4%), subjects were exposed to experimental temperatures for more than five days (and typically for their entire adult life).

A multilevel meta-analysis showed that reproductive output declines above and below the reference temperature (negative quadratic relationship between reproductive output and the deviation from the reference temperature: estimate = -0.011, 95% CI = -0.013 to -0.009, $t = -11.85$, $df = 1,384$, $p < 0.001$, $k = 1,387$; **Table S1**), with reproductive output peaking at 2.5°C below the reference temperature on average (**Figure 3A**). This effect remained after removing outliers, short-term exposure treatments, or studies where the rearing temperature was not known (Supplementary results). The quadratic effect of temperature difference explained 9.1% of variance in effect sizes (marginal R^2). Overall effect size heterogeneity was very high (I^2 [total] = 99.1%), which is typical for meta-analyses with broad taxonomic coverage such as this (Senior *et al.* 2016). Partitioning this variance showed that 58.9% is attributable to between-study differences, and the remaining 40.2% to residual (unexplained) variation.

The reproduction of individuals that were exposed to experimental temperatures before and after sexual maturity was more sensitive to temperature increases than those treated only after sexual maturity (interaction between temperature difference and life stage exposed; $t = -2.63$, $df = 1,364$, $p = 0.009$, $k = 1,370$; **Figure 3B**; **Table S5**), even after removing outliers (Supplementary results). The quadratic effect of temperature difference did not depend on whether only females were exposed or both males and females being exposed simultaneously (interaction between temperature difference and sex exposed; $t = -1.43$, $df = 1,372$, $P = 0.15$, $k = 1,378$; **Figure 3C**; **Table S8**); including after removing outliers (Supplementary results).

Thermal sensitivity of adult survival

We found only 27 studies which measured the temperature sensitivity of both reproduction and adult survival on the same species, resulting in 85 effect sizes. Most (95.3%) measured female survival, with only three effects sizes for male survival and one effect size not split by sex. For

most adult survival effect sizes (64.7%), subjects were exposed for more than five days (and typically for their entire adult life). The dataset included two extreme negative outliers of very high influence which we removed before the analysis.

A multilevel meta-analysis showed that adult survival declines above and below the reference temperature (negative quadratic relationship between adult survival and the deviation from the reference temperature: estimate = -0.008, 95% CI = -0.012 to -0.005, $t = -4.64$, $df = 1,80$, $p < 0.001$, $k = 85$; **Table S11**), peaking at 2.37°C below the reference temperature on average (**Figure 3D**). However, there were no experimental treatments greater than 10°C below the reference temperature (**Figure 3D**), so our ability to estimate the effect of cooling on adult survival is limited. This significant quadratic effect remained after removing short-term exposure treatments or studies where the rearing temperature was not known, but was no longer significant when using robust variance estimation (Supplementary results). The quadratic effect of temperature difference explained 46.3% of variance in effect sizes (marginal R^2). Overall effect size heterogeneity was very high ($I^2[\text{total}] = 99.9\%$), with 34% attributable to between-study differences, and the remaining 66% of variation attributable to residual variation.

Thermal sensitivity of adult lifespan

Adult lifespan was measured in 1,377 effect sizes (across 315 studies and 289 species). Most (93.7%) measured female lifespan, with only 5.6% measuring male lifespan (and for one study the data was not split by sex). Most studies kept males and females together for the duration of the experiment, therefore we believe it reasonable to assume that adult lifespan estimates are for mated females. For most adult lifespan effect sizes (93.3%), subjects were exposed for more than five days (and typically for their entire adult life).

A multilevel meta-analysis showed that adult lifespan follows a hump-shaped relationship with temperature (negative quadratic relationship between adult lifespan and the deviation from the reference temperature: estimate = -0.006, 95% CI = -0.008 to -0.004, $t = -6.12$, $df = 1,374$, $p < 0.001$, $k = 1,377$; **Table S14**), peaking at 18.03°C below the reference temperature on average (**Figure 3E**). Above the reference temperature, adult lifespan declines linearly with warming (**Figure 3F**). The quadratic effect of temperature difference explained 31.4% of variance in effect sizes (marginal R^2). The significant quadratic effect remained after removing outliers or short-term exposure treatments (Supplementary results). Overall effect size heterogeneity was very high ($I^2[\text{total}] = 98.7\%$), with 15.24% attributable to between-study differences, and the remaining 83.46% of variation attributable to residual variation.

The relationship between temperature difference and lifespan was not related to the life stage exposed (interaction between temperature difference and life stage exposed; $t = 0.49$, $df = 1,354$, $p = 0.62$, $k = 1,360$; **Figure 3E**; **Table S18**), including after removing outliers (Supplementary results). We did not test for an effect of sex, because almost all effect sizes considered female lifespan only.

Correlation between the thermal sensitivity of reproduction and adult lifespan

Our earlier univariate analyses indicated that, as predicted, reproduction and lifespan respond to temperature in a similar way above 25°C, but have divergent responses below 25°C. For the multivariate meta-analysis, we therefore split the dataset into experimental treatments below the reference temperature ('cool' subset) and experimental treatments above the reference temperature ('warm' subset).

For experimental treatments below the reference temperature ('cool' subset, $N = 397$ trials and 794 effect sizes), thermal sensitivity depended strongly on the life-history trait (interaction

between the quadratic effect of temperature difference and life-history trait, $t = 2.87$, $df = 788$, $p = 0.004$, $k = 794$; **Table S21, Figure 5A**). While reproduction increases towards the reference temperature, adult lifespan shows a unimodal relationship with temperature difference, peaking at 12°C below the reference temperature (**Figure 5A**). This predicted peak performance for adult lifespan is 6°C higher than the univariate analysis estimate (see above). This discrepancy is likely because the lifespan curve is asymmetric either side of the reference temperature: as the curve from the cool data subset is not constrained by what happens above the reference temperature, the analysis results in a different predicted peak. Across studies, changes in reproduction below the reference temperature were not correlated with changes in adult lifespan (between-study correlation = -0.11, 95% CI: -0.31 to 0.1, $N = 163$; **Figure 5C**), or after removing short-term exposure treatments (Supplementary results). Within each study, there was a moderate negative correlation between effect sizes from different temperature treatments (within-study correlation = -0.25, 95% CI = -0.38 to -0.11, $N = 397$), even after removing short-term exposure treatments (Supplementary results), due to the fact that reproduction effect sizes tend to be negative and lifespan effect sizes tend to be positive. However, there was no significant correlation after removing outliers (Supplementary results).

For experimental treatments above the reference temperature ('warm' subset, $N = 395$ trials and 790 effect sizes), reproductive traits were more strongly negatively impacted by a temperature increase than adult lifespan (interaction between the linear effect of temperature difference and life-history trait, $t = -7.82$, $df = 786$, $p < 0.001$, $k = 790$; **Table S25; Figure 5B**), even after removing outliers or short-term exposure treatments (Supplementary results). The slope of the relationship between temperature difference and reproduction ($\beta = -0.39$, 95% CI = -0.45 to -0.33) was more than twice as steep as the slope of the relationship between temperature difference and adult lifespan ($\beta = -0.18$, 95% CI = -0.22 to -0.15). Changes in reproduction above the reference temperature were strongly (*sensu* (Cohen 1988)) positively related to changes in

adult lifespan both across studies (between-study correlation = 0.62, 95% CI= 0.49 to 0.73, N = 174; **Figure 5D**) and across experimental treatments from the same study (within-study correlation = 0.49, 95% CI= 0.37 to 0.6, N = 395). We found weaker, but qualitatively similar correlations, after removing outliers or short-term exposure treatments (Supplementary results).

Discussion

We compared the thermal sensitivity of adult reproduction (predominantly fecundity), survival and lifespan for 306 ectothermic invertebrate species across a wide temperature range. We quantified thermal sensitivity in relation to reference temperatures assumed to be close to the optimal for population growth rate for each species. The dataset consisted of species that are mostly terrestrial, sexually-reproducing, and with internal fertilisation, and tested after long-term exposure to non-lethal temperatures (individuals typically survived long enough to reproduce). Studies typically measured adult survival or lifespan- the former following short term temperature exposure, and the latter following long-term temperature exposure. We found that reproductive output and survival were maximised close to the reference temperatures, whereas adult lifespan was maximised 12 to 18°C below reference temperatures. Importantly, we obtained enough data to compare the thermal responses of reproduction and lifespan in the same species. Below reference temperatures, the response of the two life-history traits was divergent, likely due to the opposing effect of a slowing metabolic rate: as metabolism slows, reproductive output declines, but adult lifespan lengthens. As a result, multivariate analyses found that the thermal responses of reproduction and adult lifespan are strongly positively correlated across species as temperatures increase above the reference, but there is no correlation between the two as temperatures decrease below the reference. Above the reference temperatures, both reproduction and adult lifespan decreased linearly as the temperature increased (also see Pawar *et*

486 *al.* 2024). Critically, reproductive output declined more than twice as steeply with warming than
 487 adult lifespan. This shows that reproduction is more sensitive to warming than adult lifespan in
 488 invertebrates.

489
 490 We suggest two key reasons why reproduction is more sensitive to warming than adult lifespan.
 491 First, reproductive tissues (or the gametes they produce) may be more sensitive to heat stress
 492 than other tissues. For example, high temperatures may impair sperm production in males (e.g.
 493 David *et al.* 2005; Hansen 2009; Sales *et al.* 2018), ovary and oocyte function in females (Barati *et*
 494 *al.* 2008; Li *et al.* 2016; Roth & Hansen 2005), and sperm-egg interactions (Eads *et al.* 2016; Hirao
 495 & Yanagimachi 1978; Sakatani *et al.* 2015). We could not explicitly test the sensitivity of each sex
 496 here, since most studies in this dataset simultaneously exposed both males and females, or only
 497 females, to experimental temperatures. Notably, we found no evidence for additive negative
 498 effects on reproduction when both sexes were exposed to the same test temperatures (but see
 499 e.g. Baur *et al.* 2022; Spinks *et al.* 2021). This could be explained if the reproductive costs of heat
 500 stress are predominantly borne by females, or if females compensate when encountering sub-
 501 fertile males, for example by increasing remating rates (Pembury Smith *et al.* 2025; Vasudeva *et al.*
 502 2021). Second, under stressful conditions, individuals might prioritise investment into somatic
 503 maintenance at the expense of reproduction (Stearns 1989), in which case we would predict a
 504 negative correlation between the sensitivity of reproduction and adult lifespan to warming.
 505 Instead, we found the opposite. The response of reproduction and adult lifespan to warming was
 506 positively correlated across the subset of studies that measured both traits in the same
 507 individuals, suggesting that both traits are affected by the same general breakdown of metabolic
 508 efficiency at high temperatures (albeit reproduction to a greater extent than lifespan).

509
 510 All three life history traits were characterised by very high heterogeneity. A negligible amount of
 511 this variation was explained by phylogenetic history, suggesting that thermal optima evolve

flexibly for all three life-history traits (see Buckley *et al.* 2022). Some heterogeneity probably arises due to error in the assignment of the reference temperatures, though the extent of this problem is impossible to quantify without characterising thermal performance curves for each species. However, we identified two moderator variables that explained a significant proportion of this variation. First, the response of both life-history traits strongly depended on the difference from the reference temperature, which explained 9.1% of variation for reproduction, 46.3% for adult survival, and 31.4% for adult lifespan (marginal R^2). Such a strong explanatory effect of test temperature is unsurprising, given that the dataset likely included a mix of stressful (following Ørsted *et al.* 2022) and non-stressful temperature treatments. Second, reproduction (but not adult lifespan) was more sensitive to temperature when individuals were exposed before and after sexual maturity, compared to those exposed only as adults. This effect could arise if developing reproductive tissues are particularly sensitive to heat stress (e.g. McDermott Long *et al.* 2017; Sales *et al.* 2021), or if resource acquisition is impaired during developmental heat stress. Notably, it also suggests that acclimation effects due to developmental plasticity are relatively weak (a trend that has been found in other comparative analyses in ectotherms (Pottier *et al.* 2022; Weaving *et al.* 2022), or at least not strong enough to overcome the increased thermal sensitivity of developing individuals. Importantly, for all datasets a large proportion of variance remains unexplained, suggesting other influential biological and ecological factors that we could not account for due to limitations of the dataset. For example, due to small sample size in some categories, we could not test moderators such as habitat type (aquatic vs terrestrial species), reproductive mode (sexual vs asexual reproduction), or fertilisation mode (internal vs external fertilisers).

All three life history traits are negatively affected by warming in the laboratory. However, it remains unclear whether this will translate into fitness differences for individuals or populations in the face of future warming, for several reasons. First, other traits, such as juvenile mortality,

growth rate, or adult body size, are also affected by temperature change (Atkinson 1994; Abarca *et al.* 2024; Pawar *et al.* 2024; Pörtner *et al.* 2001). These concomitant responses could either mitigate reductions in the traits we tested (Reynolds 2003; Stearns 1989) or exacerbate them (e.g. smaller body size due to developing at higher temperature may negatively impact fecundity: Verberk *et al.* 2021). Second, many species do not occupy a thermal niche that maximises reproductive output (Buckley *et al.* 2021). Therefore, warming may lead to increased fecundity for species living below their thermal optimum (Lehmann *et al.* 2020; Moore *et al.* 2023). Third, natural environments contain refugia which protect individuals from temperature extremes (Pincebourde & Woods 2020; Suggitt *et al.* 2011), and which are especially important for ectotherms that cannot regulate their body temperature physiologically. Though note that previous work has shown that the loss of fertility in the laboratory does predict current species ranges in fruit flies (van Heerwaarden & Sgrò 2021; Parratt *et al.* 2021). Finally, the extent to which thermal optima can evolve is also important (Hoffmann *et al.* 2013). Current evidence suggests that the evolvability of upper thermal limits for both survival and fertility is low (van Heerwaarden & Sgrò 2021; Kellermann *et al.* 2012), but thermal optima are evolvable (Angilletta Jr *et al.* 2002; Baur *et al.* 2022; Buckley *et al.* 2022).

Our systematic searches identified several important research gaps. First, we found few studies testing the effect of temperature on reproduction and survival, an effect partly driven by the scarcity of studies testing the effect of short-term temperature exposure. For long-term exposure studies, it is more appropriate to measure adult lifespan than survival at some arbitrary time point. Second, few studies test the thermal sensitivity of reproduction and adult lifespan/survival in ectothermic vertebrates. This is probably due to the practical difficulties of measuring lifespan or survival in species that are long-lived and have more stringent ethical controls. Third, aquatic species are also underrepresented in the dataset, with only 24 species (71 effect sizes) in the reproduction dataset and 19 species (59 effect sizes) in the adult lifespan dataset. This is despite

the fact that aquatic ectotherms may be more vulnerable to warming than terrestrial ones because they lack the ability to access thermal refugia (Pinsky *et al.* 2019). Both species groups are therefore prime targets for future research.

As climate warming continues, our results show that negative reproductive consequences will occur faster than effects on lifespan, all else being equal. This supports recent suggestions that a loss of reproductive output, and the subsequent negative effects on population persistence, is likely to be a widespread and overlooked consequence of environmental warming (Snook *et al.* 2026; Walsh *et al.* 2019). While previous work has shown thermal fertility limits may be more important than lethal limits for determining population persistence (van Heerwaarden & Sgrò 2021; Parratt *et al.* 2021), our results show that reproduction may also be impaired by long-term changes in average temperatures that are well within thermal limits. Further, a key strength of the data set is our ability to test the correlated responses of life history traits in the same species. This analysis shows that the responses of reproduction and adult lifespan to warming are strongly positively correlated, meaning that measuring one allows us to partly predict the other. However, the higher thermal sensitivity of reproduction means that studies should move away from focusing on CT_{max} as an estimate of vulnerability to future warming. A key next step for research is to link the thermal sensitivity of reproduction to population persistence in the wild, for a range of species groups, living in different parts of the world.

Author contributions

Conceptualization: AB, CF, LRD, RRS, TARP.

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Funding acquisition: AB, CF, LRD, RRS, TARP.

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Methodology: AB, CF, DWAN, FF, LRD, RRS, SN, TARP.

Project administration: AB, CF, LRD, RRS, TARP.

Visualization: DWAN, FF, LRD.

Writing – original draft: DWAN, FF, LRD.

Writing – review & editing: AB, CF, DWAN, FF, GI, JE, LRD, MG, MR, NP, PS, RRS, SN, SL, SAR.

All authors read and approved the manuscript before submission.

Data accessibility statement

All data and code are available at <https://doi.org/10.6084/m9.figshare.33183677>

Conflict of interest statement

The authors declare no conflicts of interest.

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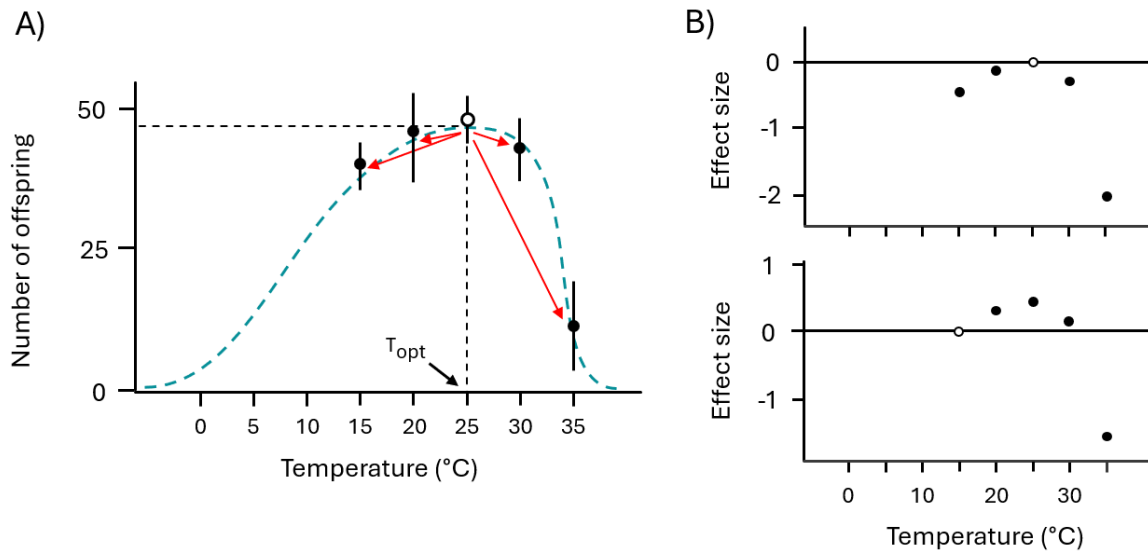


Figure 1. Using a contrast-based approach to estimate the effect of temperature on fitness. In all panels, values on the y axis are for illustration purposes only. **A)** Fitness traits such as the number of offspring typically show a non-linear thermal response curve (green dashed line), with fitness peaking at some intermediate temperature (T_{OPT} , indicated with fine dashed line). However, studies typically test relatively few temperature treatments across only part of the relevant thermal range (points). To analyse this data in a meta-analytic framework, we therefore use a contrast approach, in which experimental treatments (filled points) are compared against a control or ‘reference’ treatment (open point). Using this approach, X measurements become X-1 contrasts (red arrows). **B)** The effect sizes that are produced using this approach depend on where the reference treatment is in relation to T_{OPT} . Top panel: when the reference treatment (open point) is at T_{OPT} , all subsequent effect sizes (filled points) will be negative. Bottom panel: if the reference temperature (open point) is not at T_{OPT} , the curve will look the same, but some effect sizes (filled points) will be positive, and some will be negative.

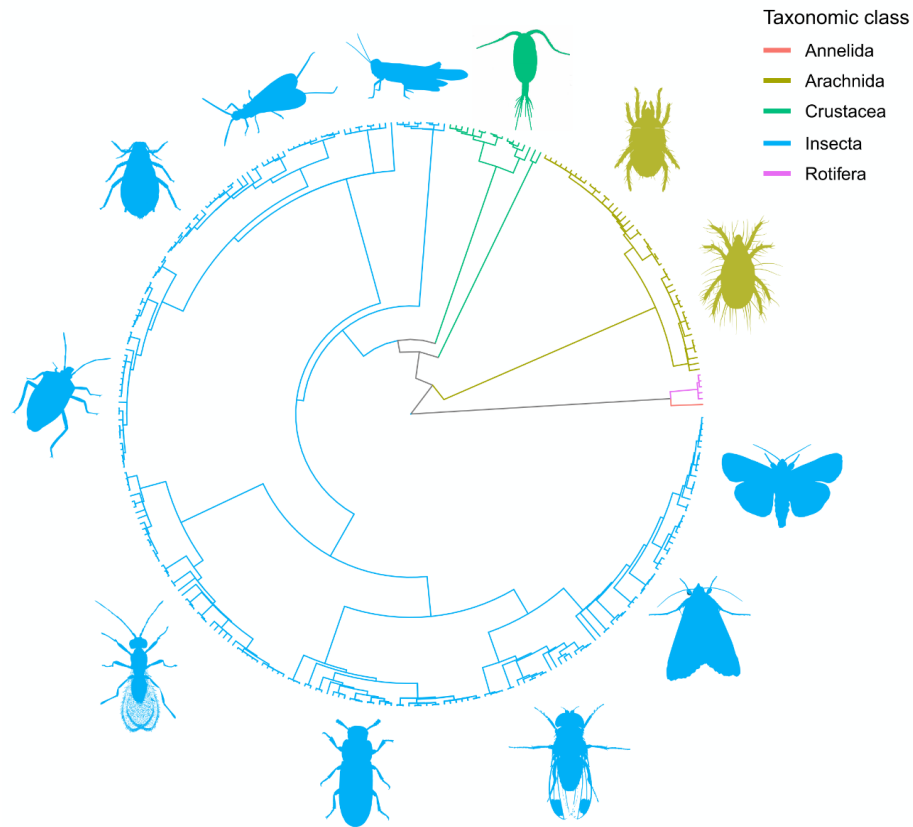


Figure 2. Phylogenetic tree showing the relationship between the 306 included species, with representative species silhouettes (phylopic.com; credit Dave Angelini, Nicholas Gompel, Gareth Monger; <https://creativecommons.org/licenses/by/3.0/>). Branch lengths are standardised.

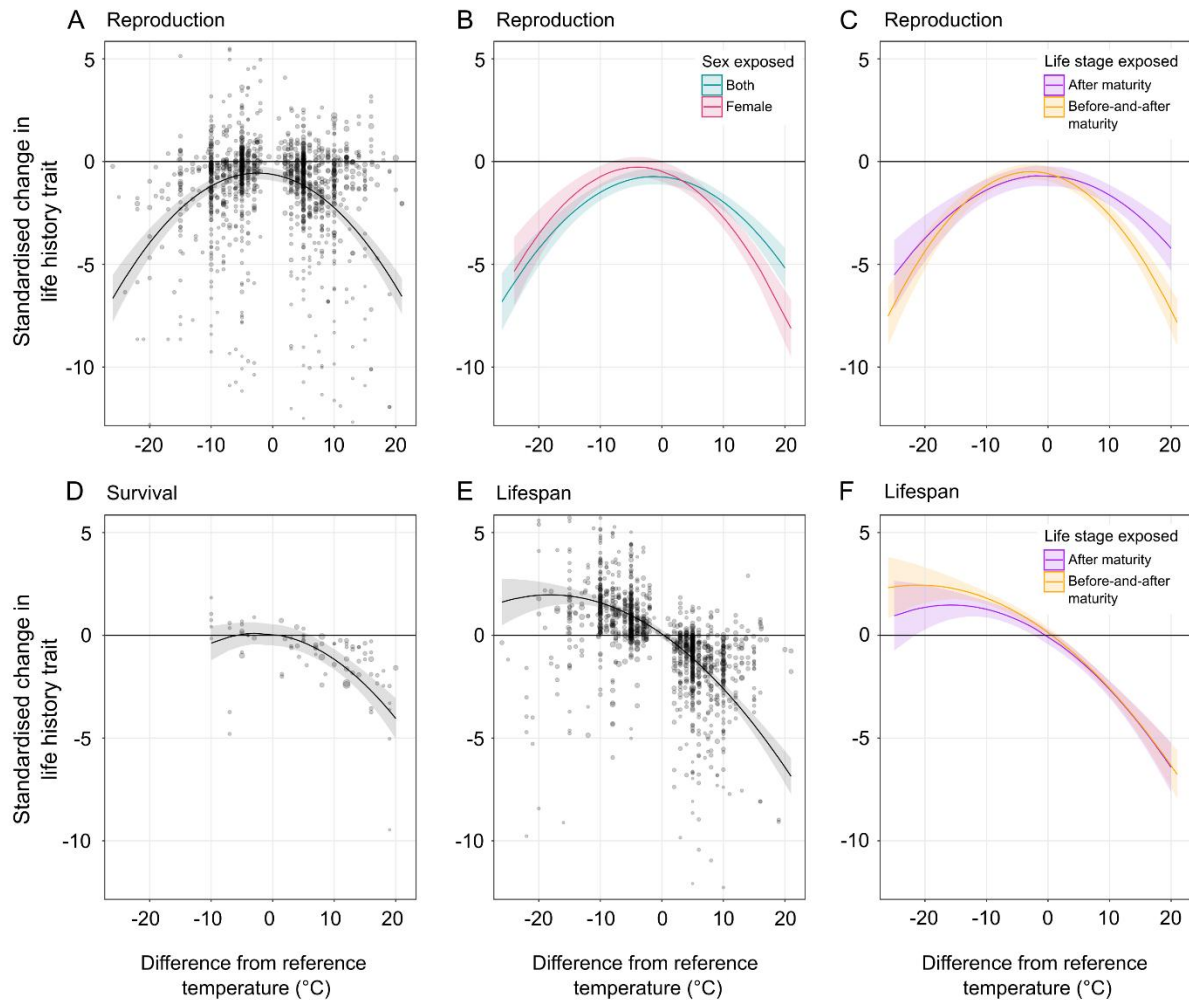


Figure 3. The thermal sensitivity of invertebrate life history. Plots show the standardised change in a life history trait in relation to temperature difference (degrees Celsius) between the reference and experimental treatments. Reference treatments are expected to be close to the temperature which maximises population growth rate for each species. Solid lines show the predicted mean from a multi-level meta-regression model, and shaded regions shows the 95% confidence intervals. In panels A, D, & E, points are scaled according to the inverse standard error (also known as ‘precision’)- larger points come from studies with larger samples sizes. Note that some raw data has been truncated for ease of visualisation, but results remain unchanged when extreme values are removed. **A)** Thermal sensitivity of reproduction (N= 1,387 effect sizes and 339 studies). **B)** Thermal sensitivity of reproduction in relation to sex exposure. Studies either exposed females only (pink) or both males and females (teal). **C)** Thermal sensitivity of reproduction in relation to life stage of exposure (N= 1,370 effect sizes and 338 studies). Individuals were exposed only as adults (after maturity category; purple) versus studies in which individuals spent at least some time in the temperature treatments before they were sexually mature (before and after maturity category; orange). **D)** Thermal sensitivity of adult survival (N= 85 effect sizes and 27 studies). **E)** Thermal sensitivity of adult lifespan. N= 1,377 effect sizes and 315 studies. **F)** Thermal sensitivity of adult lifespan in relation to life stage of exposure (N= 1,370 effect sizes and 338 studies). Individuals were exposed only as adults (after maturity category; purple) versus studies in which individuals spent at least some time in the temperature treatments before they were sexually mature (before and after maturity category; orange).

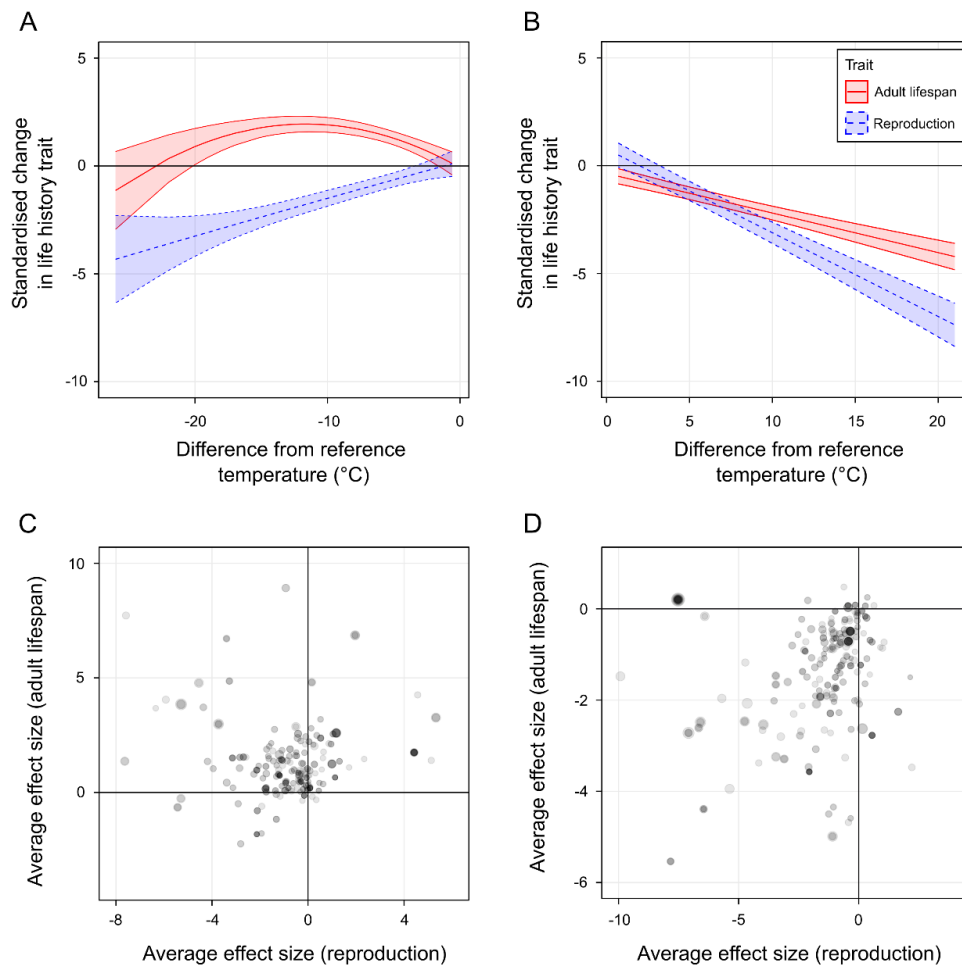


Figure 4. Predicted relationship between the difference (degrees Celsius) between the reference and experimental temperature and standardised change in reproduction (blue) and adult lifespan (red) for **A)** treatments cooler than their reference temperature ($N = 397$ for each trait), and **B)** treatments warmer than their reference temperature ($N = 395$ for each trait). Lines show the predicted mean and 95% confidence intervals from a multivariate meta-analysis model. The relationship between the average effect size for reproduction and the average effect size for adult lifespan, for **C)** treatments cooler than the reference temperature ($N = 163$ studies), and **D)** treatments warmer than the reference temperature ($N = 174$ studies). Data points scaled by inverse study variance (larger points come from studies with a larger sample size). Note that some raw data have been truncated for ease of visualisation, but results remain unchanged when extreme values are removed.

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Supplementary methods

Study inclusion criteria

We included estimates from both terrestrial and aquatic species. We initially did not restrict our search to any animal group, but found that all included studies tested invertebrates. We considered any experimental temperatures greater than 0°C, because freezing sets a hard lower limit on the completion of the life cycle for most terrestrial ectotherms (Clarke 2014). We did not assess whether treatment temperatures were stressful. Treatments did not have to expose individuals to constant temperatures, but we only included fluctuating temperature treatments which also had different average temperatures. We considered any duration of temperature exposure, ranging from short-term heat shocks of a few hours to lifetime exposure over several months. We did not limit data to thermal exposure during a specific life stage. We included experiments in which males and females were exposed to temperature treatments simultaneously or separately. We excluded studies in which temperature was confounded with another stressor (e.g. adults were deprived of food).

Effect size calculations

Standardised mean differences were calculated as Hedges' g using the following formula:

$$SMD = \frac{\bar{X}_{experimental} - \bar{X}_{reference}}{SD_{pooled}} J \quad (1)$$

$$SD_{pooled} = \sqrt{\frac{(n_{reference} - 1)S^2_{reference} + (n_{experimental} - 1)S^2_{experimental}}{n_{reference} + n_{experimental} - 2}} \quad (2)$$

$$J = 1 - \frac{3}{4(n_{reference} + n_{experimental} - 2) - 1} \quad (3)$$

where $\bar{X}_{reference}$ and $\bar{X}_{experimental}$ are the mean reproductive trait values for the reference treatment and experimental treatments, SD_{pooled} is the pooled standard deviation, J is the correction factor for small sample sizes (Hedges & Olkin 1985), and $n_{reference}$, $n_{experimental}$, $S_{reference}$, and $S_{experimental}$ are the sample sizes and standard deviations for the reference and experimental treatments, respectively. For 21 studies (101 effect sizes), we used the proportion of reproductive individuals as a measure of reproductive output, rather than means and standard deviations. In these cases, we first calculated the χ^2 test statistic, and then converted to Hedges' g using the following conversion formula (Koricheva *et al.* 2013):

$$g = \sqrt{\frac{\chi^2(n_{reference} + n_{experimental})}{n_{reference} \times n_{experimental}}} \quad (4)$$

Testing for a phylogenetic signal

It is important to account for the potential non-independence of effect sizes from closely-related species due to shared evolutionary history (Koricheva *et al.* 2013). However, a single published phylogeny including all species does not exist. We therefore used a pruned version of the tree presented in Dougherty *et al.* (Dougherty *et al.* 2024), which was produced using the Open Tree of Life (OTL) database (Hinchliff *et al.* 2015) and the *rotl* R (v3.0.12) package (Michonneau *et al.* 2016). Given the absence of accurate branch length data, all branch lengths were set to one and then made ultrametric using Grafen's method (Grafen 1989), using the *ape* (v5.3) package (Paradis *et al.* 2004). In cases where the OTL database resulted in a polytomy, we randomly resolved them using the *multi2di* function in *ape*. Phylogeny was incorporated into the univariate meta-analysis models by converting the pruned phylogenetic tree (see supplementary methods) into a correlation matrix and including this matrix in the model, assuming that traits evolve via Brownian motion. However, for both all three life history traits the best fitting model (according

to AIC) included only study ID as a random effect: phylogeny explained a negligible amount of variation in effect sizes ($I^2 < 0.001$) and so was not included in any further models.

Sensitivity tests

We ran sensitivity tests to determine the robustness of our results. First, we tested whether results could be driven by the inclusion of short-term exposure treatments. Exposure to more extreme ('stressful') temperatures is expected to result in a steeper relationship between temperature and fitness compared to exposure to less extreme ('permissive') temperatures (Ørsted *et al.* 2022), potentially skewing our results. Indeed, experimental treatments of short exposure tended to use more extreme temperatures (**Figure S2**). To account for this, we re-ran all analyses after removing effect sizes from exposure durations shorter than five days (N= 132 effect sizes for reproduction, 90 for adult lifespan). Second, to test the sensitivity of our results to the inclusion of studies in which the rearing temperature was not reported, we ran all analyses both with and without their inclusion. Third, both the reproduction and adult lifespan datasets included positive and negative effect sizes of extreme magnitude. We cross-checked that these were not due to mistakes in data extraction but could not discount the possibility that they are the result of reporting errors in the original studies. Nonetheless, to test that the results were not driven by the inclusion of these extreme values, we performed all analyses with and without the inclusion of effect sizes above a Hedges g value of 10 or below -10 (N = 61 effect sizes for reproduction, 36 for adult lifespan). Fewer than 20% of excluded outliers were from short-term exposure treatments. Fourth, we used robust variance estimation to estimate sampling covariances directly from the data (Hedges *et al.* 2010), (Yang *et al.* 2023), and adjust parameter estimates accordingly. This approach provides a test of the extent to which the VCV matrices are mis-specified, as this methods is not impacted by the choice of a value for the within study-correlation (Yang *et al.* 2023). Fifth, we tested whether the mean effect size was related to publication year, using a meta-regression model including publication year as a fixed effect. A

decline in the mean effect size over time may indicate an increase in the likelihood of publishing null results over time (Jennions & Møller 2002). To do this, we ran a meta-regression model including publication year as a fixed effect. We did not test for publication bias using methods based on funnel plot asymmetry, because the dataset is likely to show an asymmetric distribution for two reasons unrelated to publication bias. First, the way effect sizes are calculated, in relation to a reference treatment expected to be close to T_{OPT} for population growth rate, means that negative values are much more likely than positive ones. Second, there is true heterogeneity in the dataset in relation to the difference between the reference and experimental temperatures.

Supplementary results: sensitivity analyses

Reproduction

Sensitivity analysis confirmed that reproduction had a negative quadratic relationship with temperature difference after removing outliers ($t = -9.75$, $df = 1323$, $p < 0.001$; **Table S2**), short-exposure treatments ($t = -12.28$, $df = 1252$, $p < 0.001$; **Table S3**), or studies where the rearing temperature was not specified ($t = -10.69$, $df = 1051$, $p < 0.001$; **Table S4**), and after using robust variance estimation ($t = -4.77$, $df = 1384$, $p < 0.001$).

The reproduction of individuals that were exposed either when immature or both before and after sexual maturity was more sensitive to extreme temperatures than those treated only after sexual maturity after removing outliers ($t = -2.32$, $df = 1306$, $p = 0.02$; **Table S6**) or short exposure treatments ($t = -0.7$, $df = 1246$, $p = 0.48$; **Table S7**). The thermal sensitivity of reproduction did not depend on whether only females were exposed or both males and females being exposed simultaneously after removing outliers (interaction between temperature difference and sex exposed; $t = -1.75$, $df = 1311$, $P = 0.08$; **Table S9**) or short exposure

treatments ($t = 1.22$, $df = 1245$, $p = 0.22$; **Table S10**). The average effect size for reproduction was not significantly affected by publication year ($t = -1.29$, $df = 1385$, $p = 0.2$), even after removing outliers ($t = -1.46$, $df = 1324$, $p = 0.15$).

Adult survival

Sensitivity analysis confirmed that adult survival had a negative quadratic relationship with temperature difference after removing short-exposure treatments ($t = -4.45$, $df = 50$, $p < 0.001$; **Table S12**), or studies where the rearing temperature was not specified ($t = -4.07$, $df = 76$, $p < 0.001$; **Table S13**), but not after using robust variance estimation ($t = -2.11$, $df = 80$, $p = 0.063$).

Adult lifespan

Sensitivity analysis confirmed that adult lifespan had a negative quadratic relationship with temperature difference after removing outliers ($t = -7.25$, $df = 1338$, $p < 0.001$; **Table S15**), short-exposure treatments ($t = -6.94$, $df = 1284$, $p < 0.001$; **Table S16**), or studies where the rearing temperature was not specified ($t = -6.4$, $df = 1020$, $p = 0.008$; **Table S17**), and after using robust variance estimation ($t = -2.64$, $df = 1374$, $p = 0.01$).

The relationship between temperature and lifespan was not related to the life stage of exposure after removing outliers ($t = 1.36$, $df = 1318$, $p = 0.17$; **Table S19**) or short exposure treatments ($t = 0.89$, $df = 1277$, $p = 0.37$; **Table S20**). The average effect size for adult lifespan was not significantly affected by publication year ($t = -0.84$, $df = 1375$, $p = 0.4$), even after removing outliers ($t = -0.15$, $df = 1339$, $p = 0.88$).

Multivariate analysis

For treatments below the reference temperature, the interaction between the quadratic effect of temperature and life history trait was significant after removing outliers ($t = 3.48$, $df = 771$, $p <$

0.001; **Table S21**), short-term exposure treatments ($t = 2.85$, $df = 746$, $p = 0.005$; **Table S22**),
and studies where the rearing temperature was not specified ($t = 2.08$, $df = 771$, $p = 0.038$;
Table S23). The interaction between the quadratic effect of temperature and life history trait was
no longer significant when using robust variance estimation ($t = 1.28$, $df = 788$, $p = 0.22$).
However, the interaction between the linear effect of temperature and life history trait was
significant ($t = 2.62$, $df = 788$, $p = 0.01$), with reproduction showing a positive relationship with
temperature, and lifespan showing a weak negative relationship.

For treatments above the reference temperature, reproductive output was more strongly
impacted by temperature change than adult lifespan after removing outliers ($t = -5.35$, $df = 759$,
 $p < 0.001$; **Table S26**), short-term exposure treatments ($t = -6.1$, $df = 704$, $p < 0.001$; **Table**
S27), and studies where the rearing temperature was not specified ($t = -7.86$, $df = 580$, $p < 0.001$;
Table S28), and when using robust variance estimation (interaction between the linear effect of
temperature and life history trait, $t = -3.27$, $df = 786$, $p = 0.003$).

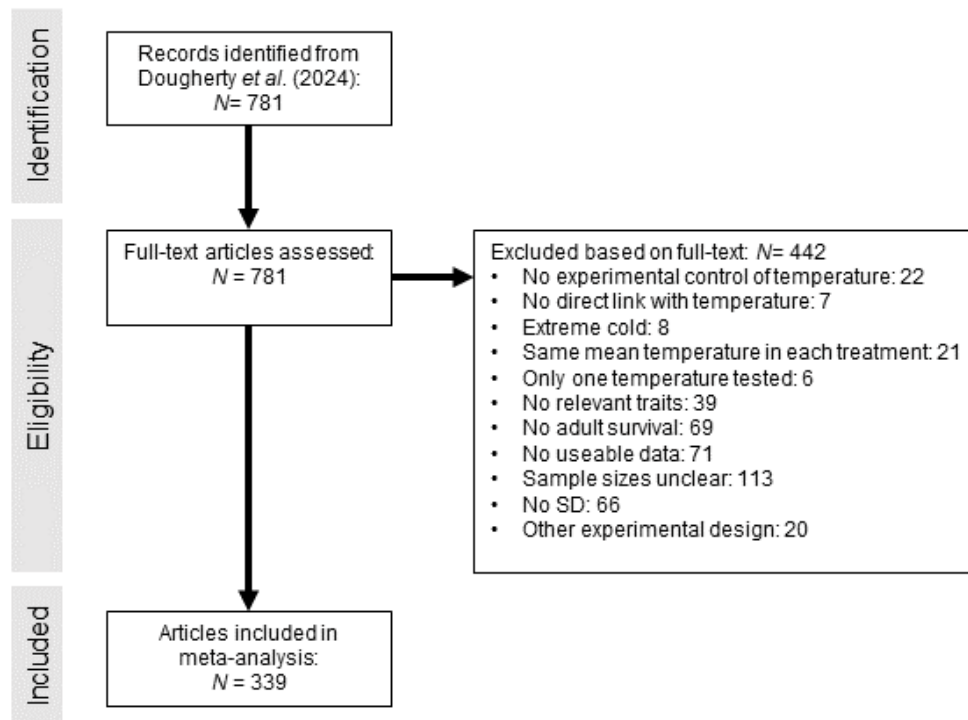


Fig. S1. PRISMA flow diagram showing the study screening process.

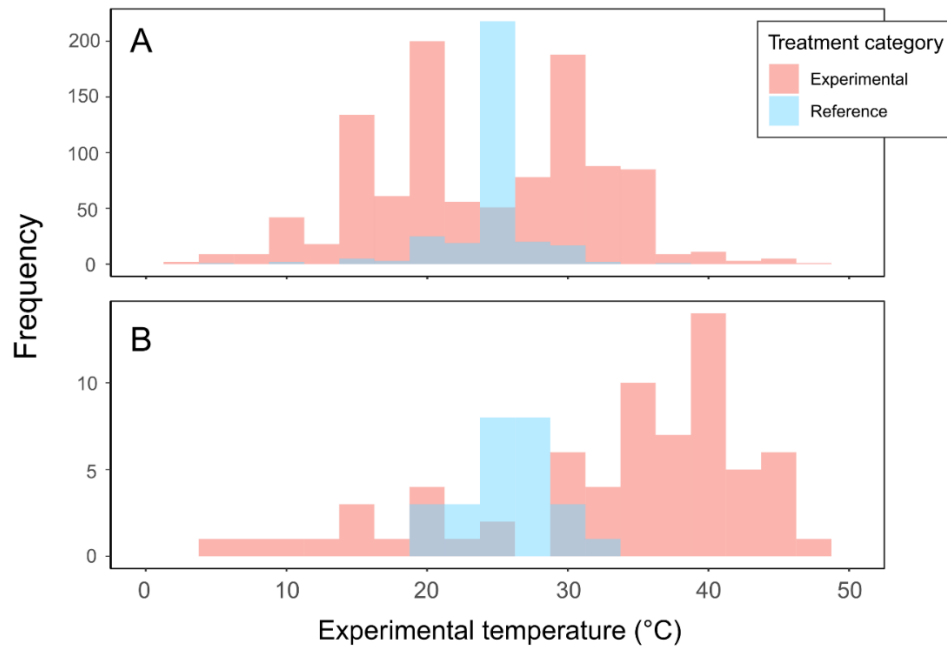


Fig. S2. Histogram showing the temperature treatment distribution (experimental temperature treatments in red, reference treatments in blue) for **A)** long-term exposures (more than five days) and **B)** short-term exposures (five days or less). Note the different y axis scale in panels A and B. Data is for all studies (N= 339).

Table S1. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on reproductive output. N= 1387 effect sizes and 339 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Reproduction (mean)	-0.624	-0.928	-0.321	-4.03	< 0.001
Linear difference from reference temperature (°C)	-0.053	-0.069	-0.036	-6.25	< 0.001
Quadratic difference from reference temperature (°C)	-0.011	-0.013	-0.009	-11.85	< 0.001

Table S2. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on reproductive output, after removing outliers. N= 1326 effect sizes and 335 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Reproduction (mean)	-0.529	-0.714	-0.345	-5.62	< 0.001
Linear difference from reference temperature (°C)	-0.027	-0.040	-0.014	-4.08	< 0.001
Quadratic difference from reference temperature (°C)	-0.007	-0.008	-0.006	-9.75	< 0.001

Table S3. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on reproductive output, after removing short-term exposure treatments. N= 1255 effect sizes and 310 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Reproduction (mean)	-0.617	-0.901	-0.334	-4.26	< 0.001
Linear difference from reference temperature (°C)	-0.042	-0.057	-0.026	-5.30	< 0.001
Quadratic difference from reference temperature (°C)	-0.011	-0.013	-0.010	-12.28	< 0.001

Table S4. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on reproductive output, after removing studies for which the rearing temperature was not specified. N= 1054 effect sizes and 253 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Reproduction (mean)	-0.584	-0.894	-0.275	-3.70	< 0.001
Linear difference from reference temperature (°C)	-0.052	-0.070	-0.033	-5.48	< 0.001
Quadratic difference from reference temperature (°C)	-0.011	-0.013	-0.009	-10.69	< 0.001

Table S5. Parameter estimates from a multilevel meta-regression model testing the effect of temperature and life stage of exposure on reproductive output. N= 1370 effect sizes and 338 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Linear difference from reference temperature (°C)	-0.012	-0.038	0.013	-0.95	0.34
Quadratic difference from reference temperature (°C)	-0.008	-0.011	-0.006	-5.84	< 0.001
After maturity	-0.686	-1.173	-0.200	-2.77	0.006
Before-and-after maturity	-0.591	-0.960	-0.222	-3.14	0.002
Difference (linear) * Life stage exposed	-0.059	-0.092	-0.027	-3.57	< 0.001
Difference (quadratic) * Life stage exposed	-0.005	-0.008	-0.001	-2.63	0.009

Table S6. Parameter estimates from a multilevel meta-regression model testing the effect of temperature and life stage of exposure on reproductive output, after removing outliers. N= 1312 effect sizes and 334 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Linear difference from reference temperature (°C)	0.010	-0.010	0.030	0.98	0.33
Quadratic difference from reference temperature (°C)	-0.006	-0.008	-0.004	-5.24	< 0.001
After maturity	-0.664	-0.969	-0.359	-4.27	< 0.001
Before-and-after maturity	-0.411	-0.639	-0.184	-3.55	< 0.001
Difference (linear) * Life stage exposed	-0.060	-0.086	-0.035	-4.65	< 0.001
Difference (quadratic) * Life stage exposed	-0.003	-0.006	-0.001	-2.32	0.02

Table S7. Parameter estimates from a multilevel meta-regression model testing the effect of temperature and life stage of exposure on reproductive output, after removing short-term exposure treatments. N= 1251 effect sizes and 310 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Linear difference from reference temperature (°C)	-0.025	-0.050	0.000	-1.97	0.05
Quadratic difference from reference temperature (°C)	-0.010	-0.013	-0.007	-6.61	< 0.001
After maturity	-0.846	-1.319	-0.374	-3.51	< 0.001
Before-and-after maturity	-0.489	-0.836	-0.142	-2.77	0.006
Difference (linear) * Life stage exposed	-0.027	-0.058	0.004	-1.71	0.09
Difference (quadratic) * Life stage exposed	-0.003	-0.006	0.001	-1.40	0.16

Table S8. Parameter estimates from a multilevel meta-regression model testing the effect of temperature and sex of exposure on reproductive output. N= 1387 effect sizes and 337 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Linear difference from reference temperature (°C)	-0.024	-0.044	-0.003	-2.23	0.03
Quadratic difference from reference temperature (°C)	-0.010	-0.012	-0.008	-8.80	< 0.001
Both sexes exposed	-0.743	-1.119	-0.368	-3.88	< 0.001
Females only exposed	-0.468	-0.968	0.032	-1.84	0.07
Difference (linear) * Sex exposed	-0.076	-0.109	-0.043	-4.54	< 0.001
Difference (quadratic) * Sex exposed	-0.003	-0.006	0.001	-1.43	0.15

Table S9. Parameter estimates from a multilevel meta-regression model testing the effect of temperature and sex of exposure on reproductive output, after removing outliers. N= 1317 effect sizes and 333 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Linear difference from reference temperature (°C)	-0.010	-0.026	0.006	-1.20	0.23
Quadratic difference from reference temperature (°C)	-0.006	-0.008	-0.004	-6.92	< 0.001
Both sexes exposed	-0.582	-0.811	-0.352	-4.97	< 0.001
Females only exposed	-0.457	-0.766	-0.148	-2.90	0.004
Difference (linear) * Sex exposed	-0.045	-0.071	-0.020	-3.45	< 0.001
Difference (quadratic) * Sex exposed	-0.003	-0.005	0.000	-1.75	0.08

Table S10. Parameter estimates from a multilevel meta-regression model testing the effect of temperature and sex of exposure on reproductive output, after removing short-term exposure treatments. N= 1252 effect sizes and 309 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Linear difference from reference temperature (°C)	-0.032	-0.052	-0.013	-3.24	0.001
Quadratic difference from reference temperature (°C)	-0.012	-0.014	-0.010	- 10.38	< 0.001
Both sexes exposed	-0.552	-0.899	-0.204	-3.11	0.002
Females only exposed	-0.760	-1.237	-0.283	-3.13	0.002
Difference (linear) * Sex exposed	-0.026	-0.058	0.006	-1.61	0.11
Difference (quadratic) * Sex exposed	0.002	-0.002	0.005	0.79	0.43

Table S11. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on adult survival. N= 83 effect sizes and 27 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Survival (mean)	0.056	-0.456	0.568	0.21	0.83
Linear difference from reference temperature (°C)	-0.040	-0.086	0.007	-1.65	0.10
Quadratic difference from reference temperature (°C)	-0.008	-0.012	-0.005	-4.64	< 0.001

Table S12. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on adult survival, after removing short-term exposure treatments. N= 53 effect sizes and 19 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Survival (mean)	0.055	-0.590	0.699	0.17	0.87
Linear difference from reference temperature (°C)	-0.059	-0.097	-0.022	-3.12	0.00
Quadratic difference from reference temperature (°C)	-0.008	-0.012	-0.005	-4.45	< 0.001

Table S13. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on adult survival, after removing studies for which the rearing temperature was not specified. N= 53 effect sizes and 19 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Survival (mean)	0.189	-0.233	0.610	0.88	0.38
Linear difference from reference temperature (°C)	-0.053	-0.100	-0.006	-2.22	0.03
Quadratic difference from reference temperature (°C)	-0.007	-0.011	-0.004	-4.07	< 0.001

Table S14. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on adult lifespan. N= 1377 effect sizes and 315 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Longevity (mean)	0.069	-0.138	0.276	0.66	0.51
Linear difference from reference temperature (°C)	-0.209	-0.226	-0.192	-23.89	< 0.001
Quadratic difference from reference temperature (°C)	-0.006	-0.008	-0.004	-6.12	< 0.001

Table S15. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on adult lifespan, after removing outliers. N= 1341 effect sizes and 313 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Longevity (mean)	0.046	-0.114	0.207	0.57	0.57
Linear difference from reference temperature (°C)	-0.179	-0.191	-0.167	-28.62	< 0.001
Quadratic difference from reference temperature (°C)	-0.005	-0.006	-0.004	-7.25	< 0.001

Table S16. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on adult lifespan, after removing short-term exposure treatments. N= 1287 effect sizes and 293 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Longevity (mean)	0.120	-0.086	0.325	1.14	0.25
Linear difference from reference temperature (°C)	-0.224	-0.242	-0.205	-23.72	< 0.001
Quadratic difference from reference temperature (°C)	-0.007	-0.010	-0.005	-6.94	< 0.001

Table S17. Parameter estimates from a multilevel meta-analysis model testing the effect of temperature on adult lifespan, after removing studies for which the rearing temperature was not specified. N= 1023 effect sizes and 231 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	z	P
Longevity (mean)	0.161	-0.069	0.390	1.37	0.17
Linear difference from reference temperature (°C)	-0.204	-0.222	-0.187	-22.65	< 0.001
Quadratic difference from reference temperature (°C)	-0.006	-0.008	-0.004	-6.40	< 0.001

Table S18. Parameter estimates from a multilevel meta-regression model testing the effect of temperature and life stage of exposure on adult lifespan. N= 1360 effect sizes and 314 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Linear difference from reference temperature (°C)	-0.195	-0.222	-0.167	-13.83	< 0.001
Quadratic difference from reference temperature (°C)	-0.006	-0.009	-0.003	-4.13	< 0.001
After maturity	-0.064	-0.419	0.291	-0.35	0.72
Before-and-after maturity	0.135	-0.121	0.389	1.03	0.30
Difference (linear) * Life stage exposed	-0.025	-0.060	0.011	-1.37	0.17
Difference (quadratic) * Life stage exposed	0.001	-0.003	0.005	0.49	0.62

Table S19. Parameter estimates from a multilevel meta-regression model testing the effect of temperature and life stage of exposure on adult lifespan, after removing outliers. N= 1324 effect sizes and 312 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Linear difference from reference temperature (°C)	-0.151	-0.171	-0.131	-15.00	< 0.001
Quadratic difference from reference temperature (°C)	-0.006	-0.008	-0.004	-5.56	< 0.001
After maturity	-0.013	-0.285	0.259	-0.09	0.93
Before-and-after maturity	0.080	-0.116	0.275	0.80	0.43
Difference (linear) * Life stage exposed	-0.045	-0.070	-0.020	-3.50	< 0.001
Difference (quadratic) * Life stage exposed	0.002	-0.001	0.005	1.36	0.17

Table S20. Parameter estimates from a multilevel meta-regression model testing the effect of temperature and life stage of exposure on adult lifespan, after removing short-term exposure treatments. N= 1283 effect sizes and 293 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Linear difference from reference temperature (°C)	-0.210	-0.240	-0.179	-13.54	< 0.001
Quadratic difference from reference temperature (°C)	-0.008	-0.012	-0.005	-5.09	< 0.001
After maturity	-0.013	-0.367	0.341	-0.07	0.94
Before-and-after maturity	0.180	-0.071	0.431	1.41	0.16
Difference (linear) * Life stage exposed	-0.022	-0.060	0.016	-1.16	0.25
Difference (quadratic) * Life stage exposed	0.002	-0.003	0.006	0.81	0.42

Table S21. Parameter estimates from a multivariate meta-analysis model testing the effect of temperature on both reproductive output and adult lifespan, for experimental temperatures below the reference temperature. N= 1588 effect sizes and 163 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Lifespan (mean)	-0.083	-0.670	0.504	-0.28	0.78
Reproduction (mean)	0.202	-0.453	0.857	0.61	0.54
Linear difference from reference temperature (°C)- Lifespan	-0.348	-0.471	-0.226	-5.58	< 0.001
Linear difference from reference temperature (°C)- Reproduction	0.168	0.029	0.306	2.37	0.02
Quadratic difference from reference temperature (°C)- Lifespan	-0.015	-0.021	-0.009	-4.74	< 0.001
Quadratic difference from reference temperature (°C)- Reproduction	0.000	-0.007	0.007	-0.07	0.94

Table S22. Parameter estimates from a multivariate meta-analysis model testing the effect of temperature on both reproductive output and adult lifespan, for experimental temperatures below the reference temperature after removing outliers. N= 1554 effect sizes and 163 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Lifespan (mean)	0.137	-0.360	0.633	0.54	0.59
Reproduction (mean)	0.309	-0.307	0.924	0.99	< 0.001
Linear difference from reference temperature (°C)- Lifespan	-0.271	-0.378	-0.165	-5.02	<.0001
Linear difference from reference temperature (°C)- Reproduction	0.200	0.068	0.332	2.98	0.003
Quadratic difference from reference temperature (°C)- Lifespan	-0.013	-0.018	-0.007	-4.68	< 0.001
Quadratic difference from reference temperature (°C)- Reproduction	0.003	-0.004	0.010	0.86	0.39

Table S23. Parameter estimates from a multivariate meta-analysis model testing the effect of temperature on both reproductive output and adult lifespan, for experimental temperatures below the reference temperature after removing short-term exposure treatments. N= 1504 effect sizes and 157 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Lifespan (mean)	-0.204	-0.878	0.470	-0.60	0.55
Reproduction (mean)	0.421	-0.255	1.096	1.23	0.22
Linear difference from reference temperature (°C)- Lifespan	-0.379	-0.527	-0.231	-5.03	< 0.001
Linear difference from reference temperature (°C)- Reproduction	0.218	0.071	0.366	2.90	0.004
Quadratic difference from reference temperature (°C)- Lifespan	-0.016	-0.024	-0.008	-4.09	< 0.001
Quadratic difference from reference temperature (°C)- Reproduction	0.001	-0.007	0.009	0.22	0.83

Table S24. Parameter estimates from a multivariate meta-analysis model testing the effect of temperature on both reproductive output and adult lifespan, for experimental temperatures below the reference temperature after removing studies in which the rearing temperature was not specified. N= 1108 effect sizes and 113 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Lifespan (mean)	-0.124	-0.670	0.422	-0.45	0.66
Reproduction (mean)	0.102	-0.775	0.979	0.23	0.82
Linear difference from reference temperature (°C)- Lifespan	-0.336	-0.447	-0.224	-5.93	< 0.001
Linear difference from reference temperature (°C)- Reproduction	0.159	-0.024	0.342	1.71	0.09
Quadratic difference from reference temperature (°C)- Lifespan	-0.014	-0.020	-0.009	-5.01	< 0.001
Quadratic difference from reference temperature (°C)- Reproduction	-0.002	-0.011	0.007	-0.41	0.68

Table S25. Parameter estimates from a multivariate meta-analysis model testing the effect of temperature on both reproductive output and adult lifespan, for experimental temperatures above the reference temperature. N= 1580 effect sizes and 174 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Lifespan (mean)	-0.361	-0.728	0.005	-1.94	0.05
Reproduction (mean)	0.771	0.193	1.350	2.62	0.009
Linear difference from reference temperature (°C)- Lifespan	-0.184	-0.220	-0.147	-9.92	< 0.001
Linear difference from reference temperature (°C)- Reproduction	-0.388	-0.449	-0.328	-12.57	< 0.001

Table S26. Parameter estimates from a multivariate meta-analysis model testing the effect of temperature on both reproductive output and adult lifespan, for experimental temperatures above the reference temperature after removing outliers. N= 1526 effect sizes and 172 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Lifespan (mean)	-0.367	-0.645	-0.088	-2.59	0.01
Reproduction (mean)	0.533	0.129	0.937	2.60	0.01
Linear difference from reference temperature (°C)- Lifespan	-0.153	-0.186	-0.120	-9.09	< 0.001
Linear difference from reference temperature (°C)- Reproduction	-0.274	-0.323	-0.225	-11.07	< 0.001

Table S27. Parameter estimates from a multivariate meta-analysis model testing the effect of temperature on both reproductive output and adult lifespan, for experimental temperatures above the reference temperature after removing short-term exposure treatments. N= 1416 effect sizes and 161 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Lifespan (mean)	-0.268	-0.654	0.119	-1.36	0.17
Reproduction (mean)	0.584	0.008	1.160	1.99	0.05
Linear difference from reference temperature (°C)- Lifespan	-0.219	-0.261	-0.176	-10.04	< 0.001
Linear difference from reference temperature (°C)- Reproduction	-0.383	-0.446	-0.319	-11.84	< 0.001

Table S28. Parameter estimates from a multivariate meta-analysis model testing the effect of temperature on both reproductive output and adult lifespan, for experimental temperatures above the reference temperature after removing studies in which the rearing temperature was not specified. N= 1161 effect sizes and 127 studies.

Term	Estimate	Lower 95% CI	Upper 95% CI	t	P
Lifespan (mean)	-0.212	-0.590	0.167	-1.10	0.27
Reproduction (mean)	1.045	0.321	1.769	2.84	0.005
Linear difference from reference temperature (°C)- Lifespan	-0.180	-0.219	-0.140	-8.98	< 0.001
Linear difference from reference temperature (°C)- Reproduction	-0.430	-0.503	-0.357	-11.60	< 0.001

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