Developmental Plasticity in Response to Temperature Aligns with Allen’s but not Bergmann’s Rule

Rachel E. Bockrath[1]*, Hailey R. Wimberly-Lehmann[1], Ned A. Dochtermann[1], Britt J. Heidinger[1]

[1]Department of Biological Sciences, North Dakota State University, North Dakota, United States of America

*Corresponding author: Rachel Elise Bockrath, rachel.bockrath@ndsu.edu

Keywords: Allen's Rule, Bergmann's Rule, Developmental Plasticity, Endotherm, Meta-Analysis, Thermal Environment

Abstract

Increases in average global temperatures have caused researchers to revisit how species and populations are expected to respond to changing temperatures. Allen’s rule and Bergmann’s rule describe two ecogeographic patterns where species in high (cold) latitudes have shorter limbs and larger bodies, respectively, than species at low (warm) latitudes. This pattern is purported to be due to the improved heat retention of short-limbed, large bodies, and improved heat dissipation of long-limbed, small bodies. While Allen’s and Bergmann’s rules are generally assumed to reflect adaptive outcomes, we sought to investigate the role of developmental plasticity in response to rearing temperature in producing these expected morphologies. To do so, we conducted a systematic review and meta-analysis to test the hypotheses that body shape and size will change plastically in response to experimentally manipulated thermal rearing environments and conform to the patterns predicted by Allen’s and Bergmann’s rules. Via a phylogenetic meta-analysis, we examined the relationship between temperature experienced by subjects during early life and subsequent body shape and size metrics. Our analysis of 40 studies included 243 estimates from 4 mammal species and 21 bird species, with some species contributing multiple estimates. Developmental plasticity generally produced morphologies in line with Allen’s rule, though not Bergmann’s rule. Changes in morphology were more prominent under artificially cold conditions than warm conditions. Mammals were generally more responsive than birds, though birds were better-represented in our final dataset. These results suggest that developmental plasticity may contribute to the ability of populations to respond to climate change and that broader biogeographical patterns may emerge from plastic responses.

Introduction

A persistent increase in global average temperatures and resulting shifts in climate can impact fitness in several ways, such as creating phenology mismatch (Visser et al. 1998; Plard et al. 2014), inducing mass casualty events (Conradie et al. 2020), reducing species' ranges (Sekercioglu et al. 2008; Morueta-Holme et al. 2010), and altering species' morphologies (Yom-Tov et al. 2006; Teplitsky and Millien 2014; Tabh and Nord 2023). Body shape (e.g. extremity length and area) and size (e.g. mass) interact with an individual's thermal environment via conduction, convection, and radiative heat transfer such that certain morphologies are advantageous under hot or cold conditions (Mitchell et al. 2018; Ryding et al. 2021). In endotherms, effective dissipation of excess body heat may affect an individual's ability to function under given environmental conditions, limiting their fitness (Speakman and Król 2010; Gardner et al. 2011; Ryding et al. 2021). Furthermore, differences in body shape and size are widely believed to be driven by thermal environment, as exemplified in Allen's and Bergmann's rules (Mayr 1956; Yom-Tov et al. 2006; Salewski and Watt 2017). Allen's rule describes the widely-observed phenomenon where species, or populations, have longer extremities at lower latitudes and in environments with high temperatures (Allen 1877; McQueen et al. 2022; Fröhlich et al. 2023; Tabh and Nord 2023). Bergmann's rule describes a similarly common phenomenon where species, or populations, possess smaller bodies at lower latitudes and in environments with high temperatures (Bergmann 1847; James 1970; McQueen et al. 2022; Fröhlich et al. 2023; Tabh and Nord 2023). Both patterns are hypothesized to result from the improved heat dissipation with greater relative surface area, and improved heat retention of bodies with low relative surface area (Bergmann 1847; Allen 1877; James 1970; Baldwin et al. 2023) but the degree to which species conform to either rule is variable (Fröhlich et al. 2023; Tabh and Nord 2023).

Implicit in many biogeographical studies of Allen's and Bergmann's rules is also the assumption that these patterns reflect adaptive responses (Tabh and Nord 2023). However, morphological changes are not always adaptive - decreases in body size and condition can also be induced by exposure to stressful early life conditions (Kraft et al. 2019; Almeida et al. 2021; Jaric et al. 2022). For example, under cold conditions the Thermal Advantage Hypothesis predicts an increase in body size for improved thermoregulation, while the Energy Efficiency Hypothesis predicts a decrease in body size due to metabolic constraints (Tabh and Nord 2023). Furthermore, some studies have called the thermal explanation for Bergmann's rule into question, proposing instead that resource availability due to the climate's influence over primary productivity is a stronger driver of endotherm body size (Rosenzweig 1968; McNab 2010). That is, in environments with abundant and widely available resources, species will tend to develop larger body sizes (Rosenzweig 1968; McNab 2010). Consistent with these predictions, studies on unmanipulated populations and museum specimens have found evidence that species and populations have developed smaller bodies and longer extremities with increasing global temperatures (Yom-Tov et al. 2006; Nudds and Oswald 2007; Van Buskirk et al. 2010; Gardner et al. 2011; DeVries et al. 2022; Shipley et al. 2022). The timeline of these changes suggests plastic responses rather than adaptive evolutionary change.

It is currently unclear whether developmental plasticity will align with biogeographic patterns and whether plasticity is sufficient to explain these patterns. Developmental phenotypic plasticity, where a trait such as morphology is shaped by the environment during early life, can aid an organism in adapting to changing environments by bringing their traits closer to the optimum for that environment (Ghalambor et al. 2007; Moczek et al. 2011). Here, via meta-analysis, we asked if the expression of developmental plasticity in response to rearing temperature aligned with the patterns described in Allen's and Bergmann's rules. To accomplish this, we analyzed studies that experimentally manipulated the thermal environment of terrestrial mammals or birds during growth phases of early life and subsequently recorded body shape or size metrics for these individuals. We limited our analysis to terrestrial endotherms as these are the species for which the rules were initially formulated (Pincheira-Donoso 2010; Gardner et al. 2011; Salewski and Watt 2017; Ryding et al. 2021).

If developmental plasticity in response to temperature is sufficient to generate the patterns described by Allen's and Bergmann's rules, we expect that 1) individuals who experienced relatively lower temperatures develop proportionally shorter or smaller appendages and larger mass or body dimensions relative to control individuals and/or 2) individuals who experienced relatively higher temperatures develop proportionally longer or larger appendages and smaller mass or body dimensions relative to control individuals. Additionally, we aimed to determine if the strength of these effects are a) influenced by the developmental timing of the thermal manipulation b) displayed more consistently by certain body structures, c) stronger in birds or mammals, and d) shown more in laboratory or field study settings.

Methods

Study acquisition and inclusion protocol

Studies in our meta-analysis were identified in three phases. First, on March 6th 2025 we searched the ISI Web of Science All Editions (WOS) with the following search terms, set as topics: (temperature* OR heat OR cold* OR cool* OR climate OR latitud* OR north* OR south* OR gradient OR thermal) AND (appendage OR mass OR volume OR "surface area" OR limb* OR "body size" OR tail OR bill OR beak OR wing OR size OR ear* OR leg* OR tars* OR body) AND ("early life" OR develop* OR increase* OR decrease* OR small* OR large* OR adjust* OR manipulate*) AND ("Bergmann's rule" OR "Allen's rule" OR allometry OR plasticity) NOT (evolution OR fossil OR observ* OR water OR ectotherm* OR altitude OR aquatic OR human OR elevation* OR fish* OR reptile OR insect OR amphibian OR invert*OR paleo*), along with the WOS

Categories of Zoology OR Evolutionary Biology OR Ecology. This search yielded a total of 1,460 papers. Three previously published review papers on this topic were also consulted, and of the 80 included references 15 were duplicates of those identified in the WOS search and were removed (Figure S1, Table S1). Second, on January 28th 2026 we reran the same search string to check for new relevant papers, which yielded a total of 1,528 papers, 65 of which were new to our data set. On February 5th 2026 22 papers that had been gathered opportunistically by HRW-L and REB in relation to other projects were added to the screening process. Finally, on May 6th 2026 a third search was conducted through PubMed. Due to the differences in article indexing in PubMed, we searched for the following terms, all set as Title/Abstract: (temperature* OR heat OR cold* OR cool* OR climate OR latitud* OR north* OR south* OR gradient OR thermal) AND (appendage OR mass OR volume OR "surface area" OR limb* OR "body size" OR tail OR bill OR beak OR wing OR size OR ear OR ears OR leg OR legs OR tars* OR body) AND ("early life" OR develop* OR increase* OR decrease* OR small* OR large* OR adjust* OR manipulate*) AND ("Bergmann's rule" OR "Allen's rule" OR allometry OR plasticity) NOT (evolution OR fossil OR observ* OR water OR ectotherm* OR altitude OR aquatic OR human* OR elevation* OR fish* OR reptile OR insect OR amphibian OR invert* OR paleo* OR plant OR tree OR grass OR flower OR drosophila OR marine OR larva OR neuro* OR cell*). This new search yielded 699 papers. 174 of these papers were duplicates of previously identified articles and were removed. Two opportunistically identified papers were also considered during this phase of study acquisition. Thus, 1,525 papers were screened during the first phase, 87 papers during the second phase, and 527 papers during the third phase, for a total of 2,139 papers (Figure S1). Paper title and abstracts were screened, and a paper was included for full text review if it met all of the following criteria: (1) the species was a terrestrial mammal or a bird; (2) included an experimental temperature manipulation during early life, with data from a control group; (3) reported means and standard deviations or standard errors, with a sample size, for at least one body measurement. Eighty-four papers met these initial screening criteria, though after full-text screening 41 papers were removed. If a study did not report the sample sizes or body size metrics in the paper, we reached out to the authors for data to calculate the necessary summary statistics (n=19) or extracted the data from a figure in the paper (n=1). If we were still unable to collect the necessary data, the paper was also excluded (n=3). Forty studies were included in our final analysis (Figure S1).

Statistical Analysis

Data Extraction and Calculation of Effect Size

We extracted sample size, means, standard deviations, and/or standard error on all measurements from all studies. Standard errors were converted into standard deviations. Additional information was extracted as potential moderator effects: measurement type (mass, head and bill length, leg length, ear size, tail length, wing length), type of treatment (warm or cold), taxonomic information (class and species), setting of study (lab or field), study year, and treatment duration. Because the studies in this analysis had distinct warm, cold, and control treatments, temperature was treated as a categorical variable.

After dataset assembly, we used R (version 4.5.0) to obtain effect sizes and conducted our meta-analysis (R Core Team 2021). Using the *escalc* function from the *metafor* package (Viechtbauer 2010), standardized mean differences (SMDH, Hedge's g) and variances were calculated using the control and experimental means and standard deviations. The measure of SMDH allows for heteroskedastic population variance between the control and treatment groups.

Base models

We analyzed the overall effect of warm and cold treatments on body size by fitting our SMDHs and variances with multilevel mixed effects models via the *metafor* package. As we did not expect a monotonic relationship across both warm and cold temperatures, we ran separate models for warm and cold treatments. Base models included random effects of species, study ID, phylogenetic relationship, and estimate ID to account for variation arising from the hierarchical structure of the data. The phylogeny was generated from the Open Tree of Life using the r package *rotl* (Figure 1, (Michonneau et al. 2016; OpenTreeOfLife et al. 2019).

Calculation of heterogeneity and Moderator variables

The random effect variance components (σ^2) — species, study, sampling, phylogeny, estimate ID — from the model output were used to assess the proportion of heterogeneity attributable to each source. These calculations were modeled on Nakagawa and Santos (2012).

Moderators for measurement type, class, timing, and study setting were individually added to the base model to determine if they improved data fit. Likelihood-ratio tests were used to assess model fit with and without each moderator to determine the significance of moderators. Our group-specific estimates are reported as μ. Regarding Allen's rule, for mammals alone we included measures of ear size and tail length as both are considered important thermal heat windows (e.g. Richardson et al. 1988; Klir and Heath 1994). Other extremities relevant to Allen's rule in mammals were wing length, leg length, and the lengths of individual limb bones (e.g. Klir and Heath 1994; Tabh and Nord 2023). In considering Bergmann's rule in mammals, we collected only mass as a measure of overall body size (e.g. Ashton et al. 2000; Tabh and Nord 2023). Regarding Allen's rule, for birds we included wing length and tarsus length as measures of extremities. Both limbs have been shown to be involved in thermoregulation and have been used as measures relevant to Allen's rule by similar analyses (e.g. Fröhlich et al. 2023; Tabh and Nord 2023; Weeks et al. 2025). In considering Bergmann's rule, we collected mass as a measure of overall body size for birds (e.g. Weeks et al. 2022; Fröhlich et al. 2023; Tabh and Nord 2023). Finally, in birds we also included measurements of the entire skull - the total length of the bill and the cranium together - as this is recognized as a proxy for skeletal size (Ardia et al. 2010; Ben-Ezra and Burness 2017).

Publication Bias

We assessed the potential for two types of publication bias, small-study biases and time-lag biases. However, typical methods for assessing small-study bias are inappropriate for models with substantive heterogeneity and non-independence (Nakagawa et al. 2022). Therefore, to test for both forms of bias, we fitted a meta-regression including the square-root of the sampling variance (for small-study bias) and year of study publication (mean-centered, for time-lag bias) following Nakagawa et al. (2022).

Results

Our final set of 40 studies included 25 species, of which 21 were birds and only 4 were mammals (Table 1, Figure 1). Of the birds, Passeriformes were by far the most represented order with 13 species. Galliformes and Anseriformes were the next most common order with 4 and 3 species, respectively, while one Charadriiform was also included. Of the mammals, two belonged to the order Rodentia, one Artiodactyla and one Chiroptera. From these studies, we extracted 243 unique estimates, mostly measures of mass and limb length. Publication year ranged from 1969 to 2025, with the majority of estimates coming from the first two decades of the 21st century. During the review process for this study, we were made aware of two additional papers that fit into the criteria of our study (Serrat 2013; Tabh et al. 2025). However, since these papers were recommended outside of our normal process (i.e. formal search or happening across them) with the results already known, we did not elect to include them in our main analysis. We have, however, included tables in the supplementary materials from an analysis that did include these papers (Table S3, S4). This additional analysis did not result in inferences different from those discussed below.

Base Models

There was a significant effect of rearing temperature on body size measurements for cold treatments, with a grand mean of the standardized mean difference of -0.58 (95% CI: -0.93 – -0.24, p=0.0009), indicating that — contrary to Bergmann's rule — individuals reared under cold treatments had smaller overall body sizes compared to controls (Figure 2A). In contrast, there was not an overall significant effect of warm treatments (grand mean = 0.06, 95% CI: - 0.11 – 0.22, p=0.692, Figure 2B).

Heterogeneity

Heterogeneity was high for both the warm treatments and cold treatments models (Table 2). In the cold model, species was the largest source of heterogeneity at 60.34%, indicating that species identity strongly influenced their response to the cold treatments (Table 2, Figure 1). In the warm model, study was the largest source of non-residual heterogeneity at 29.05%, suggesting that some of the variation is due to dissimilarities among study systems or design

(Table 2). Phylogeny contributed 7.57% and 10.93% of the heterogeneity in cold and warm studies, respectively (Table 2). In the cold model, residual heterogeneity contributed only 18.59%, while in the warm model residual heterogeneity contributed 54.54% (Table 2), indicating that the effect of moderators explained a much higher proportion of our data heterogeneity in the warm treatments (Table 2). With the additional studies, heterogeneity from species dropped slightly in the cold studies, and increased in the warm studies (Table S3).

Moderator Effects

Moderators varied in the direction and intensity of their effects under both cold and warm treatments. The inclusion of what body features were measured and the inclusion of class significantly improved both models (Table 3, Figure 1). The cold treatments had an effect during both the pre-birth and post-birth stages (μ =-0.39, p=0.004 & μ=-0.91, p<0.0001; Figure 2, Table S2). Under the cold treatments there were also significant treatment effects for both birds and mammals (μ=-0.44, p<0.0001 & μ=-1.19, p<0.0001) and under lab and field settings (μ=-0.61, p=0.004 & μ=-0.52, p=0.11; Figure 2, Table S2). Measures of mass (μ=-0.56, p<0.0001), head and bill (μ=-0.97, p<0.0001), leg (μ=-0.29, p=0.022), ear (μ=-1.82, p<0.0001,), and tail (μ=-1.12, p<0.0001,) were all significantly smaller under cold treatments (Figure 2, Table S2). Under warm treatments, neither the timing nor setting of the study were significant (Figure 2, Table S2). Under the warm treatments, there were significant effects for mammals (μ=0.63, p=0.001) and measurements of ear (μ=1.11, p=0.004), and tail (μ=0.93, p=0.027, Figure 2, Table S2). With additional measurements from the new quail study, wings also decreased significantly in cold studies (μ=-0.49, p=0.028, Table S4).

Publication Bias

Based on multilevel meta-regression analysis, there was no evidence for small-sample bias in the dataset for either cold (slope = -0.02, p = 0.968) or warm treatments (slope = 0.67, p = 0.208). There was also no evidence for time-lag bias in the cold treatments (slope = 0.03, p = 0.071) or the warm treatments (slope = 0.01, p = 0.276).

Discussion

Here, we sought to determine if the morphological patterns associated with Allen's and Bergmann's rules can be induced via developmental plasticity in response to early life environmental temperature. Our meta-analysis revealed that patterns of changes in extremities generally aligned with Allen's rule, that cold temperatures induced more changes than warm, and mammals were more responsive than birds. However, there were no effects due to the timing of the temperature treatments, nor of the study setting. This suggests greater complexity in the interplay between thermal environment and morphology than has previously been described.

Developmental phenotypic plasticity commonly generated morphological changes in line with Allen’s rule. Under cold conditions we saw significant decreases in most extremities, and under warm conditions we saw significant increases in a subset of extremities. We did not see the same support for Bergmann’s rule, as both metrics of general body size decreased rather than increased under cold conditions, and neither significantly changed under warm conditions. If plastic responses were consistent with either the Thermal Advantage Hypothesis or Bergmann’s rule, we would have observed larger body size under cold conditions (Tabh and Nord 2023). Instead, we found support for the Energy Efficiency hypothesis (Tabh and Nord 2023). Individuals exposed to cold treatments may spend more energy maintaining internal body temperature, leaving less for growth, and thus potentially generating nonadaptive phenotypes (Olson et al. 2006; Shipley et al. 2022; Tabh and Nord 2023). It is also possible that, as reported by Fröhlich et al. (2023), changes in body size and shape represent two distinct methods of responding to thermoregulatory challenges. Our study indicates that extremities are significantly larger under warm temperatures and significantly smaller under cold temperatures due to the high plasticity of these structures. Consistent with several other studies, we conclude that there is evidence for a thermal explanation for Allen’s rule (Nudds and Oswald 2007; Ryding et al. 2021; McQueen et al. 2022; Tabh and Nord 2023). However, we note that our few estimates of ear and tail measurements come exclusively from our small pool of mammals, and thus the conclusions regarding Allen’s rule under warm conditions should be considered cautiously. Furthermore, the magnitude of heterogeneity associated with species identity in the cold model indicates that responses to cold conditions in particular is likely mediated by species-specific traits such as ecology. The impact of phylogeny further indicates that differences in plasticity may also reflect evolutionary history.

Cold treatments induced more consistent changes in morphology than warm treatments. Nearly all our moderators decreased under cold conditions, while very few changed under warm conditions. Observational studies using museum specimens have found that seasonal temperature minimums are better predicters of body and extremity size than temperature maximums (Fan et al. 2019; Alhajeri et al. 2020), which aligns with our finding that cold conditions induce greater and more universal changes than warm conditions. However, most experiments included in our analysis that increased temperatures during development did so to within 2°C of controls, which may not be strong enough to trigger major changes in development due to warm conditions for some organisms. Since warm treatments were often, though not universally, smaller in magnitude than cold treatments, it is possible that the general lack of change under warm treatments is in part an artifact of study design. This asymmetry may partially explain why impacts on body size and shape were largely inconclusive for warm treatments. Further, we observed that the duration of temperature treatments, both in terms of the absolute number of days and the proportion of development in each species, ranged widely. We recommend that future studies push thermal challenges further, particularly for warm treatments, and that future reviews investigate the influence of duration.

Mammals were more responsive to thermal rearing environment than birds. While both birds and mammals were smaller under cold conditions, mammals alone had larger extremities under warm conditions. However, our study sample was heavily biased towards birds, particularly of the family *Paridae*, and only 4 species of mammals were represented (Table 1, Figure 1). Further evidence of this taxonomic imbalance can be seen with more reviews of Allen's and Bergmann's rules focusing on birds in recent years (e.g. Salewski and Watt 2017; Baldwin et al. 2023, but see Gohli and Voje 2016). This taxonomic imbalance is potentially important because analyses in other areas of evolutionary ecology have found that taxonomic bias in the studies used by meta-analyses can drastically change the generalizations made from meta-analytical results (Dochtermann et al. 2026). We believe that further empirical studies on a range of non-model species, particularly non-model mammals, will prove particularly informative. Our current taxonomic limitations unfortunately hinder our ability to generalize across many major endotherm orders. Given that the majority of the species and estimates come from passerine birds, our conclusions regarding the response of mass and limb length are strongest for this group.

The moderators of timing and setting did not improve model fit. Exposure to cold temperatures during either the pre-hatch/birth or post-hatch/birth resulted in a reduced body size. Thus, plastic responses to cold temperatures is not limited to a particular developmental phase, which agrees with observations made by Nord and Giroud (2020). Decreases in body size under the cold treatments were significant in both lab and field settings, while there was no difference under the warm treatments. This indicates that studies undertaken in either setting can sufficiently manipulate cold developmental temperature to induce plastic changes.

In this study we asked if developmental plasticity in response to thermal environment during early life generates morphologies that align with the patterns described by Allen's and Bergmann's rules in terrestrial endotherms. Our meta-analysis showed that the responses to temperature are not universal for body measurements, nor between cold and warm conditions, which lends considerable support to conclusions that have been suggested by previous reviews (Gardner et al. 2011; Teplitsky and Millien 2014; Tabh and Nord 2023). Additionally, our dataset highlights taxonomic gaps in our understanding of how endotherms plastically respond to thermal environment during early life. Our meta-analysis also showed that developmental plasticity can produce morphologies that align with Allen's rule, which may aid species' abilities to adapt to global climate change through improved thermoregulatory abilities. It is also worth noting that even when changes in morphology align with Allen's or Bergmann's rules, this does not inherently indicate that such changes are adaptive (Teplitsky et al. 2008; Tabh et al. 2025). Given the variability in our dataset, we suggest that broad generalizations may be hard to make based on individual empirical studies. To determine whether the results of developmental plasticity generally align with the patterns of Allen's and Bergmann's rules, future experimental studies should cover a greater diversity of species and a greater range of temperatures. Future biogeographical studies should also more clearly differentiate between instances where patterns are expected to be the product of genetic change and adaptation or could be produced via phenotypic plasticity.

Authors Contributions:

Rachel E. Bockrath: Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Visualization, Writing – original draft, Writing – review & editing

Hailey R. Wimberly-Lehmann: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing

Ned A. Dochtermann: Formal analysis, Methodology, Project administration, Supervision, Visualization, Writing – review & editing

Britt J. Heidinger: Project administration, Supervision, Writing – review & editing

Acknowledgements: We express our most sincere thanks to all the researchers whose data was used in this project. In particular, thank you to those who shared their raw data with us so that we could calculate the statistics necessary for this analysis; your generosity and quick replies greatly improved this analysis. We would like to thank our reviewers whose comments helped improve this manuscript.

Funding: Support for this project came from NSF IOS 1845974.

Supplementary data: Supplementary data can be found online.

Conflict of Interest Statement: The authors declare that there are no conflicts of interest.

Data Availability Statement: All data used for this meta-analysis has come from previously published articles. A summary file with all the data underlying this article and the code used in our analysis can be found on our OSF repository *https://osf.io/32xr7/overview?view_only=8a9c91e984ff47d38cd06deb55f368b0*

Citations

Alhajeri BH, Fourcade Y, Upham NS, Alhaddad H. 2020. A global test of Allen's rule in rodents. Global Ecology and Biogeography 29:2248–60.

Al-Hilli F, Wright EA. 1983. The effects of changes in the environmental temperature on the growth of bone in the mouse. Radiological and morphological study. Br J Exp Pathol 64:43–52.

Allen J. 1877. The influence of physical conditions in the genesis of species. Radical Review 1:108–40.

Almeida LZ, Hovick SM, Ludsin SA, Marschall EA. 2021. Which factors determine the long-term effect of poor early-life nutrition? A meta-analytic review. Ecosphere 12:e03694.

Álvarez E, Barba E. 2014. Behavioural responses of great tits to experimental manipulation of nest temperature during incubation. Ornis Fennica 91:220–30.

Andreasson F, Nord A, Nilsson J-Å. 2018. Experimentally increased nest temperature affects body temperature, growth and apparent survival in blue tit nestlings. Journal of Avian Biology 49:jav-01620.

Ardia DR, Pérez JH, Clotfelter ED. 2010. Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. Proc Biol Sci 277:1881–88.

Ashton KG, Tracy MC, Queiroz A de. 2000. Is Bergmann's Rule Valid for Mammals? The American Naturalist 156:390–415.

Baldwin JW, Garcia-Porta J, Botero CA. 2023. Complementarity in Allen's and Bergmann's rules among birds. Nat Commun 14:4240.

Ballinger MA, Nachman MW. 2022. The Contribution of Genetic and Environmental Effects to Bergmann's Rule and Allen's Rule in House Mice. The American Naturalist 199:691–704.

Ben-Ezra N, Burness G. 2017. Constant and Cycling Incubation Temperatures Have Long-Term Effects on the Morphology and Metabolic Rate of Japanese Quail. Physiological and Biochemical Zoology 90:96–105.

Bergmann C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Größe. Göttinger Studien 1:595–708.

Bleu J, Agostini S, Biard C. 2017. Nest-box temperature affects clutch size, incubation initiation, and nestling health in great tits. Behav Ecol 28:793–802.

Conradie SR, Woodborne SM, Wolf BO, Pessato A, Mariette MM, McKechnie AE. 2020. Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. Conservation Physiology 8:coaa048.

Corregidor-Castro A, Jones OR. 2021. The effect of nest temperature on growth and survival in juvenile Great Tits *Parus major*. Ecology and Evolution 11:7346–53.

Dawson RD, Lawrie CC, O'Brien EL. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. Oecologia 144:499–507.

DeVries MS, Waraczynski M, Baldassarre D, Slevin M, Anderson R, Jawor J. 2022. Geographic variation in morphology of Northern Cardinals: possible application of Bergmann's Rule? Journal of Field Ornithology 93.

Dochtermann NA, Sekhar MA, Nakagawa S. 2026. Ungeneralizable generalizations? A meta-meta-analysis of the influence of taxonomic bias on the study of behavior. 236:123542.

Duncan PA, Tauber AM, Sakaluk SK, Thompson CF. 2024. Interactive effects of increased nestbox temperature and vitamin E on nestling growth are attenuated by plasticity in female incubation effort. Ethology 130:e13421.

DuRant SE, Hepp GR, Moore IT, Hopkins BC, Hopkins WA. 2010. Slight differences in incubation temperature affect early growth and stress endocrinology of wood duck (*Aix sponsa*) ducklings. Journal of Experimental Biology 213:45–51.

DuRant SE, Hopkins WA, Wilson AF, Hepp GR. 2012. Incubation temperature affects the metabolic cost of thermoregulation in a young precocial bird. Functional Ecology 26:416–22.

Eiby YA, Booth DT. 2009. The effects of incubation temperature on the morphology and composition of Australian Brush-turkey (*Alectura lathami*) chicks. J Comp Physiol B 179:875–82.

Fan L, Cai T, Xiong Y, Song G, Lei F. 2019. Bergmann's rule and Allen's rule in two passerine birds in China. Avian Res 10:34.

Fröhlich A, Kotowska D, Martyka R, Symonds MRE. 2023. Allometry reveals trade-offs between Bergmann's and Allen's rules, and different avian adaptive strategies for thermoregulation. Nat Commun 14:1101.

García-del Río M, Cantarero A, Castaño-Vázquez F, Merino Y, García-Velasco J, Merino S. 2025. Experimental manipulation of nest temperature and relative humidity reduces ectoparasites and affects body condition of Blue Tits (*Cyanistes caeruleus*). Ibis 167:212–24.

Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. 2011. Declining body size: a third universal response to warming? Trends in Ecology & Evolution 26:285–91.

Ghalambor CK, McKAY JK, Carroll SP, Reznick DN. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21:394–407.

Ghimire A, Young RC, Westneat DF, Heidinger BJ. 2025. Repeated Experimental Cold Exposure During Early Life Affects Several Metrics of Success but not Telomeres in a Common Songbird. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology n/a:1–9.

Gohli J, Voje KL. 2016. An interspecific assessment of Bergmann's rule in 22 mammalian families. BMC Evol Biol 16:222.

Gurley B, Finger JW, Wada H. 2018. Sex-Specific Effects of Incubation Temperature on Embryonic Development of Zebra Finch (*Taeniopygia guttata*) Embryos. Physiological and Biochemical Zoology 91:1036–45.

Hepp GR, Kennamer RA. 2012. Warm Is Better: Incubation Temperature Influences Apparent Survival and Recruitment of Wood Ducks (*Aix sponsa*). PLoS ONE 7:e47777.

Hope SF, Kennamer RA, Moore IT, Hopkins WA. 2018. Incubation temperature influences the behavioral traits of a young precocial bird. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology 329:191–202.

James FC. 1970. Geographic Size Variation in Birds and Its Relationship to Climate. Ecology 51:365–90.

Jaric I, Voelkl B, Clerc M, Schmid MW, Novak J, Rosso M, Rufener R, Kortzfleisch VT von, Richter SH, Buettner M, Bleich A, Amrein I, Wolfer DP, Touma C, Sunagawa S, Würbel H. 2022.

The rearing environment persistently modulates mouse phenotypes from the molecular to the behavioural level. PLOS Biology 20:e3001837.

Klir JJ, Heath JE. 1994. Thermoregulatory responses to thermal stimulation of the preoptic anterior hypothalamus in the red fox (*Vulpes vulpes*). Comparative Biochemistry and Physiology Part A: Physiology 109:557–66.

Koláčková M, Kreisinger J, Albrecht T, Hořák D. 2019. Effect of incubation temperature on sex-dependent embryo mortality and morphological traits in Mallard. Journal of Thermal Biology 83:95–102.

Kraft F-LOH, Driscoll SC, Buchanan KL, Crino OL. 2019. Developmental stress reduces body condition across avian life-history stages: A comparison of quantitative magnetic resonance data and condition indices. General and Comparative Endocrinology 272:33–41.

Marks C, Nickles NE, Wise T, Mavroidis S. 2017. Incubation Temperature Alters Temperature-Dependent Oxygen Consumption in Northern Bobwhite Quail Hatchlings (*Colinus virginianus*). Physiological and Biochemical Zoology 90:478–83.

Mayr E. 1956. Geographical Character Gradients and Climatic Adaptation. Evolution 10:105–8.

McNab BK. 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. Oecologia 164:13–23.

McQueen A, Klaassen M, Tattersall GJ, Atkinson R, Jessop R, Hassell CJ, Christie M, Victorian Wader Study Group, Australasian Wader Studies Group, Symonds MRE. 2022. Thermal adaptation best explains Bergmann's and Allen's Rules across ecologically diverse shorebirds. Nat Commun 13:4727.

Michonneau F, Brown JW, Winter DJ. 2016. rotl: an R package to interact with the Open Tree of Life data. Methods in Ecology and Evolution 7:1476–81.

Mitchell D, Snelling EP, Hetem RS, Maloney SK, Strauss WM, Fuller A. 2018. Revisiting concepts of thermal physiology: Predicting responses of mammals to climate change. Journal of Animal Ecology 87:956–73.

Moczek A, Sultan S, Foster S, Ledón-Rettig C, Dworkin I, Nijhout H, Abouheif E, Pfennig D. 2011. The role of developmental plasticity in evolutionary innovation. Proceedings Biological sciences / The Royal Society 278:2705–13.

Morueta-Holme N, Fløjgaard C, Svenning J-C. 2010. Climate Change Risks and Conservation Implications for a Threatened Small-Range Mammal Species. PLoS ONE 5:e10360.

Mundinger C, Wolf JM, Gogarten JF, Fierz M, Scheuerlein A, Kerth G. 2023. Artificially raised roost temperatures lead to larger body sizes in wild bats. Current Biology 33:3977-3984.e4.

Nakagawa S, Lagisz M, Jennions MD, Koricheva J, Noble DWA, Parker TH, Sánchez-Tójar A, Yang Y, O'Dea RE. 2022. Methods for testing publication bias in ecological and evolutionary meta-analyses. Methods in Ecology and Evolution 13:4–21.

Nakagawa S, Santos ESA. 2012. Methodological issues and advances in biological meta-analysis. Evol Ecol 26:1253–74.

Nilsson JF, Stjernman M, Nilsson J-Å. 2008. Experimental reduction of incubation temperature affects both nestling and adult blue tits *Cyanistes caeruleus*. Journal of Avian Biology 39:553–59.

Nord A, Giroud S. 2020. Lifelong Effects of Thermal Challenges During Development in Birds and Mammals. Front Physiol 11.

Nord A, Nilsson J-Å. 2011. Incubation Temperature Affects Growth and Energy Metabolism in Blue Tit Nestlings. The American Naturalist 178:639–51.

Nudds RL, Oswald SA. 2007. An interspecific test of Allen's rule: Evolutionary implications for endothermic species. Evolution 61:2839–48.

Olson CR, Vleck CM, Vleck D. 2006. Periodic Cooling of Bird Eggs Reduces Embryonic Growth Efficiency. Physiological and Biochemical Zoology 79:927–36.

OpenTreeOfLife, Redelings B, Luisa L, Reyes S, Cranston KA, Allman J, Holder MT, McTavish EJ. 2019. Open Tree of Life Synthetic Tree. 12.3.

Ospina EA, Merrill L, Benson TJ. 2018. Incubation temperature impacts nestling growth and survival in an open-cup nesting passerine. Ecology and Evolution 8:3270–79.

Pincheira-Donoso D. 2010. The balance between predictions and evidence and the search for universal macroecological patterns: taking Bergmann's rule back to its endothermic origin. Theory Biosci 129:247–53.

Plard F, Gaillard J-M, Coulson T, Hewison AJM, Delorme D, Warnant C, Bonenfant C. 2014. Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer. PLoS Biol 12:e1001828.

R Core Team. 2021. R: The R Project for Statistical Computing. (https://www.r-project.org/).

Reyna KS. 2019. Acute exposure to hyperthermic oscillating temperatures during pre-incubation influences northern bobwhite development, hatching, and survival. PLoS ONE 14:e0219368.

Richardson DR, Shepherd S, McSorley T. 1988. Evaluation of the role of skin temperature in the response of cutaneous capillary blood flow to indirect heat. Microcirculation, Endothelium, and Lymphatics 4:447–67.

Rodríguez S, Barba E. 2016. Effects of Cool Nest Microclimates on Nestling Development: An Experimental Study with Mediterranean Great Tits *Parus major*. arla 63:251–60.

Rodríguez S, Diez-Méndez D, Barba E. 2016. Negative Effects of High Temperatures During Development on Immediate Post-Fledging Survival in Great Tits *Parus major*. aorn 51:235–44.

Rosenzweig ML. 1968. The Strategy of Body Size in Mammalian Carnivores. The American Midland Naturalist 80:299–315.

Ryding S, Klaassen M, Tattersall GJ, Gardner JL, Symonds MRE. 2021. Shape-shifting: changing animal morphologies as a response to climatic warming. Trends in Ecology & Evolution 36:1036–48.

Salewski V, Watt C. 2017. Bergmann's rule: a biophysiological rule examined in birds. Oikos 126.

Sant'Anna GM, Mortola JP. 2003. Thermal and respiratory control in young rats exposed to cold during postnatal development. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 134:449–59.

Sekercioglu CH, Schneider SH, Fay JP, Loarie SR. 2008. Climate Change, Elevational Range Shifts, and Bird Extinctions. Conservation Biology 22:140–50.

Serrat MA. 2013. Allen's Rule Revisited: Temperature Influences Bone Elongation During a Critical Period of Postnatal Development. The Anatomical Record 296:1534–45.

Serrat MA, King D, Lovejoy CO. 2008. Temperature regulates limb length in homeotherms by directly modulating cartilage growth. Proc Natl Acad Sci USA 105:19348–53.

Shipley JR, Twining CW, Taff CC, Vitousek MN, Winkler DW. 2022. Selection counteracts developmental plasticity in body-size responses to climate change. Nat Clim Chang 12:863–68.

Snedecor JG. 1971. Responses of Normal and Goitrogen-fed Cockerels to Different Environmental Temperatures. Poultry Science 50:237–43.

Speakman JR, Król E. 2010. The Heat Dissipation Limit Theory and Evolution of Life Histories in Endotherms—Time to Dispose of the Disposable Soma Theory? Integrative and Comparative Biology 50:793–807.

Stier A, Metcalfe NB, Monaghan P. 2020. Pace and stability of embryonic development affect telomere dynamics: an experimental study in a precocial bird model. Proc Biol Sci 287.

Tabh JKR, Nord A. 2023. Temperature-dependent Developmental Plasticity and Its Effects on Allen's and Bergmann's Rules in Endotherms. Integrative And Comparative Biology icad026.

Tabh JKR, Persson E, Correia M, Cuív CÓ, Thoral E, Nord A. 2025. Limited evidence that body size shrinking and shape-shifting alleviate thermoregulatory pressures in a warmer world. Commun Biol 8:707.

Teplitsky C, Millien V. 2014. Climate warming and Bergmann's rule through time: is there any evidence? Evolutionary Applications 7:156–68.

Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merilä J. 2008. Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. Proc Natl Acad Sci USA 105:13492–96.

Teulier L, Rouanet J-L, Rey B, Roussel D. 2014. Ontogeny of non-shivering thermogenesis in Muscovy ducklings (*Cairina moschata*). Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 175:82–89.

Ton R, Martin TE. 2024. Experimental warming of embryos accelerates metabolism of postnatal songbirds, influences growth, but has no effects on parental feeding and brooding rates. Ornithology 141:ukad058.

Van Buskirk J, Mulvihill RS, Leberman RC. 2010. Declining body sizes in North American birds associated with climate change. Oikos 119:1047–55.

Vaugoyeau M, Meylan S, Biard C. 2017. How does an increase in minimum daily temperatures during incubation influence reproduction in the great tit *Parus major*? Journal of Avian Biology 48:714–25.

Vedder O, Verhulst S, Zuidersma E, Bouwhuis S. 2018. Embryonic growth rate affects telomere attrition: an experiment in a wild bird. Journal of Experimental Biology jeb.181586.

Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36:1–48.

Villarreal JA, Schlegel WM, Prange HD. 2007. Thermal environment affects morphological and behavioral development of *Rattus norvegicus*. Physiology & Behavior 91:26–35.

Visser ME, Noordwijk AJV, Tinbergen JM, Lessells CM. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proc R Soc Lond B 265:1867–70.

Wada H, Kriengwatana B, Allen N, Schmidt KL, Soma KK, MacDougall-Shackleton SA. 2015. Transient and permanent effects of suboptimal incubation temperatures on growth, metabolic rate, immune function, and adrenocortical responses in zebra finches. Journal of Experimental Biology 2847–55.

Weaver ME, Ingram DL. 1969. Morphological Changes in Swine Associated with Environmental Temperature. Ecology 50:710–13.

Weeks BC, Harvey C, Tobias JA, Sheard C, Zhou Z, Fouhey DF. 2025. Longer Wing Bones in Warmer Climates Suggest a Role of Thermoregulation in Bird Wing Evolution. Global Ecology and Biogeography 34:e70033.

Weeks BC, Klemz M, Wada H, Darling R, Dias T, O'Brien BK, Probst CM, Zhang M, Zimova M. 2022. Temperature, size and developmental plasticity in birds. Biol Lett 18:20220357.

Woodruff MJ, Sermersheim LO, Wolf SE, Rosvall KA. 2023. Organismal effects of heat in a fixed ecological niche: Implications on the role of behavioral buffering in our changing world. Science of The Total Environment 893:164809.

Yom-Tov Y, Yom-Tov S, Wright J, J. R. Thorne C, Du Feu R. 2006. Recent changes in body weight and wing length among some British passerine birds. Oikos 112:91–101.

Figures and Tables:

Table 1: Species in our dataset with the type of temperature treatment applied, sample size ranges between groups, and the studies included.

Species	Temperature	Sample size range	Number studies	Included Studies
Mus musculus domesticus	Warm & Cold	9-10	2	Serrat et al. 2008; Ballinger and Nachman 2022
Myotis bechsteinii	Warm	52-71	1	Mundinger et al. 2023
Rattus norvegicus	Cold	9-20	2	Sant'Anna and Mortola 2003; Villarreal et al. 2007
Sus scrofa domesticus	Warm & Cold	2-4	1	Weaver and Ingram 1969
Aix sponsa	Warm & Cold	10-139	4	DuRant et al. 2010, 2012; Hepp and Kennamer 2012; Hope et al. 2018
Alectura lathami	Warm & Cold	10-15	1	Eiby and Booth 2009
Anas platyrhynchos	Warm & Cold	7-136	1	Koláčková et al. 2019
Cairina moschata	Warm	8-38	1	Teulier et al. 2014
Cardellina rubrifrons	Cold	18-20	1	Ton and Martin 2024
Colinus virginianus	Warm	6-30	2	Marks et al. 2017; Reyna 2019
Coturnix japonica	Warm & Cold	15-26	2	Ben-Ezra and Burness 2017; Stier et al. 2020
Cyanistes caeruleus	Warm & Cold	19-140	4	Nilsson et al. 2008; Nord and Nilsson 2011; Andreasson et al. 2018; García-del Río et al. 2025
Empidonax occidentalis	Warm	7-24	1	Ton and Martin 2024
Gallus gallus	Warm & Cold	8-10	1	Snedecor 1971

Junco hyemalis	Warm	5-12	1	Ton and Martin 2024
Parus major	Warm & Cold	7-247	6	Álvarez and Barba 2014; Rodríguez and Barba 2016; Rodríguez et al. 2016; Bleu et al. 2017; Vaugoyeau et al. 2017; Corregidor-Castro and Jones 2021
Passer domesticus	Cold	53-483	1	Ghimire et al. 2025
Sialia mexicana	Warm	17-56	1	Ton and Martin 2024
Sterna hirundo	Cold	39-44	1	Vedder et al. 2018
Tachycineta bicolor	Warm & Cold	17-94	3	Dawson et al. 2005; Ardia et al. 2010; Woodruff et al. 2023
Taeniopygia castanotis	Warm	77-79	1	Ton and Martin 2024
Taeniopygia guttata	Warm & Cold	9-55	3	Wada et al. 2015; Gurley et al. 2018; Ton and Martin 2024
Troglodytes aedon	Warm	10-79	2	Duncan et al. 2024; Ton and Martin 2024
Turdus migratorius	Warm & Cold	8-26	1	Ospina et al. 2018
Yuhina everetti	Warm	16-38	1	Ton and Martin 2024

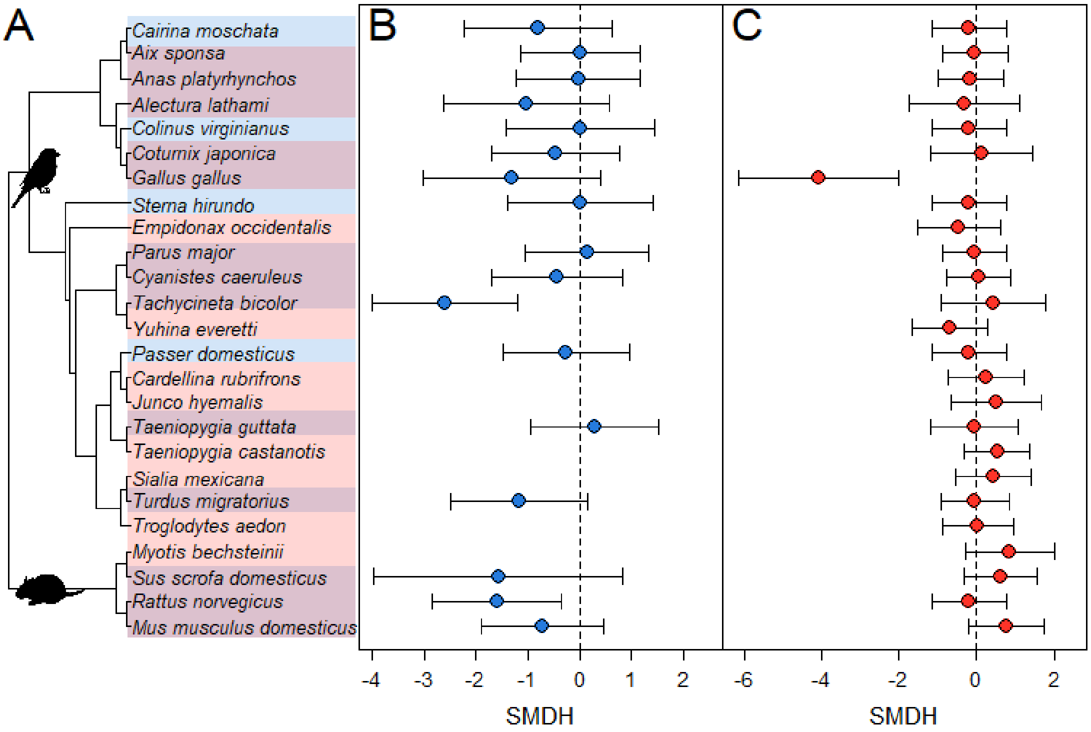
Table 2. The contributions to heterogeneity in cold and warm treatments, broken down into their tested components.

Cold treatments	
Source of Variation	Percentage
I^2_{total}	95.91
I^2_{study}	9.41
$I^2_{species}$	60.34
$I^2_{phylogeny}$	7.57
$I^2_{sampling}$	4.91
$I^2_{residual}$	18.59
Warm treatments	
I^2_{total}	94.53
I^2_{study}	29.05
$I^2_{species}$	0
$I^2_{phylogeny}$	10.93
$I^2_{sampling}$	5.47
$I^2_{residual}$	54.54

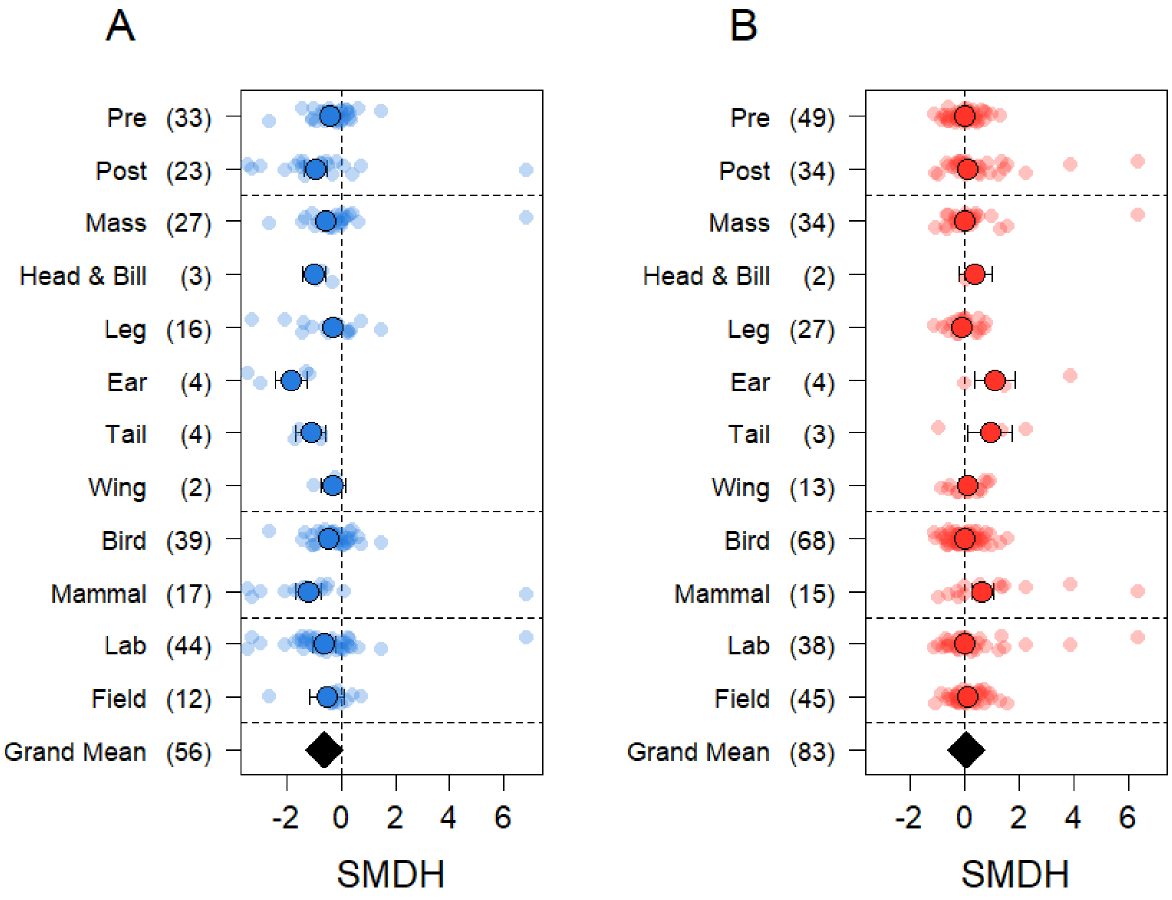
Table 3. Results of the likelihood-ratio tests for the effect of adding moderators onto the base models of the effects of cold and warm treatments. Moderators that significantly improved model fit are in bold.

Cold Treatments				
Moderator	Log-Likelihood	χ^2	df	p value
Timing	-61.59	2.83	6	0.093
Measurement	**-49.15**	**27.71**	**10**	**<0.0001**
Class	**-60.13**	**5.76**	**6**	**0.016**
Setting	-62.95	0.12	6	0.732
Base model	-61.91		5	
Warm Treatments				
Timing	-84.97	0.35	6	0.556
Measurement	**-78.44**	**13.41**	**10**	**0.020**
Class	**-80.61**	**9.06**	**6**	**0.003**
Setting	-85.03	0.22	6	0.638
Base model	-84.52		5	

Figure 1. Phylogenetic relationships among species included in meta-analyses and species-specific estimates of standardized mean differences (SMDH). (A) Phylogenetic relationships of included species. Species for which only cold treatments estimates were available are shaded in red; species for which only warm treatments estimates were available are shaded in blue; species for which both treatment estimates were available are shaded in purple. (B) Species-specific SMDH estimates and 95% confidence intervals for the effects of cold treatments. (C) Species-specific SMDH estimates and 95% confidence intervals for the effects of warm treatments.



594 Figure 2. The standardized mean differences (SMDH) for each moderator and the base model
595 from the cold treatments (A) and warm treatments (B) with confidence intervals and the means
596 of each study estimate. Sample sizes of each estimate are listed in parentheses next to the
597 moderator.



598

Supplemental Material:

Supplemental Table 1: All the papers that were considered for inclusion from other review papers. Bolded papers were included in the final dataset.

Reference Paper	Included Studies
Tabh, J. K., & Nord, A. (2023). Temperature-dependent developmental plasticity and its effects on Allen's and Bergmann's rules in endotherms.	Albustanji, L., Perez, G. S., AlHarethi, E., Aldiss, P., Bloor, I., Barreto-Medeiros, J. M., ... & Dellschaft, N. (2019). Housing temperature modulates the impact of diet-induced rise in fat mass on adipose tissue before and during pregnancy in rats.
	Andreasson, F., Nord, A., & Nilsson, J. Å. (2018). Experimentally increased nest temperature affects body temperature, growth and apparent survival in blue tit nestlings.
	Ballinger, M. A., & Nachman, M. W. (2022). The contribution of genetic and environmental effects to Bergmann's rule and Allen's rule in house mice.
	Barnett, S. A., & Dickson, R. G. (1984). Changes among wild house mice (Mus musculus) bred for ten generations in a cold environment, and their evolutionary implications.
	Burness, G., Huard, J. R., Malcolm, E., & Tattersall, G. J. (2013). Post-hatch heat warms adult beaks: irreversible physiological plasticity in Japanese quail.
	Dawson, R. D., Lawrie, C. C., & O'Brien, E. L. (2005). The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine.
	Ernst, R. A., Weathers, W. W., & Smith, J. (1984). Effects of heat stress on day-old broiler chicks.
	FRANCIS, B. S. (1909). Some effects of external conditions upon the white mouse.
	Herrington, L. P., & NELBACH, J. H. (1942). Relation of gland weights to growth and aging processes in rats exposed to certain environmental conditions.
	Johnson, J. S., Aardsma, M. A., Duttlinger, A. W., & Kpodo, K. R. (2018). Early life thermal stress: Impact on future thermotolerance, stress response, behavior, and intestinal morphology in piglets exposed to a heat stress challenge during simulated transport.
	May, J. D., & Lott, B. D. (2001). Relating weight gain and feed: gain of male and female broilers to rearing temperature.
	May, J. D., & Lott, B. D. (2001). Relating weight gain and feed: gain of male and female broilers to rearing temperature.
	Mujahid, A., & Furuse, M. (2009). Oxidative damage in different tissues of neonatal chicks exposed to low environmental temperature.
	Pérez, J. H., Ardia, D. R., Chad, E. K., & Clotfelter, E. D. (2008). Experimental heating reveals nest temperature affects nestling condition in tree swallows (Tachycineta bicolor).
	Riek, A., & Geiser, F. (2012). Developmental phenotypic plasticity in a marsupial.
	Rodríguez, S., & Barba, E. (2016). Effects of cool nest microclimates on nestling development: an experimental study with Mediterranean great tits Parus major.
	Serrat, M. A., King, D., & Lovejoy, C. O. (2008). Temperature regulates limb length in homeotherms by directly modulating cartilage growth.
	Snedecor, J. G. (1971). Responses of normal and goitrogen-fed cockerels to different environmental temperatures.

	Stawski, C., & Geiser, F. (2020). Growing up in a changing climate: how temperature affects the development of morphological, behavioral and physiological traits of a marsupial mammal. Sundstroem, E. S. (1922). Studies on the adaptation of albino mice to an artificially produced tropical climate: I. Effect of the various factors composing a tropical climate on growth and fertility of mice. Sundstroem, E. S. (1922). STUDIES ON THE ADAPTATION OF ALBINO MICE TO AN ARTIFICIALLY PRODUCED TROPICAL CLIMATE: II. Relations of the Body Form and Especially the Surface Area to the Reactions Released by and the Resistance to a Tropical Climate. Teulier, L., Rouanet, J. L., Rey, B., & Roussel, D. (2014). Ontogeny of non-shivering thermogenesis in Muscovy ducklings (Cairina moschata). Ton, R., Stier, A., Cooper, C. E., & Griffith, S. C. (2021). Effects of heat waves during post-natal development on mitochondrial and whole body physiology: an experimental study in zebra finches. Weaver, M. E., & Ingram, D. L. (1969). Morphological changes in swine associated with environmental temperature.
Weeks, B. C., Klemz, M., Wada, H., Darling, R., Dias, T., O'Brien, B. K., ... & Zimova, M. (2022). Temperature, size and developmental plasticity in birds.	**Álvarez E, Barba E. 2014 Behavioural responses of great tits to experimental manipulation of nest temperature during incubation.** **Andreasson F, Nord A, Nilsson JÅ. 2018 Experimentally increased nest temperature affects body temperature, growth and apparent survival in blue tit nestlings.** Andrew SC, Hurley LL, Mariette MM, Griffith SC. 2017 Higher temperatures during development reduce body size in the zebra finch in the laboratory and in the wild. **Ardia DR, Pérez JH, Clotfelter ED. 2010 Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows.** Auer SK, Martin TE. 2017 Parental care mitigates carry-over effects of poor early conditions on offspring growth. Beck ML, Hopkins WA, Jackson BP, Hawley DM. 2015 The effects of a remediated fly ash spill and weather conditions on reproductive success and offspring development in tree swallows. Belnap SC, Currea JP, Lickliter R. 2019 Prenatal incubation temperature affects neonatal precocial birds' locomotor behavior. **Ben-Ezra N, Burness G. 2017 Constant and cycling incubation temperatures have long-term effects on the morphology and metabolic rate of japanese quail.** **Bleu J, Agostini S, Biard C. 2017 Nest-box temperature affects clutch size, incubation initiation, and nestling health in great tits.** Cannell BL, Chambers LE, Wooller RD, Stuart Bradley J. 2012 Poorer breeding by little penguins near Perth, Western Australia is correlated with above average sea surface temperatures and a stronger Leeuwin Current. Castaño-Vázquez F, Martínez J, Merino S, Lozano M. 2018 Experimental manipulation of temperature reduce ectoparasites in nests of blue tits Cyanistes caeruleus. Chambers LE, Cullen JM, Coutin PC, Dann P. 2009 Predicting onset and success of breeding in little penguins Eudyptula minor from ocean temperatures. Cunningham SJ, Martin RO, Hojem CL, Hockey PAR. 2013 Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: A study of common fiscals.

Dawson RD, Lawrie CC, O'Brien EL. 2005 The importance of microclimate variation in determining size, growth and survival of avian offspring: Experimental evidence from a cavity nesting passerine.
Durant SE, Hepp GR, Moore IT, Hopkins BC, Hopkins WA. 2010 Slight differences in incubation temperature affect early growth and stress endocrinology of wood duck (Aix sponsa) ducklings.
DuRant SE, Hopkins WA, Wilson AF, Hepp GR. 2012 Incubation temperature affects the metabolic cost of thermoregulation in a young precocial bird.
Eiby YA, Booth DT. 2009 The effects of incubation temperature on the morphology and composition of Australian Brush-turkey (Alectura lathami) chicks.
Elsayed MA. 2016 Effects of thermal manipulation during late incubation period on post-hatch thermotolerance in ostrich.
Geiser S, Arlettaz R, Schaub M. 2008 Impact of weather variation on feeding behaviour, nestling growth and brood survival in Wrynecks Jynx torquilla.
Greño JL, Belda EJ, Barba E. 2008 Influence of temperatures during the nestling period on post-fledging survival of great tit Parus major in a Mediterranean habitat.
Gurley B, Finger JW, Wada H. 2018 Sex-specific effects of incubation temperature on embryonic development of zebra finch (Taeniopygia guttata) embryos.
Hepp GR, Kennamer RA. 2012 Warm Is Better: Incubation Temperature Influences Apparent Survival and Recruitment of Wood Ducks (Aix sponsa).
Imlay TL, Nickerson D, Horn AG. 2019 Temperature and breeding success for cliff swallows (Petrochelidon pyrrhonota) nesting on man-made structures: Ecological traps?
Jones BC, DuVal EH. 2019 Direct and indirect effects of the El Niño Southern Oscillation on development and survival of young of a tropical passerine.
Koláčková M, Kreisinger J, Albrecht T, Hořák D. 2019 Effect of incubation temperature on sex-dependent embryo mortality and morphological traits in Mallard.
Kruuk LEB, Osmond HL, Cockburn A. 2015 Contrasting effects of climate on juvenile body size in a Southern Hemisphere passerine bird.

Kvalnes T, Røberg AÅ, Jensen H, Holand H, Pärn H, Sæther BE, Ringsby TH. 2018 Offspring fitness and the optimal propagule size in a fluctuating environment.

Larson ER, Eastwood JR, Micallef S, Wehbe J, Bennett ATD, Berg ML. 2018 Nest microclimate predicts bill growth in the Adelaide rosella (Aves: Psittaculidae).
Londoño GA, Levey DJ, Robinson SK. 2008 Effects of temperature and food on incubation behaviour of the northern mockingbird, Mimus polyglottos.
Marks C, Nickles NE, Wise T, Mavroidis S. 2017 Incubation temperature alters temperature-dependent oxygen consumption in northern bobwhite quail hatchlings (Colinus virginianus).
Moreno J, González-Braojos S, Ruiz-De-Castañeda R. 2015 A spring cold snap is followed by an extreme reproductive failure event in a mountain population of Pied Flycatchers Ficedula hypoleuca.
Mueller AJ, Miller KD, Bowers EK. 2019 Nest microclimate during incubation affects posthatching development and parental care in wild birds.
Nilsson JÅ, Nord A. 2017 The use of the nest for parental roosting and thermal consequences of the nest for nestlings and parents.

	Nilsson JF, Stjernman M, Nilsson JÅ. 2008 Experimental reduction of incubation temperature affects both nestling and adult blue tits Cyanistes caeruleus. **Nord A, Nilsson JÅ. 2011 Incubation temperature affects growth and energy metabolism in blue tit nestlings.** Ospina EA, Merrill L, Benson TJ. 2018 Incubation temperature impacts nestling growth and survival in an open-cup nesting passerine. Pipoly I, Bókony V, Seress G, Szabó K, Liker A. 2013 Effects of extreme weather on reproductive success in a temperate-breeding songbird. Podlesak DW, Blem CR. 2001 Factors associated with growth of nestling Prothonotary Warblers. Wilson Bull. Potti J. 2008 Temperature during egg formation and the effect of climate warming on egg size in a small songbird. Reid JM, Monaghan P, Ruxton GD. 2000 Resource allocation between reproductive phases: The importance of thermal conditions in determining the cost of incubation. **Reyna KS. 2019 Acute exposure to hyperthermic oscillating temperatures during pre-incubation influences northern bobwhite development, hatching, and survival.** **Rodríguez S, Barba E. 2016 Effects of cool nest microclimates on nestling development: An experimental study with mediterranean great tits parus major.** Rodríguez S, Barba E. 2016 Nestling growth is impaired by heat stress: An experimental study in a mediterranean great tit population. **Rodríguez S, Diez-Méndez D, Barba E. 2016 Negative Effects of High Temperatures during Development on Immediate Post-Fledging Survival in Great Tits Parus major.** Rotenberry JT, Wiens JA. 1991 Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. Smith MG, Kaiser SA, Sillett TS, Webster MS. 2018 Variation in nest characteristics and brooding patterns of female Black-throated Blue Warblers is associated with thermal cues. **Teulier L, Rouanet JL, Rey B, Roussel D. 2014 Ontogeny of non-shivering thermogenesis in Muscovy ducklings (Cairina moschata).** **Vaugoyeau M, Meylan S, Biard C. 2017 How does an increase in minimum daily temperatures during incubation influence reproduction in the great tit Parus major?** Vedder O. 2012 Individual birds advance offspring hatching in response to increased temperature after the start of laying. **Wada H, Kriengwatana B, Allen N, Schmidt KL, Soma KK, MacDougall-Shackleton SA. 2015 Transient and permanent effects of suboptimal incubation temperatures on growth, metabolic rate, immune function and adrenocortical responses in zebra finches.** Wada H, Kriengwatana BP, Steury TD, Macdougall-Shackleton SA. 2018 Incubation temperature influences sex ratio and offspring's body composition in Zebra finches (Taeniopygia guttata).
Ryding, S., Klaassen, M., Tattersall, G. J., Gardner, J. L., & Symonds, M. R. (2021). Shape-shifting: changing	Al-Hilli, F., & Wright, E. A. (1983). The effects of changes in the environmental temperature on the growth of bone in the mouse. Burness, G., Huard, J. R., Malcolm, E., & Tattersall, G. J. (2013). Post-hatch heat warms adult beaks: irreversible physiological plasticity in Japanese quail.

animal morphologies as a response to climatic warming.	**Serrat, M. A., King, D., & Lovejoy, C. O. (2008). Temperature regulates limb length in homeotherms by directly modulating cartilage growth.** **Weaver, M. E., & Ingram, D. L. (1969). Morphological changes in swine associated with environmental temperature.**

Supplemental Table 2. Summary results from the models with each moderator individually included for cold and warm treatments. The estimates of each moderator variable and their associated confidence intervals are reported, and the significant categories are bolded.

Cold Treatment				
Moderator	Estimate Sample Size	Estimated Average Effect Size	Confidence interval	p-value
Timing				
Pre-birth	**33**	**-0.39**	**-0.66 – -0.13**	**0.004**
Post-birth	**23**	**-0.91**	**-1.34 – -0.49**	**<0.0001**
Measurement				
Mass	**27**	**-0.56**	**-0.75 – -0.37**	**<0.0001**
Head-Bill	**3**	**-0.97**	**-1.40 – -0.54**	**<0.0001**
Leg	**15**	**-0.29**	**-0.53 – 0.04**	**0.022**
Ear	**4**	**-1.82**	**-2.39 – -1.24**	**<0.0001**
Tail	**4**	**-1.12**	**-1.65 – -0.57**	**<0.0001**
Wing	2	-0.27	-0.72 – 0.18	0.243
Class				
Bird	**39**	**-0.44**	**-0.64 – -0.24**	**<0.0001**
Mammal	**17**	**-1.19**	**-1.68 – -0.69**	**<0.0001**
Setting				
Lab	**44**	**-0.61**	**-1.03 – -0.20**	**0.004**

Field	**12**	**-0.52**	**-1.16 – -0.12**	**0.11**
Warm Treatment				
Timing				
Pre-birth	49	0.02	-0.19 – 0.23	0.836
Post-birth	34	0.11	-0.14 – 0.37	0.396
Measurement				
Mass	34	0.01	-0.18 – 0.20	0.941
Head-Bill	2	0.39	-0.23 – 1.01	0.215
Leg	27	-0.10	-0.31 – 0.12	0.381
Ear	**4**	**1.11**	**0.36 – 1.87**	**0.004**
Tail	**3**	**0.93**	**0.11 – 1.75**	**0.027**
Wing	13	0.08	-0.21 – 0.37	0.602
Class				
Bird	68	-0.02	-0.16 – 0.13	0.809
Mammal	**15**	**0.64**	**0.25 – 1.03**	**0.001**
Setting				
Lab	38	-0.02	-0.22 – 0.26	0.887
Field	45	0.10	-0.14 – 0.33	0.420

Supplemental Table 3. Summary results for the models from the dataset which includes two papers suggested during review, with each moderator individually included for cold and warm treatments. The estimates of each moderator variable and their associated confidence intervals are reported, and the significant categories are bolded.

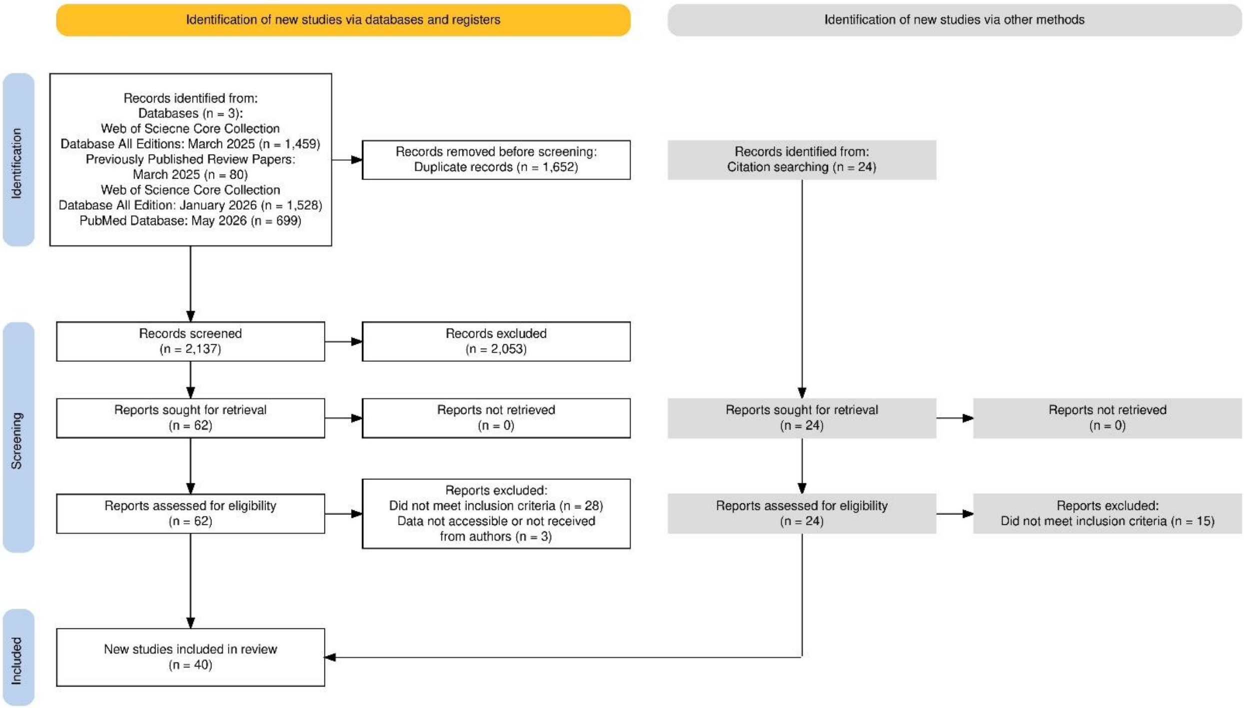
Cold Treatment				
Moderator	Estimate Sample Size	Estimated Average Effect Size	Confidence interval	p-value
Timing				
Pre-birth	**33**	**-0.39**	**-1.08 – -0.05**	**0.030**
Post-birth	**27**	**-0.57**	**-0.93 – -0.15**	**0.006**
Measurement				
Mass	**29**	**-0.54**	**-0.75 – -0.33**	**<0.0001**
Head-Bill	**3**	**-1.01**	**-1.48 – -0.54**	**<0.0001**
Leg	**16**	**-0.25**	**-0.52 – 0.02**	**0.065**
Ear	**4**	**-1.76**	**-2.36 – -1.15**	**<0.0001**
Tail	**5**	**-1.01**	**-1.55 – -0.47**	**0.0003**
Wing	**3**	**-0.49**	**-0.92 – -0.05**	**0.028**
Class				
Bird	**42**	**-0.41**	**-0.63 – -0.20**	**0.0002**
Mammal	**15**	**-1.17**	**-1.68 – -0.67**	**<0.0001**
Setting				
Lab	**43**	**-0.61**	**-1.03 – -0.20**	**0.004**

Field	**12**	**-0.52**	**-1.16 – -0.12**	**0.11**
Warm Treatment				
Timing				
Pre-birth	30	0.02	-0.18 – 0.22	0.858
Post-birth	57	0.16	-0.07 – 0.39	0.164
Measurement				
Mass	36	0.003	-0.18 – 0.19	0.978
Head-Bill	2	0.39	-0.23 – 1.01	0.217
Leg	27	-0.07	-0.28 – 0.14	0.506
Ear	**4**	**1.16**	**0.41 – 1.91**	**0.002**
Tail	**4**	**1.13**	**0.42 – 1.85**	**0.002**
Wing	14	0.04	-0.23 – 1.01	0.217
Class				
Bird	71	-0.0004	-0.14 – 0.13	0.996
Mammal	**13**	**0.63**	**0.27 – 0.99**	**0.0007**
Setting				
Lab	42	0.08	-0.17 – 0.33	0.532
Field	45	0.11	-0.14 – 0.36	0.380

Table S4. The contributions to heterogeneity in cold and warm treatments, broken down into their tested components from the dataset which includes two papers suggested during review.

Cold treatment	
Source of Variation	Percentage
I^2_{total}	95.98
I^2_{study}	15.49
$I^2_{species}$	48.79
$I^2_{phylogeny}$	13.50
$I^2_{sampling}$	4.02
$I^2_{residual}$	18.20
Warm treatment	
I^2_{total}	94.58
I^2_{study}	2.06
$I^2_{species}$	24.94
$I^2_{phylogeny}$	6.99
$I^2_{sampling}$	5.42
$I^2_{residual}$	60.59

Figure S1. PRISMA diagram of the searching, screening, and inclusion of the articles considered in the meta-analysis. Figure made using PRISMA Flow Diagram (Haddaway et al. 2022).



Supplemental References:

Haddaway NR, Page MJ, Pritchard CC, McGuinness LA. 2022. PRISMA2020: An R package and Shiny app for producing PRISMA 2020-compliant flow diagrams, with interactivity for optimized digital transparency and Open Synthesis. Campbell Systematic Reviews 18:e1230.