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Global change biology

Developmental environments do not affect thermal physiological traits in reptiles: an experimental test and meta-analysis

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On a global scale, organisms face significant challenges due to climate change and anthropogenic disturbance. In many ectotherms, developmental and physiological processes are sensitive to changes in temperature and resources. Developmental plasticity in thermal physiology may provide adaptive advantages to environmental extremes if early environmental conditions are predictive of late-life environments. Here, we conducted a laboratory experiment to test how developmental temperature and maternal resource investment influence thermal physiological traits (critical thermal maximum: CT_{max} and thermal preference: T_{pref}) in a common skink (*Lampropholis delicata*). We then compared our experimental findings more broadly across reptiles (snakes, lizards and turtles) using meta-analysis. In both our experimental study and meta-analysis, we did not find evidence that developmental environments influence CT_{max} or T_{pref} . Furthermore, the effects of developmental environments on thermal physiology did not vary by age, taxon or climate zone (temperate/tropical). Overall, the magnitude of developmental plasticity on thermal physiology appears to be limited across reptile taxa suggesting that behavioural or evolutionary processes may be more important. However, there is a paucity of information across most reptile taxa, and a broader focus on thermal performance curves themselves will be critical in understanding the impacts of changing thermal conditions on reptiles in the future.

1. Introduction

Climate warming and anthropogenic stressors pose significant challenges to organisms on a global scale [1,2]. Rapidly increasing temperatures are a particularly significant threat for ectothermic species. Indeed, increasing temperatures can drive fitness declines due to physiological intolerance [3] and alter the distribution of species [4]. Inevitably, these impacts are primarily mediated by how organisms change their behaviour and physiology through development and evolutionary time in response to shifting environments. Phenotypic changes that occur during an animal's lifetime in response to changing environments (i.e. phenotypic plasticity) are important mechanisms by which ectotherms can cope with climate change over short timescales [5]. However, the magnitude of plastic responses is widely trait- and species-specific [5–7]

Temperature can also have transgenerational effects by impacting parental generations [8,9]. For instance, recent evidence indicates that some ectotherms can tolerate heat events for long periods [5,10]. Thermal ecology of ectotherms can also be shaped by other factors, such as diet or maternal investment, which can influence physiological traits that are temperature dependent [11–13]. For example, a diet high in nutrients (carbohydrate or protein) leads to higher metabolic rates and critical thermal maximum (CT_{max}), while a diet low in these nutrients can result in lower physiological trait values [14–16]. Additionally, the resources a mother invests in her offspring (i.e. the energetic provisioning of eggs) can influence metabolic processes like growth and development [17]. Determining how thermal and resource environments during development affect key thermal physiological traits in various taxa may provide an understanding of how species are likely to cope with changing environments.

While phenotypic plasticity can adjust phenotypes throughout life, developmental plasticity—plasticity occurring during early embryonic development—can have organizational effects on phenotypes that can affect responses later in life [6]. For vertebrates in particular, such effects may be adaptive or maladaptive depending on whether early-life environments are predictive of late-life environments. While temperature and early resource provisioning can influence thermal traits in ectotherms [18], most research effort has focused on temperature, which is known to have a profound effect on fitness [19,20]. In reptiles, temperatures during embryonic development are known to affect phenotypes throughout ontogeny [7]. For example, incubation conditions of developing reptile embryos can impact a variety of traits including sex, growth rate, morphology, behaviour and cognition [7,20,21]. However, there is a dearth of evidence linking developmental factors more generally to thermal traits, and whether these differences persist through various stages of ontogeny in reptiles [22,23].

Here, we aim to determine how early developmental environments affect thermal physiology (CT_{max} and thermal preference: T_{pref}) in reptiles. CT_{max} and T_{pref} are two common thermal indices used as proxies for how the environment influences individual fitness and are used to predict how species distributions are predicted to shift with climate change [3,24,25]. We first conduct a laboratory experiment to test how maternal investment and developmental temperature both influence CT_{max} and T_{pref} in a common skink (*Lampropholis delicata*). We then compare our experimental findings with quantitative results testing this same question more broadly in reptiles using a meta-analysis.

2. Method and materials

(a) Consequences of incubation temperature and resource allocation on thermal physiology: an experimental manipulation

We collected gravid *Lampropholis delicata* (common garden skink, $n=100$) from populations in Sydney (Australia) and transported them back to the Australian National University, where females were housed until eggs ($n=40$) were laid. We then pseudo-randomly (to ensure equal sample sizes) assigned eggs ($n=20$) to both a resource allocation treatment ('R'—yolk removal or 'C'—control) and an incubation temperature (23°C or 28°C s.d. ± 3.0) treatment (see electronic

supplementary material for details on husbandry of hatchlings). Egg incubation temperatures were chosen to mimic conditions experienced at extremes of natural nest temperatures in nature while also showing natural thermal fluctuations throughout the day [26]. Yolk removal treatments followed Sinervo [16], with 15–20% of the total egg mass being removed via a sterilized syringe. Control treatments were punctured with the syringe without any yolk removal. For further description of husbandry conditions of adults and incubation details, see Kar *et al.* [27].

Hatchlings from their respective treatment were housed in mixed treatment groups of 5–6 within 20 plastic enclosures [40 cm (l) \times 29.5 cm (w) \times 20.5 cm (h)], with UVA/UVB lighting and a 20 W heat lamp in each enclosure. Water was provided *ad libitum*, with enclosures misted daily. Lizards were fed calcium and vitamin-dusted crickets (*Acheta domesticus*) every second day. At eight to eleven months post-hatching, lizards were selected at random, and thermal traits (CT_{max} and T_{pref}) were measured. Briefly, after undergoing a 24 h fasting period, animals were transferred into individual lanes of a thermal gradient (5°C to 55°C) to measure T_{pref} . A FLIR T640 thermal camera was used to take thermal images of all lanes every 15 min over an 8 h observation period. T_{pref} was defined as the mean skin surface temperature (on the neck) over the 8 h observation period. Given the small size of lizards (i.e. 1.3 g), we assumed skin surface temperature reflected body temperature, which has been shown for many small lizards [28]. For CT_{max} , we followed the same fasting period used for T_{pref} experiments. Here, lizards were placed in Falcon tubes in a water bath for 5 min at a temperature of 30°C. The water temperature was increased to 38°C at a rate of 1°C min⁻¹. We used a control Falcon tube with a thermal couple attached to the bottom of the tub where lizards were positioned to record the temperature of the tube surface, which we took to be the temperature experienced by the lizards. This approach was needed because it was not possible to have a thermal couple in each lizard's Falcon tube when measuring righting responses in the CT_{max} procedure [29]. CT_{max} was defined as the temperature at which an individual lost their righting reflex (for further details in collection methods, see electronic supplementary material).

All statistical analyses were conducted using the R environment, ver. 4.1.0 (<https://www.r-project.org/>). We used linear mixed-effects models to analyse thermal traits (T_{pref} and CT_{max}). We constructed models that contained the main effects of body mass, sex, incubation temperature and resource treatment. We also tested for the interaction between incubation temperature and resource treatment (see electronic supplementary material for more details). If the interaction was not significant, we removed it and presented the full main effects model.

(b) Meta-analysis of early thermal effects on thermal physiology in reptiles

To understand more broadly the impact of developmental environments on thermal physiology, we systematically searched for studies manipulating early developmental environments and subsequently measuring thermal physiological traits. Unfortunately, few studies manipulated egg resource investment and measured thermal tolerance. As such, it was only possible to focus on developmental temperature manipulations. Our meta-analysis collected data on offspring T_{pref} and CT_{max} in lizards, snakes, tortoises, turtles

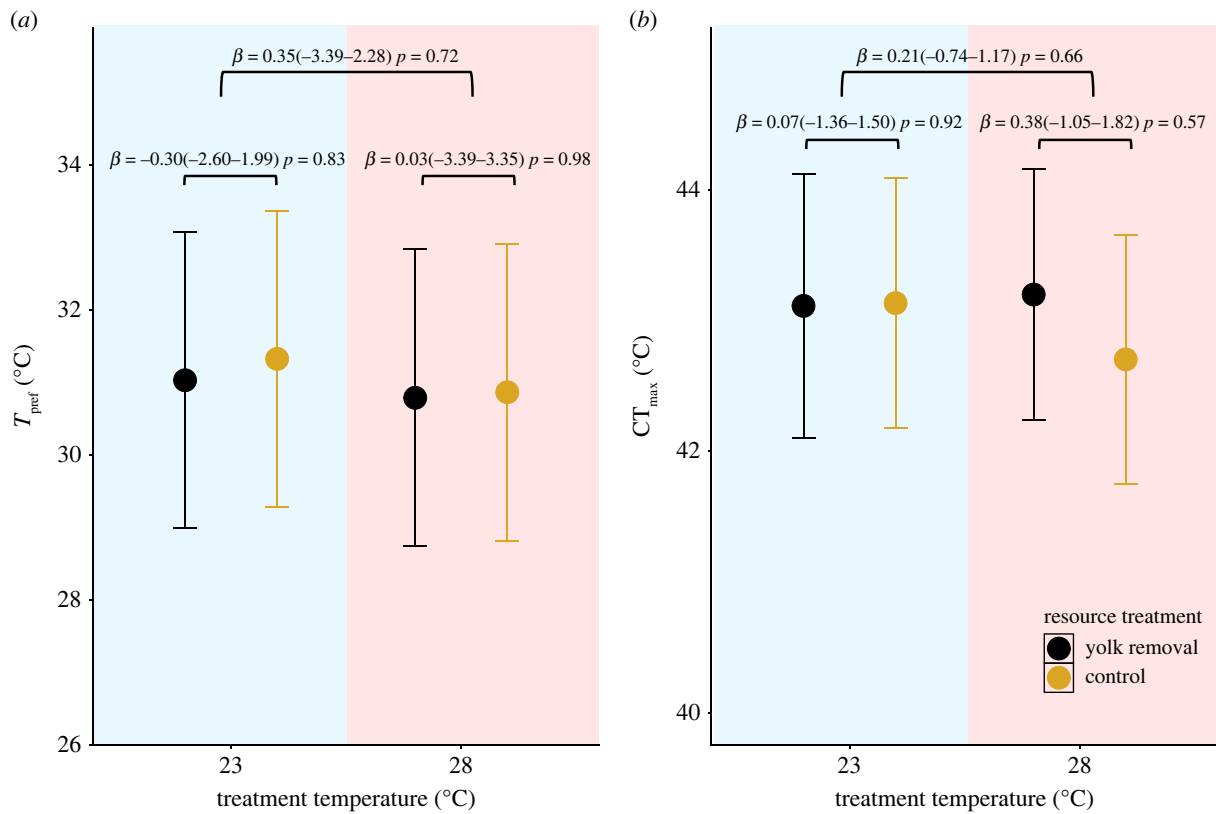


Figure 1. Thermal indices across different incubation temperatures and resource treatments for hatchling *Lampropholis delicata* ($n = 10$ per temperature and treatment). (a) Thermal preference (T_{pref}) in lizards incubated at 23 and 28°C for each resource treatment (yolk ablation and control). (b) Critical thermal maximum (CT_{max}) in lizards incubated at 23 and 28°C for each resource treatment. Bars above plots indicate pairwise comparisons of thermal indices between temperature and resource treatments. Means and 95% confidence intervals are provided along with the p -value for each contrast.

and tuatara. Our search string included cold tolerance (i.e. critical thermal minimum, CT_{min}), but there were too few studies that manipulated developmental environments and measured this trait to conduct a formal meta-analysis. As such, we focus on T_{pref} and CT_{max} .

In brief, we conducted a systematic literature search in Scopus, ISI Web of Science (core collection), and ProQuest (dissertations and thesis) and did not apply a timespan limit. We followed the PRISMA-EcoEvo (Preferred Reporting Items for Systematic Reviews & Meta-Analyses in Ecology and Evolutionary biology) guidelines for reporting [30]. Full search strings, search methods and selection criteria are described in detail in electronic supplementary material, figures S1 and S2. We obtained 485 original records, and 15 articles satisfied our selection criteria [31–42].

Multi-level meta-analytic models were constructed using the *rma.mv* function in the *metafor* package (version 3.8) [43]. To determine the ability of an organism to acclimate to changes in the environment, we used the acclimation response ratio (ARR) as our effect size [44]. Sampling variance for the ARR was derived in Pottier *et al.* [45]. Study, phylogeny and species were designated as random effects and we included an observation-level random effect (effect size ID). A model that included only study, species and effect size ID was best supported over one with phylogeny, so we present meta-analytic results from a model without phylogeny. Studies often had more than two temperature treatments. As such, we derived all pairwise effect size comparisons. This, however, does induce a correlation between effect size sampling errors, which we controlled for through the inclusion of a sampling (co)variance matrix derived by assuming effect sizes are correlated by $r = 0.5$ [46]. Thermal trait (T_{pref} or CT_{max}), life

stage at measurement (hatchling, juvenile or adult), climate zone (temperate or tropical) and major taxonomic group (lizard, snake, tuatara or turtle) were included as fixed factors in separate multi-level meta-regression (MLMR) models. We also tested for publication bias using a MLMR model with sampling variance and standard error as predictors [47] and was visually inspected using a funnel plot (see electronic supplementary material for more details). We present effect size heterogeneity by constructing prediction intervals [48] and presenting I^2 using the *orchaRd* package (version 2.0) [49].

3. Results

(a) Incubation temperature and resource allocation consequences on thermal preference and critical thermal maximum

Mean T_{pref} was $31.0^\circ\text{C} \pm 0.47$ (mean \pm s.e.) and ranged from 20.99 to 34.26°C. Mean CT_{max} was $43.04^\circ\text{C} \pm 0.23$ and ranged from 38.6 to 45.2°C. We did not detect any effect of incubation temperature, yolk treatment, sex or body mass on T_{pref} or CT_{max} (figure 1a,b; table 1).

(b) Meta-analysis of early thermal effects on thermal physiology in reptiles

Across reptiles, developmental temperatures did not influence thermal traits (T_{pref} or CT_{max}), but heterogeneity was high (ARR = 0.05, 95% CI: -0.28–0.37; $I^2_{\text{total}} = 99.53\%$, prediction interval: -1.23–1.32; figure 2a, $n = 69$ effects from 14 species). Overall, we found no evidence for publication

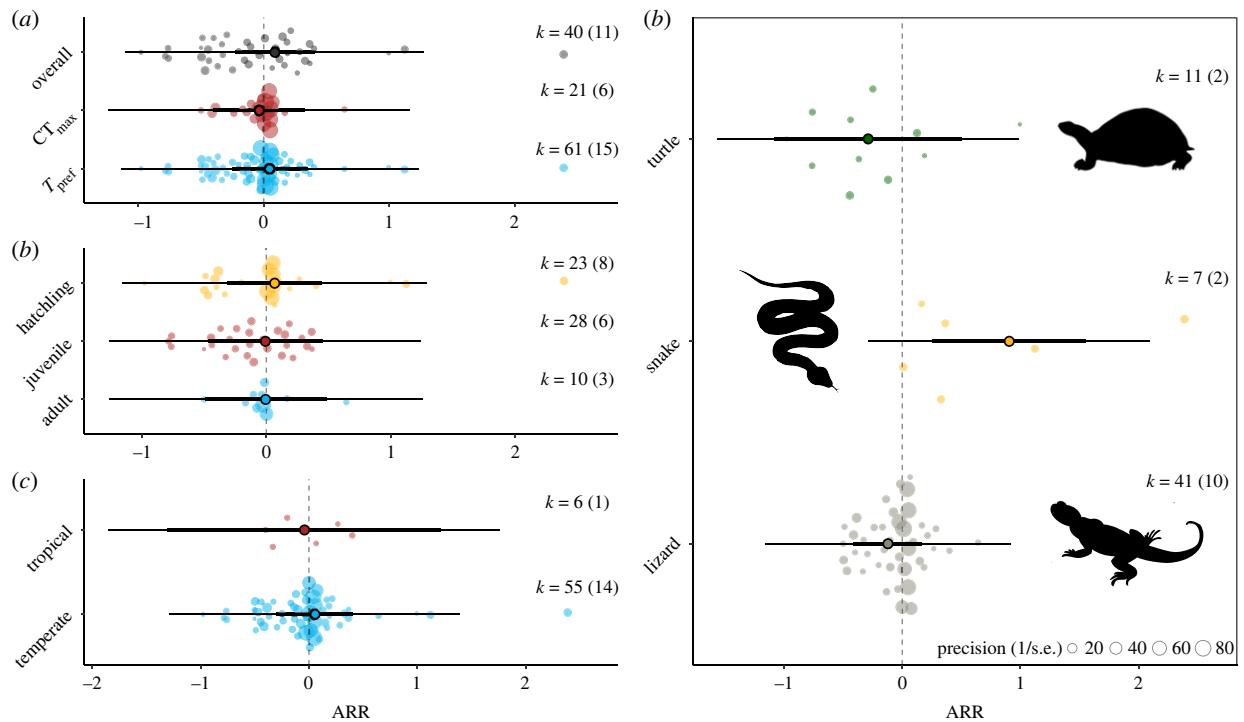


Figure 2. The magnitude of the effect of developmental temperature on thermal indices (T_{pref} and CT_{max}) in reptiles (a) concerning age class of thermal physiological measurement (b), climate zone (c) and taxon (d). Mean meta-analytic ARR estimates (circles) with their 95% confidence intervals (thicker error bars) and prediction intervals (thinner error bars). Data points from each study from the meta-analysis are scaled by precision (inverse of s.e.), and k is the number of effect sizes with the number of species in brackets. ARR is the acclimation response ratio. Ninety-five per cent confidence intervals not overlapping 0 are statistically significant. Graphs were constructed using the *orchaRd* package [50]. Tuatara was removed for visual purposes due to the small number of effect sizes ($n = 3$).

Table 1. Model outputs coefficients for testing whether sex, body mass, incubation temperature, resource or the interaction between resource and temperature had an effect on T_{pref} or CT_{max} in hatchling *Lampropholis delicata*. Estimate value describes the estimated coefficient value and 95% CI describes the lower and upper bound of the 95% credible interval for each coefficient value. Intercept is the estimated mean of each thermal trait from the null model. Italics indicate coefficients that are significant at $p < 0.05$.

thermal index	covariate	estimate	l-95% CI	u-95% CI	p-value
T_{pref}	<i>(intercept)</i>	30.94	28.67	33.20	<0.01
	body mass	0.44	-0.97	1.86	0.53
	sex	0.30	-2.50	3.09	0.83
	incubation temperature	-0.35	-2.36	1.66	0.72
	resource	0.19	-1.83	2.20	0.85
	incubation temperature \times resource	-0.22	-4.31	3.87	0.91
CT_{max}	<i>(intercept)</i>	43.27	42.17	44.37	<0.01
	body mass	-0.41	-1.08	0.25	0.21
	sex	-0.03	-1.35	1.28	0.96
	incubation temperature	-0.18	-1.14	0.78	0.70
	resource	-0.24	-1.20	0.71	0.61
	incubation temperature \times resource	-0.52	-2.47	1.44	0.59

biases ($\beta = -0.81$, 95% CI = -1.92 – 0.3 , $p = 0.15$; electronic supplementary material, figure S3; for further details see electronic supplementary material). Species effects ($I_{\text{Species}}^2 = 70.57\%$) drove most of the heterogeneity in ARR, but thermal traits were not influenced by life stage, climate zone or major taxonomic group (i.e. snakes, turtles and lizards) (figure 2b,c). While there was a significant increase in thermal traits in snakes (figure 2d), this was driven by a single species (*Nerodia sipedon*), and given the small

sample sizes, we need to caution whether any true differences between snakes and other groups exist.

4. Discussion

Genetic adaptation and phenotypic plasticity are two hypotheses for how ectotherms can cope with warming temperatures associated with anthropogenic climate change

[3,51–53]. Plastic responses occurring early in development can have long-lasting effects on organisms, with significant implications for how they cope with environmental stressors.

We show that early developmental environments do little to modify thermal physiological traits (CT_{max} and T_{pref}) in most reptile taxa. Both our experimental and meta-analytic approaches suggest that the magnitude of developmental plasticity on thermal indices appears to be canalized. For example, our meta-analysis indicated that for every 1°C change in developmental temperature, we only expect a 0.05°C change in thermal physiological response. Our findings are consistent with those of other ectotherm systems, which show that developmental plasticity has little impact on adult heat tolerance [6,54–56]. Nonetheless, we detected significant species-specific heterogeneity ($I^2_{Species} = 70.57\%$), suggesting substantial differences across species that cannot be ignored. Such variability may be driven by species differences in: (1) micro-habitat selection of nests; (2) nesting phenology; (3) the propensity for local adaptation in the wild and/or (4) the different conditions chosen for laboratory experiments across species. It has been indicated in other studies [57–60] that differences in nest depth, nest location, clutch density or maternal condition may select for developmentally plastic responses in offspring. Together, these data highlight that further ecological data on developmental environments in nature is needed to test if static manipulations in the laboratory provide a functional link to how species can cope with environmental change.

While there are still limited empirical studies, across reptile taxa, plasticity in thermal physiology did not differ by age, taxon or climate zone. We expected that the earlier the age at which thermal traits were measured would make it more likely that effects of early environments would be detected because of the tighter connection between egg and post-hatchling experiences. In addition, tropical species are expected to maintain body temperatures near their thermal limits, and an increase in temperature can push these species to physiological extremes compared to temperate species [3,53,61]. Greater thermal variability in temperate regions may also select for greater plasticity. However, our meta-analysis does not support these hypotheses. Instead, the microthermal environments chosen, along with behavioural flexibility (or lack thereof) in nest site selection, may be more important driving mechanisms in determining whether species respond plastically to developmental environments or not [3,51]. Future studies looking at the autocorrelation between early and late developmental environments would be fruitful in helping elucidate species-specific responses to thermal environments.

Overall, our results suggest that many reptiles may have limited developmental plasticity in thermal traits, relying instead on energetically expensive behaviours (i.e. thermoregulation) [3,62] or responses that operate on slower timescales (i.e. local adaptation) [52,63]. Given the small effect sizes we observed, statistical power is likely an issue in ours and others' empirical work. However, ethical constraints in measuring thermal limits in large numbers of animals will mean such studies are likely to be common. As such, we will need to rely on meta-analysis to help circumvent power limitations in individual studies (as we have done here) [64]. We have also identified clear gaps in the literature that should help pave the way for future research. First, we encourage measuring thermal physiology under different developmental manipulations across a greater diversity of reptile taxa. Greater taxonomic diversity will clarify when developmental environments matter and allow us to explore the reasons for this heterogeneity. Second, we encourage measuring CT_{min} , in addition to other thermal physiological traits (i.e. CT_{max} , T_{pref} , etc.), as it is often more environmentally flexible than upper thermal limits. Despite these gaps, our results provide valuable insights into possible responses that are plausible under changing thermal conditions.

Ethics. All experimental procedures followed approved protocols by the ANU Animal Ethics Committee (ARA2019/17). Lizards were caught under NPWS permit LT201917.

Data accessibility. Experimental and meta-analytic datasets and code are available from the Zenodo repository: <https://doi.org/10.5281/zenodo.7700383> [65].

The data are provided in the electronic supplementary material [66].

Authors' contributions. R.Y.Z.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, writing—original draft and writing—review and editing; K.H.W.: data curation, formal analysis, investigation, methodology, writing—original draft and writing—review and editing; P.P.: conceptualization, data curation, formal analysis, investigation, methodology and writing—review and editing; M.I.C.: conceptualization, data curation, investigation, methodology, supervision and writing—review and editing; S.N.: conceptualization, funding acquisition, methodology, resources, validation and writing—review and editing; D.W.A.N.: conceptualization, data curation, formal analysis, funding acquisition, project administration, supervision, writing—original draft and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Parmesan C. 2006 Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
2. Sala OE *et al.* 2000 Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774. (doi:10.1126/science.287.5459.1770)
3. Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012 Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Phil. Trans. R. Soc. B* **367**, 1665–1679. (doi:10.1098/rstb.2012.0005)
4. Peralta-Maraver I, Rezende EL. 2021 Heat tolerance in ectotherms scales predictably with body size. *Nat. Clim. Chang.* **11**, 58–63. (doi:10.1038/s41558-020-00938-y)
5. Seebacher F, White CR, Franklin CE. 2015 Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Chang.* **5**, 61–66. (doi:10.1038/nclimate2457)
6. Pottier P, Burke S, Zhang RY, Noble DWA, Schwanz LE, Drobnik SM, Nakagawa S. 2022 Developmental plasticity in thermal tolerance: ontogenetic variation, persistence, and future directions. *Ecol. Lett.* **25**, 2245–2268. (doi:10.1111/ele.14083)
7. Noble DWA, Stenhouse V, Schwanz LE. 2018 Developmental temperatures and phenotypic plasticity in reptiles: a systematic review and

- meta-analysis. *Biol. Rev.* **93**, 72–97. (doi:10.1111/brv.12333)
8. Sales K *et al.* 2018 Experimental heatwaves compromise sperm function and cause transgenerational damage in a model insect. *Nat. Commun.* **9**, 4771. (doi:10.1038/s41467-018-07273-z)
 9. Salinas S, Munch SB. 2012 Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. *Ecol. Lett.* **15**, 159–163. (doi:10.1111/j.1461-0248.2011.01721.x)
 10. Kirchof S *et al.* 2017 Thermoregulatory behavior and high thermal preference buffer impact of climate change in a Namib Desert lizard. *Ecosphere* **8**, e02033. (doi:10.1002/ecs2.2033)
 11. Burton T, Killen SS, Armstrong JD, Metcalfe NB. 2011 What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proc. R. Soc. B* **278**, 3465–3473. (doi:10.1098/rspb.2011.1778)
 12. Tobler M, Nilsson JÅ, Nilsson JF. 2007 Costly steroids: egg testosterone modulates nestling metabolic rate in the zebra finch. *Biol. Lett.* **3**, 408–410. (doi:10.1098/rsbl.2007.0127)
 13. Zhao CL *et al.* 2022 Temperature and diet acclimation modify the acute thermal performance of the largest extant amphibian. *Animals* **12**, 531.
 14. Hardison EA, Kraskura K, van Wert J, Nguyen T, Eliason EJ. 2021 Diet mediates thermal performance traits: implications for marine ectotherms. *J. Exp. Biol.* **224**, jeb242846. (doi:10.1242/jeb.242846)
 15. Bujan J, Kaspari M. 2017 Nutrition modifies critical thermal maximum of a dominant canopy ant. *J. Insect. Physiol.* **102**, 1–6. (doi:10.1016/j.jinsphys.2017.08.007)
 16. Sinervo B. 1990 The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* **44**, 279–294. (doi:10.2307/2409407)
 17. Mousseau TA, Fox CW. 1998 The adaptive significance of maternal effects. *Trends Ecol. Evol.* **13**, 403–407. (doi:10.1016/S0169-5347(98)01472-4)
 18. Angilletta Jr MJ, Angilletta MJ. 2009 *Thermal adaptation: a theoretical and empirical synthesis*. New York, NY: Oxford University Press.
 19. Huey RB, Berrigan D. 2001 Temperature, demography, and ectotherm fitness. *Am. Naturalists* **2**, 158–210. (doi:10.1086/321314)
 20. Sibly RM, Atkinson D. 1994 How rearing temperature affects optimal adult size in ectotherms. *Ecology* **8**, 486–493.
 21. Bull JJ. 1980 Sex determination in reptiles. *Q. Rev. Biol.* **55**, 3–21. (doi:10.1086/411613)
 22. Refsnider JM, Clifton IT, Vazquez TK. 2019 Developmental plasticity of thermal ecology traits in reptiles: trends, potential benefits, and research needs. *J. Therm. Biol.* **84**, 74–82. (doi:10.1016/j.jtherbio.2019.06.005)
 23. Bodensteiner BL *et al.* 2021 Thermal adaptation revisited: how conserved are thermal traits of reptiles and amphibians? *J. Exp. Zool. A Ecol. Integr. Physiol.* **335**, 173–194. (doi:10.1002/jez.2414)
 24. Hoffmann AA, Chown SL, Clusella-Trullas S. 2013 Upper thermal limits in terrestrial ectotherms: how constrained are they? *Funct. Ecol.* **27**, 934–949. (doi:10.1111/j.1365-2435.2012.02036.x)
 25. Sinervo B *et al.* 2010 Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899. (doi:10.1126/science.1184695)
 26. Cheetham E, Doody JS, Stewart B, Harlow P. 2011 Embryonic mortality as a cost of communal nesting in the delicate skink. *J. Zool.* **283**, 234–242. (doi:10.1111/j.1469-7998.2010.00764.x)
 27. Kar F, Nakagawa S, Noble DWA. 2022 Impact of developmental temperatures on thermal plasticity and repeatability of metabolic rate. *Evol. Ecol.* **36**, 199–216. (doi:10.1007/s10682-022-10160-1)
 28. Garrick D. 2008 Body surface temperature and length in relation to the thermal biology of lizards. *Biosci. Horizons* **1**, 136–142. (doi:10.1093/biohorizons/hzn014)
 29. Llewelyn J, Macdonald SL, Hatcher A, Moritz C, Phillips BL. 2016 Intraspecific variation in climate-relevant traits in a tropical rainforest lizard. *Divers. Distrib.* **1**, 1000–1012. (doi:10.1111/ddi.12466)
 30. O’Dea RE *et al.* 2021 Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biol. Rev.* **96**, 1695–1722. (doi:10.1111/brv.12721)
 31. Abayarathna MG. The effect of incubation temperature on offspring phenotypes and survival of velvet gecko, *Amalasia lesueurii*. PhD thesis, University of Technology, Sydney, Australia.
 32. Alberts AC, Perry AM, Lemm JM, Phillips JA. 1997 Effects of incubation temperature and water potential on growth and thermoregulatory behavior of hatchling Cuban rock iguanas (*Cyclura nubila*). *Copeia* **1997**, 766–776. (doi:10.2307/1447294)
 33. Arnold SJ, Peterson CR, Gladstone J. 1995 Behavioural variation in natural populations. VII. Maternal body temperature does not affect juvenile thermoregulation in a garter snake. *Anim. Behav.* **50**, 623–633. (doi:10.1016/0003-3472(95)80124-3)
 34. Beltrán I, Durand V, Loiseleur R, Whiting MJ. 2020 Effect of early thermal environment on the morphology and performance of a lizard species with bimodal reproduction. *J. Comp. Physiol. B* **190**, 795–809. (doi:10.1007/s00360-020-01312-2)
 35. Blouin-Demers G, Kissner KJ, Weatherhead PJ. 2000 Plasticity in preferred body temperature of young snakes in response to temperature during development. *Copeia* **2000**, 841–845. (doi:10.1643/0045-8511(2000)000[0841:PIPBTO]2.0.CO;2)
 36. Dayananda B, Murray BR, Webb JK. 2017 Hotter nests produce hatchling lizards with lower thermal tolerance. *J. Exp. Biol.* **220**, 2159–2165. (doi:10.1242/jeb.152272)
 37. Goodman RM, Walguarnery JW. 2007 Incubation temperature modifies neonatal thermoregulation in the lizard *Anolis carolinensis*. *J. Exp. Zool. Part A* **307**, 439–448. (doi:10.1002/jez.397)
 38. Llewelyn J, Macdonald SL, Moritz C, Martins F, Hatcher A, Phillips BL. 2018 Adjusting to climate: acclimation, adaptation and developmental plasticity in physiological traits of a tropical rainforest lizard. *Integr. Zool.* **13**, 411–427. (doi:10.1111/1749-4877.12309)
 39. Nelson NJ, Keall SN, Hare KM. 2017 Temperature selection by juvenile tuatara (*Sphenodon punctatus*) is not influenced by temperatures experienced as embryos. *J. Therm. Biol.* **69**, 261–266. (doi:10.1016/j.jtherbio.2017.08.008)
 40. O’Steen SH. 1998 Embryonic temperature influences juvenile temperature choice and growth rate in snapping turtles *Chelydra serpentina*. *J. Exp. Biol.* **201**, 439–449. (doi:10.1242/jeb.201.3.439)
 41. Qualls CP, Andrews RM. 1999 Cold climates and the evolution of viviparity in reptiles: cold incubation temperatures produce poor-quality offspring in the lizard, *Sceloporus virgatus*. *Biol. J. Linn. Soc.* **67**, 353–376.
 42. Spotila JR, Zimmerman LC, Binckley CA, Grumbles JS, Rostal DC, List Jr A, Beyer EC, Phillips KM, Kemp SJ. 1994 Effects of incubation conditions on sex determination, hatching success, and growth of hatchling desert tortoises, *Gopherus agassizii*. *Herpetol. Monogr.* **1**, 103–116. (doi:10.2307/1467074)
 43. Viechtbauer W. Conducting meta-analyses in R with the metafor Package. *J. Stat. Softw.* 2010; **36**, 1–48. (doi:10.18637/jss.v036.i03)
 44. Clausen DL. 1977 Thermal acclimation in ambystomatid salamanders. *Comp. Biochem. Physiol.* **58**, 333–340. (doi:10.1016/0300-9629(77)90150-5)
 45. Pottier P, Burke S, Drobnik SM, Lagisz M, Nakagawa S. 2021 Sexual (in)equality? A meta-analysis of sex differences in thermal acclimation capacity across ectotherms. *Funct. Ecol.* **35**, 2663–2678. (doi:10.1111/1365-2435.13899)
 46. Noble DWA, Lagisz M, O’Dea RE, Nakagawa S. 2017 Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. *Mol. Ecol.* **26**, 2410–2425. (doi:10.1111/mec.14031)
 47. 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 Ecol. Evol.* **13**, 4–21. (doi:10.1111/2041-210X.13724)
 48. Noble DWA, Pottier P, Lagisz M, Burke S, Drobnik SM, O’Dea RE, Nakagawa S. 2022 Meta-analytic approaches and effect sizes to account for ‘nuisance heterogeneity’ in comparative physiology. *J. Exp. Biol.* **225**, jeb243225. (doi:10.1242/jeb.243225)
 49. Nakagawa S, Lagisz M, O’Dea RE, Pottier P, Rutkowska J, Senior AM, Yang Y, Noble DW. 2023 orchard 2.0: An R package for visualizing meta-analyses with 2 orchard plots. *EcoEvoRxiv*. (doi:10.32942/X2QC7K)
 50. Nakagawa S, Lagisz M, O’Dea RE, Rutkowska J, Yang Y, Noble DWA, Senior AM. 2021 The orchard plot: cultivating a forest plot for use in ecology,

- evolution, and beyond. *Res. Synth. Methods* **12**, 4–12. (doi:10.1002/jrsm.1424)
51. Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB. 2014 Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl Acad. Sci. USA* **111**, 5610–5615. (doi:10.1073/pnas.1316145111)
 52. Kellermann V, van Heerwaarden B, Sgrò CM, Hoffmann AA. 2009 Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science* **325**, 1244–1246.
 53. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)
 54. MacLean HJ, Sørensen JG, Kristensen TN, Loeschke V, Beedholm K, Kellermann V, Overgaard J. 2019 Evolution and plasticity of thermal performance: an analysis of variation in thermal tolerance and fitness in 22 *Drosophila* species. *Phil. Trans. R. Soc. B* **374**, 20180548. (doi:10.1098/rstb.2018.0548)
 55. Enriquez-Urzelai U, Sacco M, Palacio AS, Pintanel P, Tejedo M, Nieceza AG. 2019 Ontogenetic reduction in thermal tolerance is not alleviated by earlier developmental acclimation in *Rana temporaria*. *Oecologia* **189**, 385–394. (doi:10.1007/s00442-019-04342-y)
 56. Gunderson AR, Fargevieuille A, Warner DA. 2020 Egg incubation temperature does not influence adult heat tolerance in the lizard *Anolis sagrei*. *Biol. Lett.* **16**, 20190716. (doi:10.1098/rsbl.2019.0716)
 57. Shine R, Harlow PS. 1996 Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology* **77**, 1808–1817. (doi:10.2307/2265785)
 58. Mitchell TS, Warner DA, Janzen FJ. 2013 Phenotypic and fitness consequences of maternal nest-site choice across multiple early life stages. *Ecology* **94**, 336–345. (doi:10.1890/12-0343.1)
 59. Bonduriansky R, Head M. 2007 Maternal and paternal condition effects on offspring phenotype in *Telostylinus angusticollis* (Diptera: Neriidae). *J. Evol. Biol.* **20**, 2379–2388. (doi:10.1111/j.1420-9101.2007.01419.x)
 60. Parker GA, Begon M. 1986 Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am. Nat.* **128**, 573–592. (doi:10.1086/284589)
 61. Janzen DH. 1967 Why mountain passes are higher in the tropics. *Am. Nat.* **101**, 233–249. (doi:10.1086/282487)
 62. Kearney M, Shine R, Porter WP. 2009 The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proc. Natl Acad. Sci. USA* **10**, 3835–3840. (doi:10.1073/pnas.0808913106)
 63. Gunderson AR, Stillman JH. 2015 Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proc. R. Soc. B* **282**, 20150401. (doi:10.1098/rspb.2015.0401)
 64. Nakagawa S, Noble DWA, Senior AM, Lagisz M. 2017 Meta-evaluation of meta-analysis: ten appraisal questions for biologists. *BMC Biol.* **15**, 1–14. (doi:10.1186/s12915-016-0343-5)
 65. Zhang RY, Wild KH, Pottier P, Carrasco MI, Nakagawa S, Noble DWA. 2023 Code for: Developmental environments do not affect thermal physiology in reptiles: an experimental test and meta-analysis. Zenodo. (doi:10.5281/zenodo.7700383)
 66. Zhang RY, Wild KH, Pottier P, Carrasco MI, Nakagawa S, Noble DWA. 2023 Developmental environments do not affect thermal physiology in reptiles: an experimental test and meta-analysis. Figshare. (doi:10.6084/m9.figshare.c.6620541)