Electronic supplementary material (ESM): Developmental environments do not affect thermal physiology in reptiles: An experimental test and meta-analysis

Supplementary Materials and Methods
1. Experimental manipulations of early thermal environment

(a)Optimal body temperature – T_{pref}
Animals (n =40) were randomly sampled to form five trial groups (n=8) such that two animals, one male and one female, from each treatment were in each trial group. Before T_{pref} trials, trial animals were moved from mating enclosures to individual enclosures undergoing a 24-hour fasting period. After this period, the mass of all trial animals was measured, after which animals were transferred into individual lanes of a thermal gradient plate spanning temperatures of 5°C to 55°C. The thermal profiles across the thermal gradient were generated from an immersion cooler, copper tubing, and an electric heating pad. Infrared images were obtained in 15- minute intervals over an eight-hour observation period with a FLIR T640 thermography camera. Animals were returned to individual enclosures after T_{pref} trials. *Lampropholis delicata* body temperatures were extracted from infrared images using Flir Tools, version 5.13. T_{pref} was defined as the mean body temperature (T_b) over the eight-hour observation period.

(b) Critical Thermal Maximum
Critical thermal maximum (CT_{max}) was determined for all individuals at least 24 hours after their T_{pref} trials. For each trial, individual skinks were placed in 50 mL Falcon tubes. Tubes were perforated lengthwise with holes to maintain airflow, while being weighted on the opposite side to maintain stable, horizontal buoyancy (Figure S1). Once lizards were in tubes, they were placed in a water bath for 5 min at a temperature of 30°C. This ensured that each lizard T_b was 30°C before trials started. To obtain the most accurate T_b for skinks, temperature was monitored with a thermocouple probe secured within a Falcon tube and an additional thermal couple that was placed in the bath. Water temperature was increased to 38° C at a rate of 1° C/min. If trial temperatures were above 38°C, the heating rate was reduced to 0.5° C/min. Every 1 min tubes were rotated to check righting reflex of skinks. CT_{max} was defined as the temperature at which an individual lost their righting reflex. Once CT_{max} was reached, skinks were removed from the tube and placed into room temperature water for cooling.

(c) Statistical analysis
For the experimental analysis (T_{pref} and CT_{max}) on *L. delicata*, we used linear mixed-effects models using the lme4 package (version 1.1)[1]. Each model was constructed with a thermal index (T_{pref} or CT_{max}) as the response variable and body mass, sex, incubation temperature, resource treatment, and the interaction between incubation temperature and resource treatment as predictor variables. Model assumptions were checked using the *performance* package (version 0.10)[2]. Finally, the package *emmeans* (version 1.80)[3] was used to extract marginal means (least-squares means) and standard error for figure purposes.

2. Meta-analysis
(a) Initial literature search and record screening process
We developed search strings to capture experimental studies which measured the thermal traits (in the form of CT_{max} or T_{pref}) of reptiles exposed to different developmental temperatures. We focused only on temperatures given that too few studies manipulated egg resources and measured thermal physiology of offspring. The search strings used in the two databases screened in this study are below:

ProQuest and Scopus:
("temperature*" OR "thermal" OR "cold" OR "cool*" OR "heat*" OR "acclimat*") AND ("incubat*" OR "rear*" OR "development*" OR "ontogen*" OR "nest*" OR "embryo*" OR "early*" OR "juvenile*" OR "hatchling*" OR "young*" OR "egg*" OR "life history stage*" OR "life stage*") AND ("thermal tolerance*" OR "thermotolerance*" OR "cold tolerance*" OR "heat tolerance*" OR "tolerance* to heat*" OR "tolerance* to cold*" OR "tolerance* to temperature*" OR "temperature* tolerance*" OR "physiological tolerance*" OR "critic* thermal" OR "critic* temperature*" OR "thermal limit*" OR "thermal breadth*" OR "tolerance breadth*" OR "thermal range*" OR "performance breadth*" OR "thermal window*" OR "tolerance window*" OR "warming tolerance*" OR "tolerance* to warming" OR "cooling tolerance*" OR "tolerance* to cooling*" OR "CTmax" OR "CTmin" OR "heat coma" OR "chill coma" OR "lethal temperature*" OR "lethal limit*" OR "SCP" OR "supercooling point*" OR "crystal* temperature*" OR "freez* *tolerance*" OR "frost tolerance*" OR "freezing point*" OR "preferred temperature*" OR "preferred body temperature*" OR "selected body temperatures" OR "temperature preference*" OR "thermal preference*" OR "selected temperature*" OR "selected body temperature*" OR "thermal prefer*" OR "temperature* prefer*" OR "temperature* select*" OR "thermal select*" OR "equilibr* temperature*" OR "temperature* at equilibrium") AND ("squamat*" OR "lizard*" OR "reptil*" OR "snake*" OR "serpent*" OR "turtle*" OR "crocodil*", OR "iguan*", OR "anol*" OR "skink*" OR "chameleon*" OR "chamaeleon*" OR "gecko*" OR "tortoise*" OR "adder*" OR "viper*" OR "python*" OR "boa" OR "boas" OR "colubrid*" OR "amphisbaenia*" OR "rhynchocephal*" OR "testudin*" OR "chelon*" OR "alligator*" OR "caiman*" OR "gavial**" OR "garhial" OR "tuatar*" OR "sphenodon*") AND NOT ("endotherm*" OR "bird*" OR "avia*" OR "aves" OR "mammal*" OR "rodent*" OR "mouse" OR "mice" OR "rat" OR "rats" OR "cattle*" OR "livestock*" OR "domesticated" OR "cow" OR "cows" OR "pig" OR "pigs" OR "sheep*" OR "goat*" OR "horse*" OR "rabbit*" OR "chicken*" OR "duck*" OR "turkey*" OR "cat" OR "cats" OR "dog" OR "dogs" OR "plant" OR "plants" OR "plantule*" OR "cultivar*" OR "arabidopsis" OR "leaf" OR "leaves" OR "root*" OR "seed*" OR "tree*" OR "fungi" OR "fungal" OR "alga" OR "algae" OR "algal" OR "seaweed*" OR "seagrass" OR "*phyt*" OR "*bacteri*" OR "unicellular" OR "protist*" OR "archae*" OR "woman" OR "women" OR "man" OR "men" OR "volunteer*" OR "athlete*" OR "military" OR "*fish*" OR "amphib*" OR "frog*" OR "toad*" OR "salamander*" OR "newt*" OR "invertebrate*" OR "insect*" OR "arthropod*" OR "arachnid*" OR "crustacea*" OR "myriapod*" OR "mollus*" OR "annelid*" OR "*worm*" OR "cnidar*" OR "coral*")

ISI Web of Science:
("temperature*" OR "thermal" OR "cold" OR "cool*" OR "heat*" OR "acclimat*") AND ("incubat*" OR "rear*" OR "development*" OR "ontogen*" OR "nest*" OR "embryo*" OR "early*" OR "juvenile*" OR "hatchling*" OR "young*" OR "egg*" OR "life history stage*" OR "life stage*")) AND ("thermal tolerance*" OR "thermotolerance*" OR "cold tolerance*"

OR "heat tolerance*" OR "tolerance* to heat*" OR "tolerance* to cold*" OR "tolerance* to temperature*" OR "temperature* tolerance*" OR "physiological tolerance*" OR "critic* thermal" OR "critic* temperature*" OR "thermal limit*" OR "thermal breadth*" OR "tolerance breadth*" OR "thermal range*" OR "performance breadth*" OR "thermal window*" OR "tolerance window*" OR "warming tolerance*" OR "tolerance* to warming" OR "cooling tolerance*" OR "tolerance* to cooling*" OR "CTmax" OR "CTmin" OR "heat coma" OR "chill coma" OR "lethal temperature*" OR "lethal limit*" OR "SCP" OR "supercooling point*" OR "crystal* temperature*" OR "freez* *tolerance*" OR "frost tolerance*" OR "freezing point*" OR "preferred temperature*" OR "preferred body temperature*" OR "selected body temperatures" OR "temperature preference*" OR "thermal preference*" OR "selected temperature*" OR "selected body temperature*" OR "thermal prefer*" OR "temperature* prefer*" OR "temperature* select*" OR "thermal select*" OR "equilibr* temperature*" OR "temperature* at equilibrium")) AND ("squamat*" OR "lizard*" OR "reptil*" OR "snake*" OR "serpent*" OR "turtle*" OR "crocodil*", OR "iguan*", OR "anol*" OR "skink*" OR "chameleon*" OR "chamaeleon*" OR "gecko*" OR "tortoise*" OR "adder*" OR "viper*" OR "python*" OR "boa" OR "boas" OR "colubrid*" OR "amphisbaenia*" OR "rhynchocephal*" OR "testudin*" OR "chelon*" OR "alligator*" OR "caiman*" OR "gavial**" OR "garhial" OR "tuatar*" OR "sphenodon*")) NOT ("endotherm*" OR "bird*" OR "avia*" OR "aves" OR "mammal*" OR "rodent*" OR "mouse" OR "mice" OR "rat" OR "rats" OR "cattle*" OR "livestock*" OR "domesticated" OR "cow" OR "cows" OR "pig" OR "pigs" OR "sheep*" OR "goat*" OR "horse*" OR "rabbit*" OR "chicken*" OR "duck*" OR "turkey*" OR "cat" OR "cats" OR "dog" OR "dogs" OR "plant" OR "plants" OR "plantule*" OR "cultivar*" OR "arabidopsis" OR "leaf" OR "leaves" OR "root*" OR "seed*" OR "tree*" OR "fungi" OR "fungal" OR "alga" OR "algae" OR "algal" OR "seaweed*" OR "seagrass" OR "*phyt*" OR "*bacteri*" OR "unicellular" OR "protist*" OR "archae*" OR "woman" OR "women" OR "man" OR "men" OR "volunteer*" OR "athlete*" OR "military" OR "*fish*" OR "amphib*" OR "frog*" OR "toad*" OR "salamander*" OR "newt*" OR "invertebrate*" OR "insect*" OR "arthropod*" OR "arachnid*" OR "crustacea*" OR "myriapod*" OR "mollus*" OR "annelid*" OR "*worm*" OR "cnidar*" OR "coral*")

On 2021/01/28 a literature search using Scopus returned 289 records. On 2021/02/01 an additional search was performed using ISI Web of Science (core collection) and ProQuest (dissertation and theses) returning 346 records. During this search, four additional records were obtained from a review paper[4] and two unpublished records from additional studies were also included. These were combined to generate 639 records. Within these records, we removed 154 duplicates and obtained 485 unique documents. RZ screened titles, abstracts, and key words in Rayyan QCRI[5]. We selected studies based on eight eligibility criteria: (i) the study was done on a non-avian reptile (lizard, snake, turtle/tortoise, crocodile/alligator, or tuatara), (ii) the study was experimental, (iii) CT_{max} or T_{pref} (also referred to as T_{sel}) was measured, (iv) studies experimentally manipulated two or more incubation temperatures, (v) measurements of T_{pref} and CT_{max} were performed on individuals acclimated to the same temperatures, (vi) means, sample sizes and variances were reported. Full details of our selection criteria at the abstract and full-text screening stages are provided in Table S1 and Figure S2.

The PRISMA flowchart illustrating the systematic literature search and workflow is also shown in Figure S3. Following preliminary selection, full-text eligibility criteria were used to screen 52 full-text documents (Figure S3). Of the full-text documents, 19 documents fulfilled all eligibility criteria. We contacted the primary authors of five different studies to request unprocessed data that was not included in the publication but received no responses.

(b) Data extraction
Overall, we obtained a total of 69 unique effect sizes from 14 studies spanning 13 different species. All data were extracted by RZ. Data presented in the text or tables were directly extracted from the study. Data shown in the figures were digitised using the *metaDigitise* package[6] in R (version 1.0.1). Alongside effect size data, we also extracted any available information regarding experimental species, life stage at the time of measurement (hatchling, juvenile, or adult), life history (latitude of origin, terrestrial, or aquatic), and reptilian class (lizard, snake, turtle, or tuatara).

(c) Statistical analysis
We analysed our data using multi-level meta-analysis (MLMA) (i.e., intercept only models with random effects) and multi-level meta-regression (MLMR) models (i.e., models with 'fixed' and random effects). The acclimation response ratio (ARR) was used as our effect size and was defined as the variation in heat tolerance associated with a one-degree change in developmental temperature. Acclimation response ratio was defined as:

$$ARR = \frac{\mu HT_{T2} - \mu HT_{T1}}{T_2 - T_1}$$

Where HT is the mean heat tolerance estimates (CTmax or Tpref), and T is the incubation temperature in Celsius. T_1 is defined as the control developmental temperature and T_2 is defined as the warm or treatment developmental temperature. When ARR = 0 the heat tolerance measurement remains static, and no acclimation occurs as developmental temperature increases. In contrast, perfect compensation would be considered when ARR =1, where heat tolerance changes in concordance with developmental temperature. The sampling variance for AAR was derived as:

$$s^2 ARR = \left(\frac{1}{T_2 - T_1}\right)^2 \left(\frac{sd_{[T1]}^2}{n_{[T1]}} + \frac{sd_{[T2]}^2}{n_{[T2]}}\right)$$

Where s^2(ARR) is the sampling variance of AAR, *sd* is the standard deviation and n is the sample size (number of individuals). In studies with more than two temperatures we calculated a pairwise effect between each developmental temperature comparison. Given the same data are used to derive different effect sizes this induces non-independence between effect size sampling errors and the effects themselves (*See* Noble et al.[7]). We accounted for this through the inclusion of a sampling (co)variance matrix derived assuming effect sizes are correlated by r = 0.5[7]. We also re-fit models using robust variance estimation methods as these do not make assumptions about the nature of correlation within studies and have been shown to perform extremely well with complex sources of non-independence [8,9]. In all cases, RVE did not make any difference to conclusions. As such, we only included the sampling covariance matrices in our models.

All meta-analytic models were constructed using the '*rma.mv*' function in the package *metafor* (version 3.8-1)[10]. In all models we included phylogeny, species, study, and observation as random effects. We created a phylogenetic correlation matrix of species in the data set using the Open Tree of Life [11]. We used the *rotl* package (version 3.0.12) [12] to access the Open Tree of Life in R. Branch lengths were calculated for trees using the 'compute.brlen' function in the *ape* package (version 5.6.2)[13]. Using the *ape* '*vcv*' function, we built a correlation matrix of phylogenetic relatedness among species which was included in our models. We compared three intercept models where we accounted for 1) species, 2)

phylogeny, and 3) species and phylogeny (Table S2). [7]we used the function AIC scores from *metafor*[4] *to* evaluate which model was the best fit for the data.

We estimated the overall meta-analytic mean and calculated measures of heterogeneity by constructing prediction intervals and calculating I^2 from our MLMA models (Nakagawa & Santos 2012; Noble et al. 2022). I^2 allowed us to estimate the proportion of variation explained by species differences, phylogeny, and study-specific effects while accounting for known sampling variance[14,15]. Prediction intervals were calculated using *metafor* whereas I^2 was calculated using the *orchaRd* package (version 2.0).

We then fit MLMR models by including the same random effects, but adding in a single moderator (i.e., predictor) at a time. The models included those with the following moderator variables: thermal trait measurement type (T_{pref} or CT_{max}), climate zone (temperate or tropical), and life stage when thermal physiological trait measurements took place (hatchling, juvenile or adult). We explored publication bias using visual interpretation using a funnel plot and a modified version of Eggers regression [16] that included a multi-level meta-regression model with sampling variance or sampling standard error as a moderator[14].

Supplementary Results

1. Meta-analysis

We found minimal difference in AIC support for our intercept-only MLMA models when accounting for phylogeny, species, or phylogeny and species (Table S2). Therefore, we selected species in our final intercept model. We did not find evidence for developmental temperatures to influence CT_{max} (ARR = -0.08, 95%CI: -0.75–0.58; *p = 0.79*) or T_{pref} (ARR = 0.08, 95%CI: -0.36–0.53; *p = 0.68;* Table S3). We also did not find evidence for developmental temperatures affecting ARR across age classes in reptiles, where the confidence intervals overlapped with zero for hatchlings, juveniles, and adults (Table S4). We did not find differences in plasticity between animals found in the tropics (ARR = -0.08, 95%CI: -1.39–1.24; *p = 0.90*), and temperate animals (ARR = 0.04, 95%CI: -0.35–0.43; *p = 0.81;* Table S5). We acknowledge, however, that the sample size for tropical species was low and these results must be considered preliminary. We also did not find evidence for differences in plasticity between turtles, lizards, and tuataras (Table S6). In snakes, however, developmental temperatures did have a significant increase effect on thermal traits, but this effect is primarily driven by one species, *Nerodia sipedon*. Visual inspection of funnel plots did not show data distribution of publication bias (Figure S4), and statistically, we found no evidence for publication biases (*β*=-0.81, 95%CI=-1.92-0.3, *p=0.15*).

Table S1. Description of the inclusion criteria used to screen full texts of studies used in Figure S2 (decision tree).

Term	Definition
1. Reptile	Only included studies where the study species belonged to the class *Reptilia*. Studies examining bacteria, fungi, plants, invertebrates, non-reptilian vertebrates, or cells isolated from reptilian animals were excluded.
2. Experimental study	Only studies were included where researchers performed manipulative laboratory experiments. As a result, data obtained from field experiments, theoretical studies, observational laboratory experiments and qualitative reviews or models were excluded.
3. Measurement of T_{pref} or CT_{max}	Thermal preference (T_{pref}) and critical thermal maximum (CT_{max}) were selected as the two desired measures of thermal traits. Accordingly, we excluded experimental studies measuring other thermal traits like the lethal temperature for 50% of animals (LT_{50}), critical thermal minima (CT_{min}), heat knockdown time (HKT), or thermal optima (T_{opt}) of reptiles. Studies that measured preferred body temperature (PBT) or preferred temperature (T_p) were included, as these are analogous measures to T_{pref}.
4. Manipulation of developmental temperature	Only studies were included where independent groups of animals were exposed to two or more controlled (laboratory setting) temperatures during their embryonic development and subsequently assessed for thermal tolerance. A brief (e.g. less than 24hrs) exposure to a particular temperature condition was not considered to be sufficient manipulation of developmental temperature. Studies containing fluctuating developmental temperature treatments were permitted so long as the mean temperature between treatments differed. In circumstances where embryos were collected from the wild, we only included studies that performed a subsequent developmental temperature manipulation. Any studies which manipulated juvenile or adult developmental temperature were excluded. We also excluded any studies where juveniles or adults were collected from the wild and subsequently measured for T_{pref} or $CT_{max,}$ but included studies where embryos were collected for controlled developmental temperature manipulation.
5. Developmental temperature not confounded with adult acclimation	Studies were excluded where other known factors like chemical exposure, hormone addition and humidity were confounded with developmental temperature treatments. We included studies that manipulated developmental temperature alongside one or more factors in a fully factorial design, as it is possible to have independent manipulations of developmental temperature.

6. Is developmental temperature not confounded with additional factors?	Studies were excluded where other known factors like chemical exposure, hormone addition and humidity were confounded with developmental temperature treatments. We included studies that manipulated developmental temperature alongside one or more factors in a fully factorial design, as it is possible to have independent manipulations of developmental temperature.
7. Sample sizes and variances reported	Only included studies where measures of dispersion in the form of standard deviation or standard error were reported for each group of animals. If such data were not reported, the study's primary author was contacted for further information.

Table S2. Multi-level meta-analysis (MLMA) (i.e., intercept only models with random effects) of phylogeny, species, or phylogeny and species. Akaike information criterion was used to compare model fits.

Model name	AIC	est	ci.lb	ci.ub	pi.lb	pi.ub	pvalue	I^2_{Total}	$I^2_{study\_ID}$	I^2_{phylo}	I^2_{spp}	I^2_{obs}
Phylogeny	77.38	0.03	-0.28	0.34	-1.23	1.28	0.86	99.52	0.52	0.00	-	20.99
Species	78.11	0.05	-0.28	0.37	-1.23	1.32	0.76	99.53	7.87	-	70.57	21.10
Species and Phylogeny	80.11	0.05	-0.28	0.37	-1.23	1.32	0.76	99.53	7.87	0.00	70.57	21.10

Table S3. The magnitude of the effect of developmental temperature on ARR on CTmax and Tpref of reptiles. The number of effect sizes is denoted by k and n indicates the number of species. Estimates are species mean meta-analytic estimates with their 95% confidence intervals (lowerCL = lower bound & upperCL = upper bound) and prediction intervals (lowerPR = lower bound & upperPR = upper bound). P values indicate if values are significantly different from zero. The conditional r^2 (0.79) and the marginal r^2 (0.01).

Thermal metric	k	n	Estimate	upperCL	lowerPR	upperPR	p value
Ctmax	21	6	-0.04	0.33	-1.2	1.2	0.84
Tpref	61	15	0.09	0.41	-1.1	1.3	0.58

Table S4. The magnitude of the effect of developmental temperature on ARR when accounting for age class. The number of effect sizes is denoted by k and n indicates the number of species. Estimates are species mean meta-analytic estimates with their 95% confidence intervals (lowerCL = lower bound & upperCL = upper bound) and prediction intervals (lowerPR = lower bound & upperPR = upper bound). P values indicate if values are significantly different from zero. The conditional r^2 (0.80) and the marginal r^2 (0.01).

Age class	k	n	Estimate	upperCL	lowerPR	upperPR	p value
Adult	10	3	-0.01	0.48	-1.3	1.3	0.98
Juvenile	28	6	-0.01	0.45	-1.3	1.2	0.97
Hatchling	23	8	0.07	0.45	-1.2	1.3	0.72

Table S5. The magnitude of the effect of developmental temperature on ARR when accounting for the species origin. The number of effect sizes is denoted by k and n indicates the number of species. Estimates are species mean meta-analytic estimates with their 95% confidence intervals (lowerCL = lower bound & upperCL = upper bound) and prediction intervals (lowerPR = lower bound & upperPR = upper bound). P values indicate if values are significantly different from zero. The conditional r^2 (0.80) and the marginal r^2 (0.01).

Geographic zone	k	n	Estimate	upperCL	lowerPR	upperPR	p value
Temperate	55	14	0.06	0.41	-1.3	1.4	0.74
Tropical	6	1	-0.04	1.22	-1.9	1.8	0.94

Table S6. The magnitude of the effect of developmental temperature on ARR when accounting for reptile taxa. The number of effect sizes is denoted by k and n indicates the number of species. Estimates are species mean meta-analytic estimates with their 95% confidence intervals (lowerCL = lower bound & upperCL = upper bound) and prediction intervals (lowerPR = lower bound & upperPR = upper bound). P values indicate if values are significantly different from zero. The conditional r^2 (0.80) and the marginal r^2 (0.38).

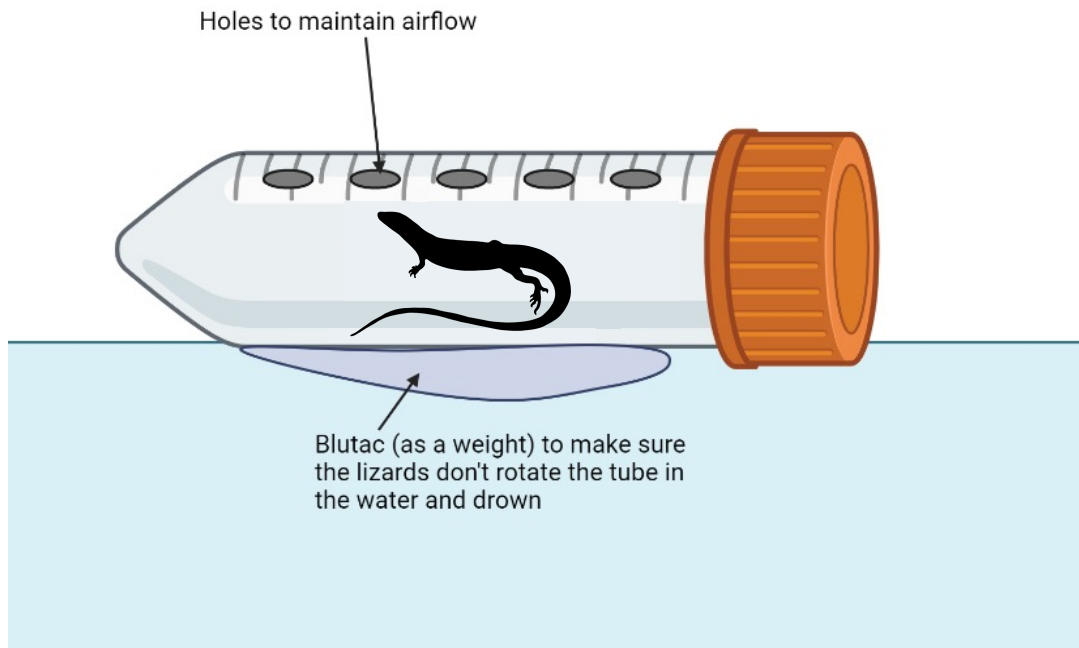| Taxa	k	n	Estimate	upperCL	lowerPR	upperPR	p value
Lizard	41	10	-0.12	0.17	-1.16	0.92	0.37
Snake	7	2	0.91	1.55	-0.28	2.10	0.01
Tuatara	2	1	0.37	2.08	-1.60	2.35	0.63
Turtle	11	2	-0.29	0.51	-1.56	0.99	0.44

Figure S1. Methods for collecting CT_{max} in *Lampropholis delicata*. Lizards were placed in Falcon tubes in a temperature-controlled bath. To obtain the most accurate T_b for skinks, temperature was monitored with a thermocouple probe secured within Falcon tube and an additional thermal couple that was placed in the bath. Water temperature was increased to $38°$ C at a rate of $1°$ C/min intervals. Every 1min tubes were rotated to check righting reflex of skinks. CT_{max} was defined as the temperature at which an individual lost their righting reflex.
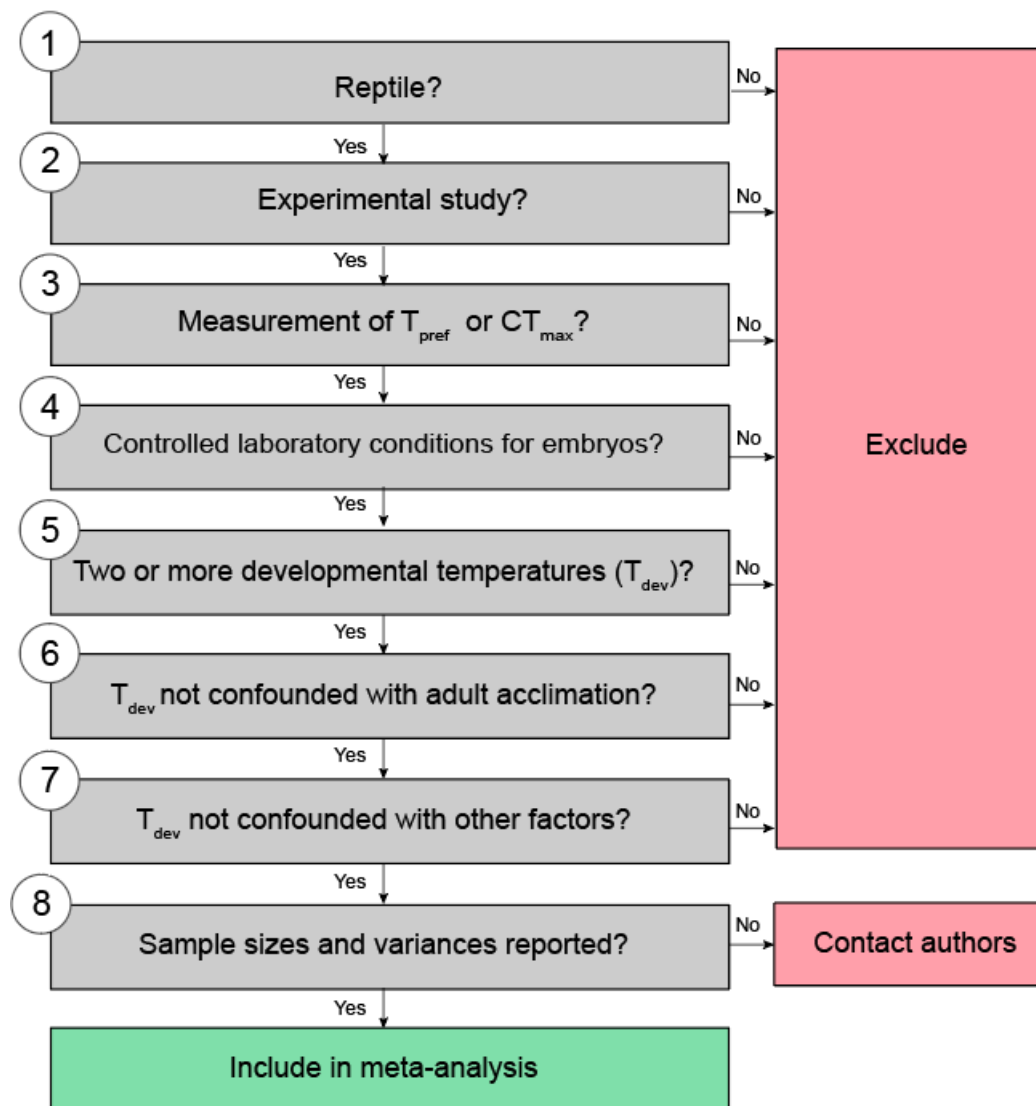
Figure S2. Decision tree showing the eligibility criteria used to assess full-text articles.
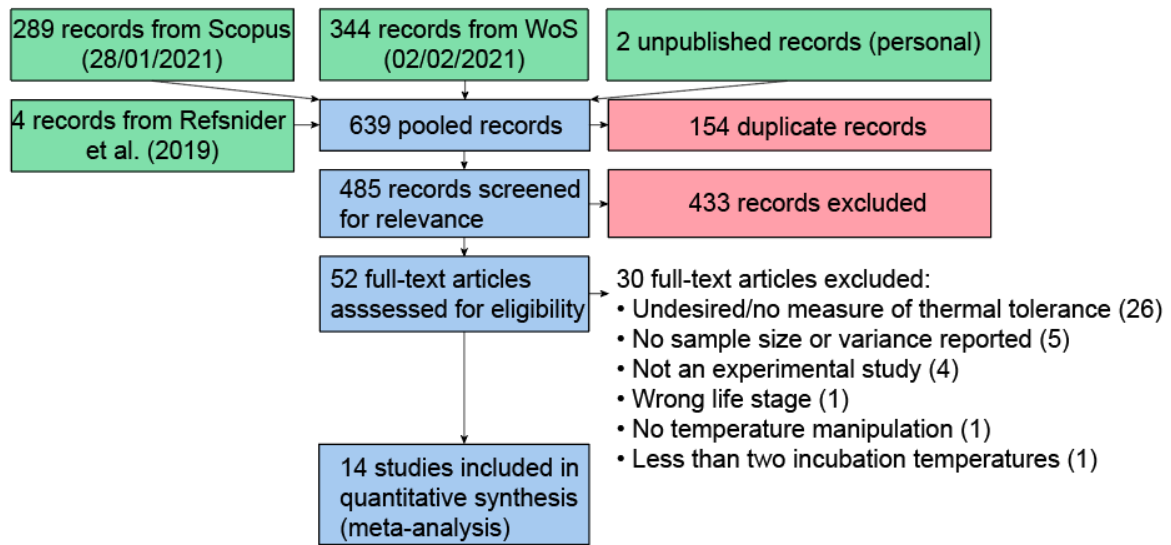
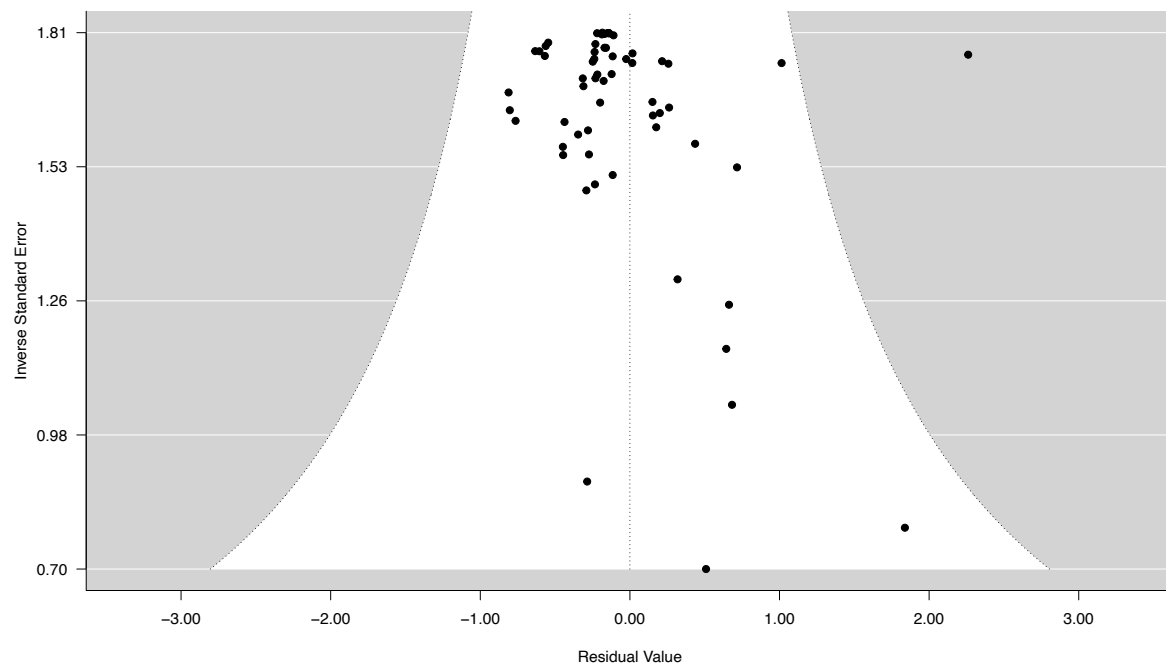Figure S3. PRISMA flowchart illustrating the systematic literature search and record screening process.

Figure S4. Funnel plot of the meta-analytic residuals against precision (1/SE) to test for publication bias. Each point represents a pair-wise temperature comparison. There is no detectable asymmetry across our samples.

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