Natural developmental temperatures of ectotherms: A systematic map and comparative analysis

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Abstract

In ectothermic animals, physiological processes are highly sensitive to environmental temperatures. Developmental temperatures, in particular, have large and long-lasting impacts on ectotherm phenotypes. However, most phenotypic responses are studied in the laboratory, and may not accurately reflect ecological impacts in natural environments. In this study, we provide the first synthesis of natural oviposition site temperatures in wild ectothermic populations by collating and analysing 64 years (1958-2022) of published data. First, we conducted a systematic review to explore the history and trends in the field. Second, we examined how the mean and among-site variation in temperatures varied across latitude, habitats (land/water), and taxonomic groups (arthropods, fish, amphibians, and reptiles). Third, we performed a meta-analysis to investigate the extent to which temperatures of natural oviposition sites influence the phenotypes of newly hatched ectotherms. We found a large taxonomic bias towards reptile model species, with few studies from fishes, amphibians, and arthropods. This bias towards reptile species can be explained by a historical focus on targeted research questions (e.g. temperature-dependent sex determination) and a lag in technological developments required to measure nest temperatures in other taxa (e.g. waterproof miniature dataloggers). We found no evidence for a correlation between mean oviposition site temperatures and latitude, but the temperature variability among oviposition sites within a population increases significantly with latitude. We also found that ectotherms laying eggs in water have a steeper decline in oviposition site temperatures with latitude than those that lay their eggs on land. These findings suggest that mothers select oviposition site temperatures that likely optimise embryonic development regardless of local climate, yet maternal selection behaviour may be less effective for those laying eggs in the water and at higher latitudes. Strikingly, studies quantifying the impacts of natural oviposition site temperatures on hatchling development or hatching success are rare (N = 46 studies) and biased towards a few (N = 19) reptile or arthropod species. However, our meta-analysis revealed small-to-large negative correlations between oviposition site temperatures and incubation duration and hatching success (Zr = -0.580 and -0.076, respectively). This suggests that the widely reported impacts of developmental temperatures on hatchling phenotype described in laboratory studies will translate to impacts in the wild. However, existing taxonomic biases challenge the generalisability of these findings across ectotherms. We provide recommendations and highlight novel technological advances that will help fill knowledge gaps and complement our understanding of the impacts of temperature on wild ectotherms.

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Introduction

The embryonic stage is a particularly vulnerable life stage for ectotherms, as the lack of post-oviposition parental care in most species leaves embryos exposed to unmodulated environmental conditions. Yet despite our appreciation that environmental temperatures vary considerably, we have only limited and species-specific understanding of natural developmental temperatures and the extent to which they impact offspring phenotype in the wild (e.g. Bowden et al., 2014). This means that knowledge regarding developmental plasticity and thermal adaptation gained from laboratory measurements (e.g. Pottier et al, 2022a; Hoffmann & Sgrò, 2011; Verberk et al., 2016; Noble et al., 2018) often has uncertain relevance for natural populations. Greater knowledge of variation in natural oviposition site temperatures and how they impact ectotherm development in the wild would help transfer knowledge acquired in the laboratory to natural environments, thus expanding our understanding of thermal ecology and adaptation. This knowledge expansion is particularly urgent given the current rate of climatic warming.

Laboratory evidence shows that embryonic developmental temperatures have large and long-lasting impacts on future phenotypes of ectotherms, including hatching success, developmental time, physiology, morphology, and behaviour (Colinet et al., 2015; Noble et al., 2018; Bodensteiner et al., 2021; Massey and Hutchings, 2020). However, phenotypic responses to constant or periodically fluctuating thermal regimes used in laboratory settings may not mirror phenotypic responses that occur in natural populations (Bowden et al., 2014; Hall and Warner, 2020; Paitz et al., 2010; Raynal et al., 2020). In nature, temperature can be highly variable within the developmental embryonic period, as well as among years and micro-habitats (Colinet et al., 2015; Booth, 2018; Bowden and Paitz, 2018; Suggitt et al., 2011). The increased frequency and intensity of extreme weather events, such as heatwaves, cold snaps, or droughts, is likely to increase the environmental variation that embryos are exposed to in natural environments (Kikstra et al., 2022). Moreover, environmental conditions other than temperature (e.g. moisture, pH; Bowden et al., 2014; Frouz, 2000; Noble et al., 2018; Santi et al., 2020) can modulate the impact of temperature on phenotype. Thus, it cannot be assumed that results from controlled lab experiments translate directly to temperature effects occurring in the wild.

If oviposition site temperature plays a role in shaping hatching success in wild populations, then selection on ovipositing behaviour and life-history strategies may have occurred in response to temperature variation. First, maternal oviposition behaviour can help avoid exposure to suboptimal or stressful temperatures (Refsnider & Janzen, 2010). For example, mothers can oviposit in shadier sites or earlier in the breeding season to avoid exceeding thermal maxima in warmer environments, or expose eggs to greater solar radiation to reach warmer temperatures in cool environments (Angilletta et al., 2004; Bennett et al., 2015; Bose et al., 2019; Doody, 2009; Löwenborg et al., 2012; Radder and Shine, 2007; Rodrigues et al., 2020; Shine and Harlow, 1996; Wisenden et al., 2009). Second, geographic variation in temperature could lead to local adaptation of embryonic physiologies or life histories (Doody et al., 2006; Laugen et al., 2003; Du and Shine, 2015). For example, populations from cooler environments often have faster developmental rates at a given temperature compared with populations from warmer environments, allowing embryos to complete development at low temperatures (i.e., countergradient developmental rate; Hourigan and Radtke, 1989; Laugen et al., 2003; Mitchell and Seymour, 2000; Shine, 1999; Thompson et al., 1996). Alternatively, prolonged developmental time (Danks, 2007; Shine, 2004), diapause (insects, fish and reptiles; Armbruster, 2016; Bale and Hayward, 2010; Danks, 2007; Thompson et al., 1996; Wourms, 1972), or over-wintering within the oviposition site (Costanzo et al., 1995) obviate the need to develop quickly. Despite the large literature examining global patterns of thermal adaptation (Angilletta et al., 2004; Buckley et al., 2015; Hoffmann and Sgrò, 2011; Huey and Stevenson, 1979), there are very few geographic comparisons of thermal conditions of natural oviposition sites (Bennett et al., 2015; Bodensteiner et al., 2023; Carter et al., 2019; Doody et al., 2006).

In this study, we synthesised oviposition site temperatures globally and analysed their impacts on the phenotype of wild ectotherms. We performed a systematic review of the literature – the first to our knowledge – encompassing studies published in the last 64 years (1958-2022). Our synthesis provides novel insight into thermal ecology and adaptation through three objectives. First, we assess the history and trends in the literature on ectotherm oviposition sites using quantitative data from our collated dataset. This historical review describes the drivers dictating progress in the field, including the conceptual history behind research on oviposition site temperatures and the technological advances that opened avenues for new research questions and increased the quality, resolution, and quantity of data.

Second, we analyse how ectotherm oviposition site temperatures vary with latitude, oviposition habitat (land vs. water), and between taxonomic groups (reptiles, fishes, amphibians, arthropods). Air temperatures are warmer and less variable (across days and seasons) at low absolute latitudes relative to higher latitudes (Mahlstein et al., 2011). Therefore, we predicted that that oviposition site temperatures would decrease with latitude. Alternatively, adaptations in maternal site selection for optimal temperatures may reduce or mask the variation in oviposition site temperatures across latitudes. Additionally, aquatic ectotherms tend to experience lower and less variable temperatures than terrestrial ectotherms from similar geographical locations (Barber, 2013; Mitchell and Seymour, 2000). Therefore, we predicted that the mean and variation in temperature among oviposition sites will be lower in aquatic environments compared with terrestrial environments.

Lastly, using a subset of our collated data we perform a meta-analysis to assess the correlation between natural oviposition site temperature and phenotypic traits of newly hatched ectotherms (development time, hatching success). Previous meta-analyses using laboratory studies have demonstrated that higher constant incubation temperatures reduce development time and hatching success (e.g., Noble et al., 2018; O’Dea et al., 2019). However, thermal fluctuations can influence the magnitude of responses to incubation temperatures, particularly at low or high mean temperatures (Noble et al. 2018; Raynal et al., 2022; but see Stocker et al., 2024). Therefore, we expect as temperatures increase in a natural setting, hatching success and incubation duration will decrease. We conclude with recommendations to fill existing knowledge gaps and increase our understanding of how temperature impacts ectotherms in the wild.

Methods

Literature search

We conducted a systematic review of published studies that measured the oviposition site temperatures of ectotherms. Following PRISMA-EcoEvo guidelines (O’Dea et al. 2021), searches were conducted in both Web of Science (core collection) and Scopus using the University of New South Wales library subscription (Nakagawa, Ivimey-Cook, et al., 2023). The basic search string used was as follows: ("thermal*" OR "temperat*") AND ("oviposit*" OR "egg site" OR "nest" or “nests” OR "egg laying") (see supplement for full search string details). Additionally, certain categories were excluded to reduce the number of unrelated studies (see supplementary material). This resulted in 4846 records from Web of Science and 5027 records from Scopus. These records were imported into Rayann (Ouzzani et al., 2016) and duplicates were removed (3030), leaving 6843 unique records that were screened (by RR) based on their title, abstract, and keywords (Figure S1). To check for inclusion accuracy, LS and RR independently analysed 100 abstracts in Rayann and were 95% aligned (Ouzzani et al., 2016). One author (RR) screened 637 full-texts, of which 251 studies were included in the systematic historical review and comparative study, and 46 studies in the meta-analysis (Figure S1). We included additional previously-unreported mean nest temperatures for several reptile species that were compiled by Schwanz et al (2020) (N = 7 studies).

To be included in the systematic review and comparative macroecology analysis, studies must have recorded the temperature of fixed oviposition sites containing live eggs and reported the population mean oviposition site temperature (or minimum and maximum, see methods below for converting these to mean). We also included studies that reported a single temperature if only one temperature recording was made. The temperature must have been measured where the eggs were laid (not in the ground next to the oviposition site or the air temperature above the oviposition site). We included sea turtle egg relocation studies if the hatcheries were located on the same beach where the turtles naturally nest. In these cases, the temperatures included in the present study were the temperatures from the most natural treatment. Temperatures from treatments or studies where oviposition sites were manipulated with high levels of shading or water were not included.

Most studies that matched our inclusion criteria measured multiple oviposition sites from a population, often recording a time-series of temperature measurements for each oviposition site and calculating a mean temperature for each site. Typically, these studies then reported oviposition temperature as the population mean across sites and the standard deviation of individual oviposition site means. We extracted these values as the “mean temperature” and “standard deviation among sites” for each population. In addition, we extracted any data on the minimum and maximum site (mean) temperature for the population. Some studies measured temperature for only a single oviposition site, such that the standard deviation among sites was not available. Some studies reported data for multiple populations or for the same population across multiple years. These separate ‘sample populations’ were included as unique data points and hereafter referred to as ‘populations’ for simplicity. We additionally extracted the following information about each population: Taxonomic order, species, population location, and oviposition site habitat (terrestrial vs. aquatic). Data was extracted from both in-text and figures. These data were used for the systematic map and macroecological analysis.

A subset of the above studies was used for the meta-analysis. To be included in the meta-analysis, animals must have spent at least 80% of their development in the oviposition site. When not reported in the included study, species average developmental times reported in the literature were used. Studies must have also reported a statistical relationship between oviposition site temperature and offspring outcome (incubation duration, hatching success, hatchling phenotype) and reported the sample size of oviposition sites. We emailed authors of studies that reported correlations between mean oviposition site temperatures and hatchling phenotype to inquire regarding unpublished correlations with hatching success and incubation duration. As a result of these enquiries, we received unpublished correlations from W.S Huang and S. Kobayashi and raw data from K. Bonach, J. Riley, I. Reboul, G. González Desales and D. Booth. For all studies, we extracted correlation coefficients between mean site temperature and offspring outcome.

Systematic map

To analyse which research topics motivate ectotherm oviposition site research for our historical review, we assessed each study in the systematic map to generate categories of topics that appear most commonly. We then assigned the following broad research categories to each paper: evolutionary transitions, thermoregulation, general ecology, climate change, and species management. Most of the studies in the dataset have multiple aims; therefore, categories were chosen based on the main perceived motivation of the paper.

Macroecological patterns

The goal of our macroecological analysis was to examine the variation in ectotherm oviposition site temperatures across latitude, habitat (terrestrial vs. aquatic), and taxa. This was to determine if local environmental conditions directly drive oviposition site temperatures, or if maternal oviposition behaviour limits the variation across latitudes. Some studies (N = 32) presented the minimum and maximum oviposition site temperature, rather than the overall mean. To include these in the analysis, we calculated the population mean temperature by averaging the minimum and maximum values presented. We verified that this approach was accurate using 20 studies that presented minimum, maximum, and mean. Averaging the minimum and maximum temperatures from these studies predicted the population mean temperature accurately (r = 0.9863, slope = 1.06). For studies that did not report the latitude of the study population, these were obtained using the description of the location and Google Maps.

All analyses were performed in R (Version 4.2.0) (R Core Team, 2020). First, we checked if the relationship between mean temperature and latitude was linear, by comparing the fit of a generalised additive model and a linear model using the *mgcv*

(Version 1.8.42) (Wood and Wood, 2015) and *lme4* (Version 1.1.34) (Bates et al., 2014) packages, respectively. Using visual inspection and AIC model selection, we found that the linear model was a better fit to the data (ΔAIC = 223.8). We ran separate Bayesian linear mixed models using the *MCMCglmm* package (Version 2.35) (Hadfield, 2010) to examine the relationship between latitude (absolute value; predictor) and two measures of ectotherm oviposition site temperatures: mean temperature across oviposition sites and standard deviation among sites within each population. Due to standard deviation being bounded by 0 and having a right-skewed distribution, we natural-logged this variable before running the models. Model estimates and predictions were back-transformed for visualisation. Additionally, we ran separate models to examine if the variation in oviposition site temperatures (mean or standard deviation) and latitude varied between taxonomic groups. We first created major groupings based on higher-level taxonomy, though the groups are not monophyletic clades. The major groups were arthropods, fish, amphibians, and reptiles.

Due to the much larger sample sizes of reptiles found in the literature, we also analysed reptile groups separately, by dividing this group into secondary categories: sea turtles, crocodilians, freshwater turtles (including tortoises), and squamates (snakes and lizards). Lastly, we categorised ectotherms based on whether they oviposit their eggs in the water or on land. All models included the random effects of study identity, species and the phylogeny. To create the phylogenetic tree containing all the species in the dataset, we used the Tree of Life (http://itol.embl.de/) via the *rotl* package (Version 3.1.0) (Michonneau et al., 2016). Branch lengths were estimated using the '*compute.brlen*' function from the *ape* package (Paradis and Schliep, 2019). To analyse relationships with latitude among the different taxa, we ran separate models with each taxonomic group as the reference level. We generated predictions from statistical model outputs using the *'emmeans'* function from the *emmeans* package (Version 1.8.7) (Lenth and Lenth, 2018).

Meta-analysis

Although we collected data on any offspring outcome from all ectotherm groups, only hatching success and incubation duration had sample sizes large enough for a meta-analytic approach. This resulted in the meta-analysis including data from only reptiles and amphibians.

Correlations reported in studies were converted from F values, Chi square, Spearman's rank correlation coefficient (ρ) and r^2 values to Pearson's correlation coefficients (r) as per Koricheva et al., (2013). Pearson's correlation coefficients (r) were then converted to "*Zr*" effect sizes using the *'escalc'* function from the *metafor* package (Version: 4.2.0) (Viechtbauer, 2010) to be used in meta-analytic models. A phylogeny was created for the meta-analysis dataset using similar methods as for the macroecology analysis (see above).

To obtain an overall estimate of how natural nest temperatures affect incubation duration and hatching success, we first ran a multi-level meta-analysis (MLMA) with all Zr effect sizes (N = 70, from N=46 studies overall) as the response variable (i.e., including both incubation duration and hatching success) and three random effects (effect size ID, species, and phylogeny). This model was estimated using residual maximum likelihood (REML) using the '*rma.mv'* function from the *metafor* package. We then split the dataset between effects on incubation duration (N= 38 effect sizes) and hatching success (N= 32 effect sizes) and ran separate models for each trait using three random effects (effect size ID, species, and phylogeny). As only four studies contributed multiple effect sizes to each of these datasets, we chose to not include study ID as a random effect to avoid overfitting the models (14 studies contributed effect sizes to both datasets). These separate models were used to calculate the amount of heterogeneity, I^2, and the overall strength of the effect in each of the two datasets. I^2 is the percentage of variance among effect sizes not explained by sampling error alone. Heterogeneity estimates over 75% are considered high, 50% medium, and 20% small (Higgins et al., 2003). However, large levels of heterogeneity (>90%) are common in multispecies analyses such as ours (Senior et al., 2016). We used the function *'orchard_plot'* from the *orchard 2.0* package (Nakagawa et al., 2023) to back transform the Zr effect sizes to correlation coefficient (r) and plot the meta-analysis results.

To test for publication bias over time in each dataset, we ran a model using the function *'rma.mv'* from the *metafor* package (Viechtbauer, 2010) that included all moderators and random effects in each response variable's full model along with Z-transformed publication year and precision (wi, the inverse of the variance). We found no evidence of publication bias in the hatching success and incubation duration datasets. All data and R code used in these analyses can be found at: https://github.com/RRaynal/naturalnestsMA.

Results

Systematic map: History of the field of research

Research that is conducted and published is driven by many factors, such as government policy and funding (Clark, 1993; Culumber et al., 2019), technology availability, model species suitability and availability (taxonomic bias; Jenner & Wills, 2007; Kim & Byrne, 2006), publication bias (Dickersin & Min, 1993; Lortie et al., 2007; Møller & Jennions, 2001), and choice of research topics (Kim & Byrne, 2006; Lortie et al., 2007; Møller & Jennions, 2001). Here, we review the history and current state of the field of natural oviposition site temperatures in the context of some of these drivers: technology availability, choice of research topics, and taxonomic bias. By identifying patterns within these areas, we aim to highlight recommendations to advance the field.

Technology

The early history of studying natural oviposition site temperatures was largely driven by the technology available at the time. Up until 1985, it was very common for oviposition temperatures to be measured rather erratically, with spot temperatures taken a few times a week, or even just once or twice in total (Greenwood, 1958; Magnusson, 1979; Omo, 1977). Many of these earlier studies used thermographs or large wired dataloggers with probes. These tools required a person to be at the oviposition site to read the thermometer every time a measurement was recorded. This meant measurement intervals could be impacted by access to the site, number of research assistants available, weather, or parental guarding.

The first record we found of a natural oviposition site temperature for an ectotherm was published in 1934 (McIlhenny, 1934). This study was not retrieved in our systematic search, highlighting the challenges of finding early literature with modern indexing tools. In McIlhenny’s study, the temperature of a single alligator nest (species unreported) was monitored using a double registering thermometer (with a bulb) buried in the nest (McIlhenny, 1934). The first study retrieved in our systematic search (from 1958) investigated the breeding habitats and nests of the East African lungfish (*Protopterus aethiopicus*) and used a simple thermometer to monitor natural developmental temperatures (Greenwood, 1958). For the next 25 years studies mainly used technology such as simple thermometers, thermistors, or thermocouples to monitor temperatures at natural egg sites (Jay & Frankson, 1972; Josens, 1971; Lévieux, 1972; Magnusson, 1979; Omo, 1977; Siefert, 1968).

In the mid-1980's, great advances were made in monitoring temperature at many oviposition sites within a population and for longer timespans. For example, Bull (1985) monitored 75 map turtle (*Graptemys geographica, G. ouachitensis, G. psuedogeographica*) nests simultaneously with frequent datalogging, using a copper-constant thermocouple with a datalogger that had 100 independent channels (arrow 1, figure 1). Similarly, Rosengren et al. (1987) continuously monitored the internal temperatures of a wood ant nest for 5 years, using a thermograph and 3 mercury sensors. However, these forms of technology still required wires and relatively large logger equipment to be left outside – either dug into holes near the oviposition site (Christian and Lawrence, 1991) or protected in a weatherproof container.

In the mid-1990's miniaturized, weather resistant dataloggers (such as iButtons and Hobo Pendants) were introduced (arrow 2, figure 1). These dataloggers were small enough (approximately 16.3mm diameter x 5.9mm tall) to be left within larger oviposition sites to record temperatures at pre-set intervals without any intervention from a researcher. This revolutionised the resolution of thermal data and facilitated a boom in research on the natural nest temperatures of turtles, which quickly dominated the world of oviposition site thermal research (Figure 1). With the increased feasibility of oviposition site research, more sites could be monitored and with greater frequency of sampling and over longer periods of time. Animals were also not disturbed while attending their nest or laying additional eggs. Advances in technology had a defining role in research on oviposition sites temperatures by increasing the resolution and repeatability of research, which in turn increased the range of questions that could be addressed.

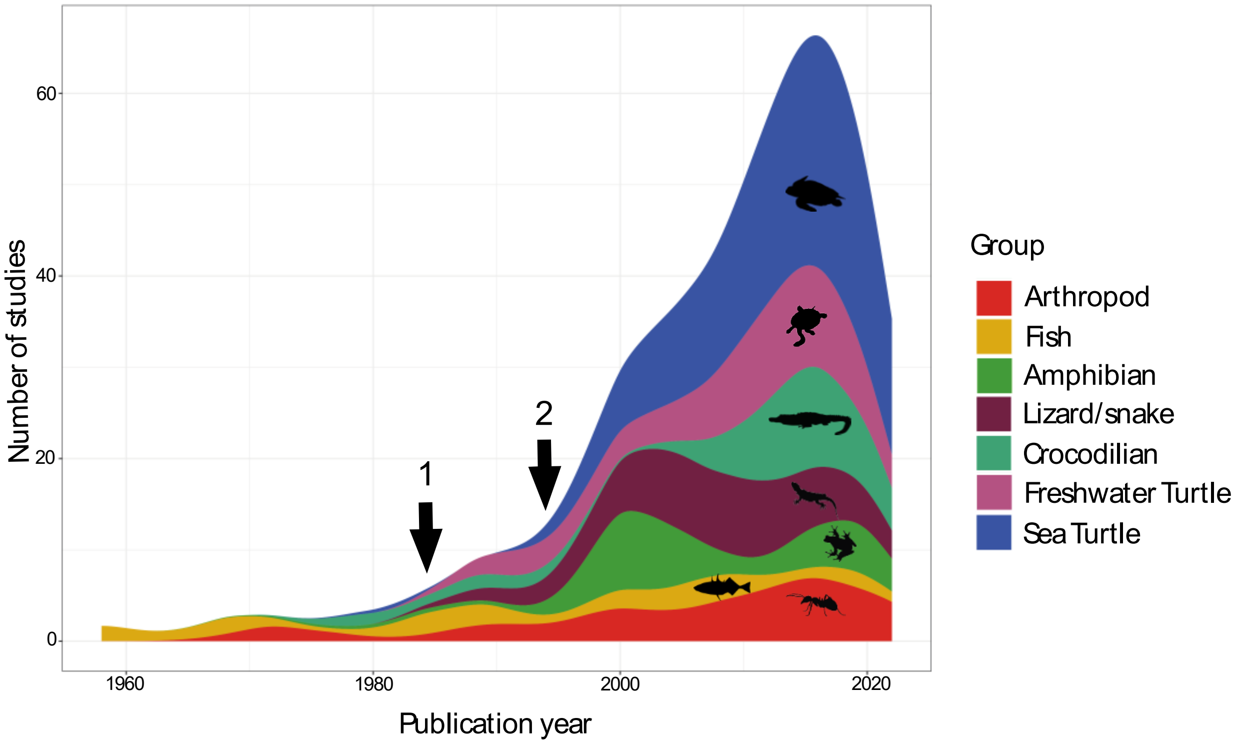

Figure 1. Number of published studies that investigate natural oviposition site temperatures in ectotherms over time. '1' denotes the first found study that monitored multiple oviposition sites at the same time, '2' denotes the first found study that used miniature dataloggers. Colours represent ectotherm groups (N = 251 studies). Tortoises are included in the Freshwater Turtle group. First paper for; Arthropod: 1971, Fish:1958, Amphibian: 2000, Lizard/snake: 1988, Crocodilian: 1979, Freshwater Turtle: 1988, Sea Turtle: 1982. Silhouette images obtained from PhyloPic (https://www.phylopic.org).

Topics of research

The motivations behind research, including emerging academic questions or applied outcomes often play a large role in shaping the progression of a field. Although most studies included in this systematic map were motivated by multiple questions and themes, there were a handful of primary motivating research topics that appeared frequently across taxa: evolutionary transitions, thermoregulation (including thermal tolerance and egg temperature regulation), general ecology, climate change and species management (Figure 2).

Ectotherm clades often serve as model clades for studying repeated evolutionary transitions between life-history strategies (e.g. oviparity-viviparity, level of sociality, sex-determining mechanism), as they facilitate addressing questions of adaptive evolution (Franks, 1989; Shine, 1995) (evolutionary transitions: N=41 studies). For example, the evolution of viviparity from oviparity has been studied in reptile taxa that have both viviparous and oviparous populations, and this phenomenon has been hypothesized to be driven by selection for modulation of embryonic developmental temperatures (Shine, 1995). Similarly, theories of the evolution of temperature-dependent sex determination (TSD), where developmental temperatures directly affect the sex of individuals, posit that TSD is adaptive when oviposition site temperatures influence offspring fitness-related traits (e.g. hatching success and size) (Shine, 1995; Schwanz & Georges 2021). Indeed, the discovery of TSD in 1966 (Charnier, 1966) led to increased interest in monitoring the temperature of oviposition sites to look for TSD in other reptiles (Bull, 1985). Thus, interest in these two major evolutionary questions gave rise to studies on sex ratios, offspring phenotypes, and nest site selection. While many studies investigating TSD and viviparity are conducted in the laboratory, natural oviposition temperatures provide crucial information about processes occurring in wild populations. Therefore, it is not surprising such topics are well-represented in our systemic map.

Interest in animal thermoregulation has driven studies investigating thermoregulation within ectotherm-constructed nests (N=54/56 studies), and to a lesser extent thermal tolerance of eggs (N=2/56 studies). Thermoregulation within the nests of eusocial insects make up the largest portion of studies on arthropods in our systematic map (Figure 2). These studies aim to understand the diverse strategies employed by social insects to maintain optimal brood temperatures in variable, cool, and hot environments. For example, in very large colonies, the metabolism of thousands of workers maintains tolerable nest temperatures (Franks, 1989), while in some smaller colonies, behavioural adaptations such as fanning and foraging for water play similar roles (Jay and Frankson, 1972). In addition to investigating the thermal condition inside nests, many studies explore the role of nest-site selection on nest temperatures, such as nest spatial location, substrate type, and nest depth (Christian and Lawrence, 1991; Swiggs et al., 2018). For example, a study using water dragons (*Intellagama lesueurii*) across the east coast of Australia found that animals from warmer climates laid their eggs deeper to protect them from lethally high temperatures (Doody et al., 2006).

Studies that fall within the general ecology topic include broad, natural history studies where the measurement of oviposition site temperature often takes a secondary role in the study (General ecology: N=64 studies). These studies generally gather foundational information on understudied amphibians, fish and reptile species (Amoah et al., 2021; Greenwood, 1958; McCarty et al., 2022; Poulin & FitzGerald, 1989). They aim to address knowledge gaps on overall breeding ecology, such as mating and nesting behaviours (Amoah et al., 2021; Antelo et al., 2010; Fischer, 2023; Nakao et al., 2006), embryonic development (Magalhaes et al., 2017; N. J. Mitchell & Seymour, 2000; Monsinjon et al., 2017), and how disease impacts reproduction and life history (Kraus et al., 1998; Tapilatu et al., 2020).

Studies included in the climate change category are often motivated more narrowly on examining whether populations will be able to respond to climate change via trait plasticity or evolution, or whether population management is necessary (Climate change: N = 38 studies). Studies investigating plasticity, such as changes in thermal reaction norms and nest site selection behaviours are particularly prevalent (Monsinjon et al., 2017; Tapilatu et al., 2020; Weisrock and Janzen, 1999). Research projecting the impacts of climate change on biodiversity loss suggest the overall impact will be negative (Habibullah et al., 2022). However, studies on individual species have yielded variable findings. For example, studies suggest that some arthropod pest species respond to higher natural temperatures with increased fecundity, shorter generation times, and prolonged length of breeding seasons, in turn producing more clutches annually (Casañas-Arango et al., 1990, see also Colinet et al., 2015). Whether the effect of climate change will be positive or negative for certain taxa will likely be dependent on whether the temperatures experienced in nature are permissive or detrimental.

Threatened species management has motivated many studies (N=52 studies), though these studies cross over with the topics of evolutionary transitions and climate change. Within this category, all of the studies focus on species that have been defined as threatened species at some point, have temperature-dependent sex determination, and are predicted to be substantially impacted by future climate predictions (Eisemberg et al., 2017; Escobedo-Galván et al., 2016; Pazira et al., 2016). Studies aiming to develop or refine management strategies for conserving endangered species in a changing climate often involve directly regulating oviposition site temperature in an attempt to stabilise sex ratios, such as egg relocations, nest shading and nest watering, or relocating populations to areas with more conducive oviposition site temperature options (Başkale and Kaska, 2005; Milton et al., 1997; Tuttle and Rostal, 2010).

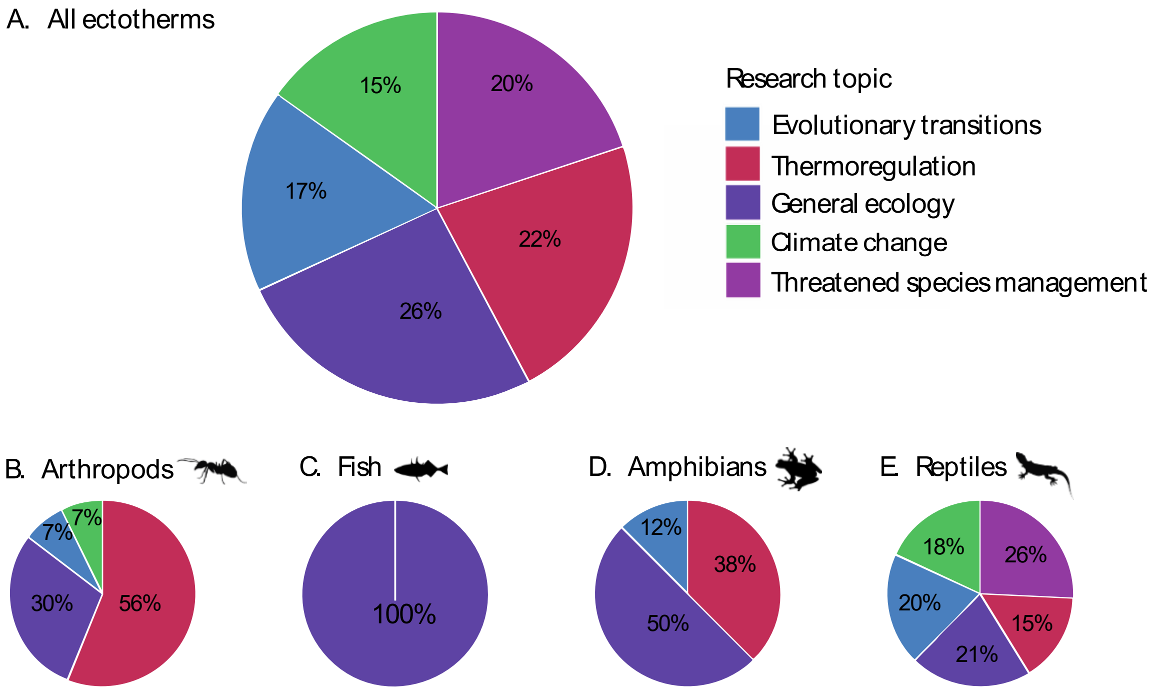

Figure 2. The percentages of each primary topic of inquiry (colour) within studies of ectotherm oviposition site temperatures included in the systematic review and macroecological analysis. A) All ectotherms (N = 251 studies), B) Arthropods (N = 41 studies), C) Fish (N = 8 studies), D) Amphibians (N = 8 studies), and E) Reptiles (N = 194 studies). Silhouette images obtained from PhyloPic (https://www.phylopic.org).

Taxonomy and phenotype

Reptiles make up the largest percentage of our dataset (77.3% of studies, N = 62 species, Figure 3). Within reptiles, sea turtles (56% of reptile studies, N= 6 species) and freshwater turtles (18% of reptile studies, N= 18 species) make up the largest proportion of studies. Lizards (11% of reptile studies, N= 17 species) and crocodilians (9.2% of reptile studies, N = 11 species) constitute the next largest group followed by snakes (4% of reptile studies, N= 7 species) and tortoises (2% of reptile studies, N= 3 species). It is evident sea turtles are popular model species; however, most studies in our dataset use only two of the seven extant species: loggerhead turtle (18% of reptile studies, N = 46 studies) and green turtle (20.6% of reptile studies, N = 41 studies). This highlights that much of what is known about oviposition site temperatures of ectotherms originates from data on two reptile species from a small monophyletic group with large geographic distributions (29% of all studies; 38.7% of reptile studies).

Arthropods constitute one of the most species diverse groups in the animal kingdom and represent the second largest group in our dataset (16.6% of studies, N = 36 species, Figure 3). However, like the reptile dataset, we also found taxonomic biases within the arthropod group. Most studies on arthropods use eusocial insects as model species (84% of arthropods). Within arthropods, the largest group was ants (39%), followed by bees (22%), termites (13%) and wasps (10%). Other groups were only represented by a single or two studies each (butterflies, aquatic insects, moths, spiders and beetles; Figure 3).

Amphibians are the most threatened group of vertebrates (see Luedtke et al., 2023), but studies investigating the oviposition site temperatures of amphibians are rare (3% of studies, N = 8 studies, 8 species, Figure 3). Additionally, frogs were the only group of amphibians represented in this dataset (Figure 3). Studies on this taxon were only found starting from the year 2000 (Figure 1) and were broader studies in the general ecology topic category (Figure 2). Of the 8 species included in this dataset, 5 build nests, suggesting that the construction of nests provides some opportunity or impetus for studying amphibian oviposition sites (Rodrigues et al. 2020; Mitchell et. al 2000; Rodriguez et al. 2019; Shepard et al. 2005; Luza et al. 2005).

Despite fish being diverse (>30,000 species), our search retrieved few studies that have investigated the temperature of their oviposition sites (3% of studies, N = 8 studies, 7 species). Like amphibians, all studies using fish were motivated by the broader topic of general ecology (Figure 2). It is likely that the amphibian and fish studies included in this dataset needed to have broader aims due to lack of foundational information on natural nest ecology. All fish model species included in our dataset build nests and often exhibit parental care via male guarding and/or oxygenating eggs (Bose et al., 2019; Greenwood, 1958; Nakao et al., 2006; Poulin and FitzGerald, 1989; Reebs et al., 1984; Siefert, 1968; Walters et al., 2000; Wisenden et al., 2009).

Studying offspring phenotype is crucial in evolutionary biology and ecology as it provides insights into selection, adaptation, and impacts of environmental change. Despite the relatively large number of studies that measured oviposition site temperatures in nature, these studies rarely provide any direct links to offspring phenotypes. Within the dataset, 59.8% (150/251) of studies measured an offspring outcome, of which 39.3% (59/150) statistically analysed the covariation between an outcome and oviposition site temperatures (Figure S2). Thus, fewer than a quarter of studies that measured oviposition site temperature also linked temperatures to offspring outcomes (23.9%; 60/251, i.e., hatching success, incubation duration, sex ratio, morphology and behaviour). Of the studies that statistically compared an offspring outcome to oviposition site temperature, 56 used reptiles, 2 used amphibians and 2 used arthropods as a model species.

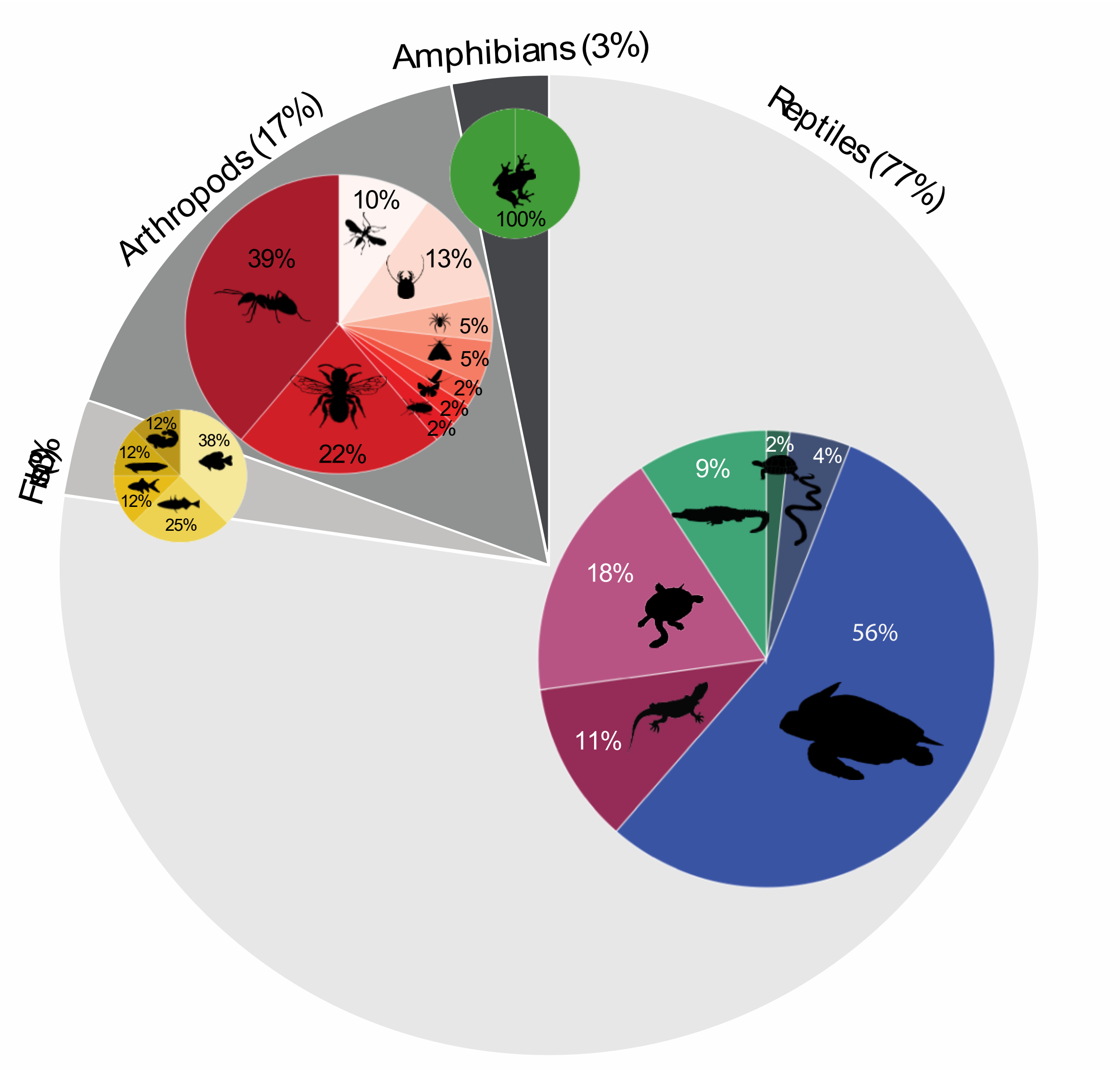

Figure 3. Percentages of studies that were in included in the systematic review and macroecological analysis, presented as a function of their focal ectotherm taxa (colour; N=251 studies). Silhouette images obtained from PhyloPic (https://www.phylopic.org).

Macroecological Patterns

On a global scale, we found no relationship between oviposition site temperatures and absolute latitude (Figure 4; Table 1). Amphibian oviposition site temperatures decreased with latitude at a faster rate than the other major taxonomic groups (slope = -0.77, CI= -1.216, -0.353, P<0.05, Table 1, Figure 5). Similarly, ectotherms laying eggs in water had a steeper decline in oviposition site temperatures with latitude than those that lay their eggs on land (Table 1, Figure 5). All other comparisons of slope between major taxonomic groups were non-significant (all posthoc pairwise comparisons P > 0.05). However, the results regarding latitudinal clines should be interpreted in the context of the availability of data across latitude. Specifically, the majority of amphibian (N=6/8) and fish (N=7/8) studies, as well as the majority of studies on aquatic egg-layers in general (N = 12/16), focused on populations that live above 30 degrees absolute latitude (Greenwood, 1958; Rodrigues et al., 2020; Shepard and Caldwell, 2005; Figure 5). In contrast, major reptile groups had much greater latitudinal representation (though sea turtle and crocodile populations were more equatorial in their distribution than freshwater turtle populations; Figure 5). Finally, at 0 degrees latitude (intercept), mean oviposition site temperatures of snakes and lizards were significantly lower, by about 8 degrees, than those of sea turtles (-8.08, CI= -17.4, -0.1; Table 1).

Among-site standard deviation in temperatures (i.e. oviposition sites within a sample population) increased significantly with absolute latitude regardless of taxonomic group or habitat (Table 1, p <0.05, Figure 6). We found no significant interactions between taxonomic group and latitude for among-site standard deviation in oviposition site temperatures.

Table 1. Results of Bayesian linear mixed models testing the relationship between the mean and standard deviation (among site) temperature of ectotherm oviposition sites and absolute latitude. We present posterior means (Post mean), lower and upper bound of the 95% confidence interval (CI) and p-values for each fixed effect within each model. Significant effects are bolded.

Mean					***ln(Standard Deviation)***				
Fixed effects	**Post mean**	**L CI**	**U CI**	**P-value**	**Fixed effects**	**Post mean**	**L CI**	**U CI**	**P-value**
All taxa – taxonomic grouping									
(Intercept: Reptile) (N=309)	**26.951**	**20.854**	**32.116**	**<0.001**	*Intercept (Reptile) (N= 221)*	-0.475	-1.240	0.415	0.229
Latitude (absolute) (N=392)	0.009	-0.018	0.037	0.534	***Latitude (absolute) (N=255)***	**0.019**	**0.007**	**0.033**	**0.004**
Amphibian (N=8)	15.139	-1.780	31.304	0.080	*Amphibian (N=5)*	-2.188	-5.471	1.427	0.206
Fish (N=10)	-3.142	-15.784	9.414	0.595	*Fish (N=5)*	-0.944	-8.809	6.096	0.802
Arthropod (N=65)	1.097	-5.397	8.473	0.739	*Arthropod (N=24)*	-0.695	-2.346	0.980	0.379
Lat*Amphibian	**-0.779**	**-1.234**	**-0.316**	**0.001**	*Lat*Amphibian*	0.051	-0.056	0.147	0.330
*Lat*Fish*	-0.132	-0.474	0.163	0.411	*Lat*Fish*	0.031	-0.142	0.199	0.723
*Lat*Arthropod*	-0.054	-0.128	0.024	0.142	*Lat*Arthropod*	0.008	-0.026	0.040	0.641
Reptiles – taxonomic grouping									
Intercept (Sea turtle) (N=185)	**30.818**	**24.234**	**38.203**	**<0.001**	*Intercept (Sea turtle) (N=149)*	-0.754	-1.758	0.419	0.157
Latitude (absolute) (N=309)	0.016	-0.010	0.044	0.241	***Latitude (absolute) (N=218)***	**0.016**	**0.000**	**0.031**	**0.043**
Crocodilian (N=18)	-0.047	-8.245	8.513	0.990	*Crocodilian (N=12)*	0.997	-1.180	3.058	0.365
Freshwater turtle (N= 54)	-3.002	-9.100	2.165	0.266	*Freshwater turtle (N=27)*	0.261	-1.169	1.616	0.677
Lizard/Snake (N=49)	**-8.080**	**-17.364**	**-0.104**	**0.049**	*Lizard/Snake (N=30)*	-0.190	-1.924	1.333	0.821
*Lat*Crocodilian*	0.044	-0.190	0.241	0.702	*Lat*Crocodilian*	-0.011	-0.124	0.086	0.839
*Lat*Freshwater turtle*	-0.047	-0.117	0.032	0.231	*Lat*Freshwater turtle*	0.000	-0.032	0.040	0.982
*Lat*Lizard/snake*	0.038	-0.066	0.150	0.496	*Lat*Lizard/snake*	0.022	-0.018	0.061	0.305
All taxa - Land/Water									
Intercept (Land, N=370)	**26.948**	**20.412**	**32.139**	**<0.001**	*Intercept (Land) (N=245)*	-0.621	-1.266	0.058	0.080
Latitude (absolute) (N=392)	0.003	-0.025	0.031	0.846	***Latitude (absolute) (N=255)***	**0.020**	**0.009**	**0.032**	**<0.001**
Water (N=22)	2.775	-7.706	14.947	0.654	*Water (N=10)*	-2.082	-4.726	1.093	0.185
Lat*Water	**-0.346**	**-0.640**	**-0.044**	**0.013**	*Lat*Water*	0.055	-0.019	0.129	0.167

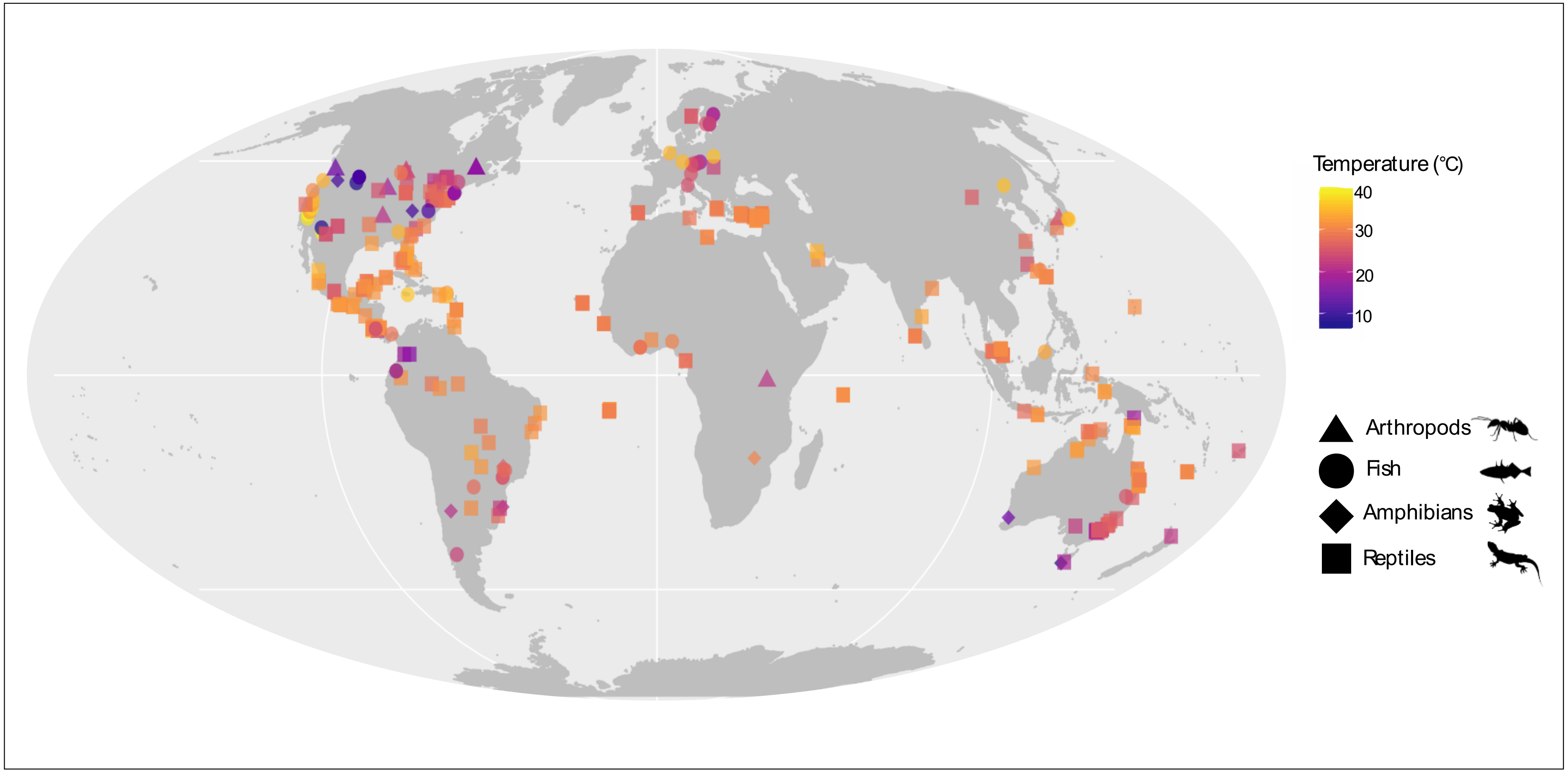

Figure 4. Global distribution of mean oviposition site temperature (symbol colour) within ectotherm populations, separated by higher taxonomy (symbol shape; N=392 populations from 251 studies). Silhouette images obtained from PhyloPic (https://www.phylopic.org).

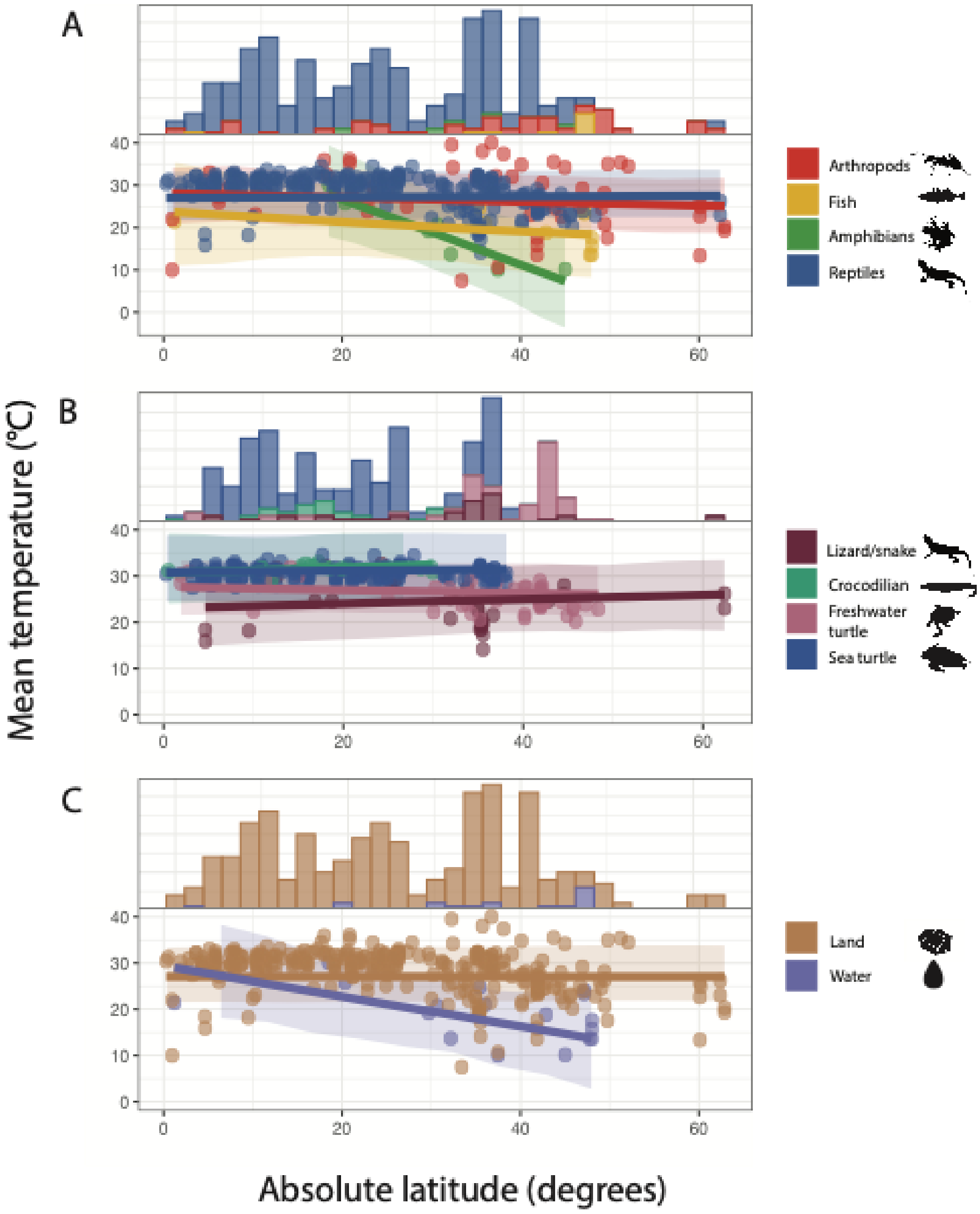

Figure 5. Mean oviposition site temperature within a sample population as a function of absolute latitude for A) major ectotherm groups (N=392 populations from 251 studies), B) reptiles (N=309 data points), and C) ectotherms that lay their eggs in the water (N=22 data points) or on land (N=370 data points). Freshwater turtles include tortoises (N=4 data points). Trend lines and shaded error bars (Highest Posterior Density (HPD) intervals) were predicted from Bayesian linear mixed models. Histograms reflect the number of data points for each category across latitude. Silhouette images obtained from PhyloPic (https://www.phylopic.org).

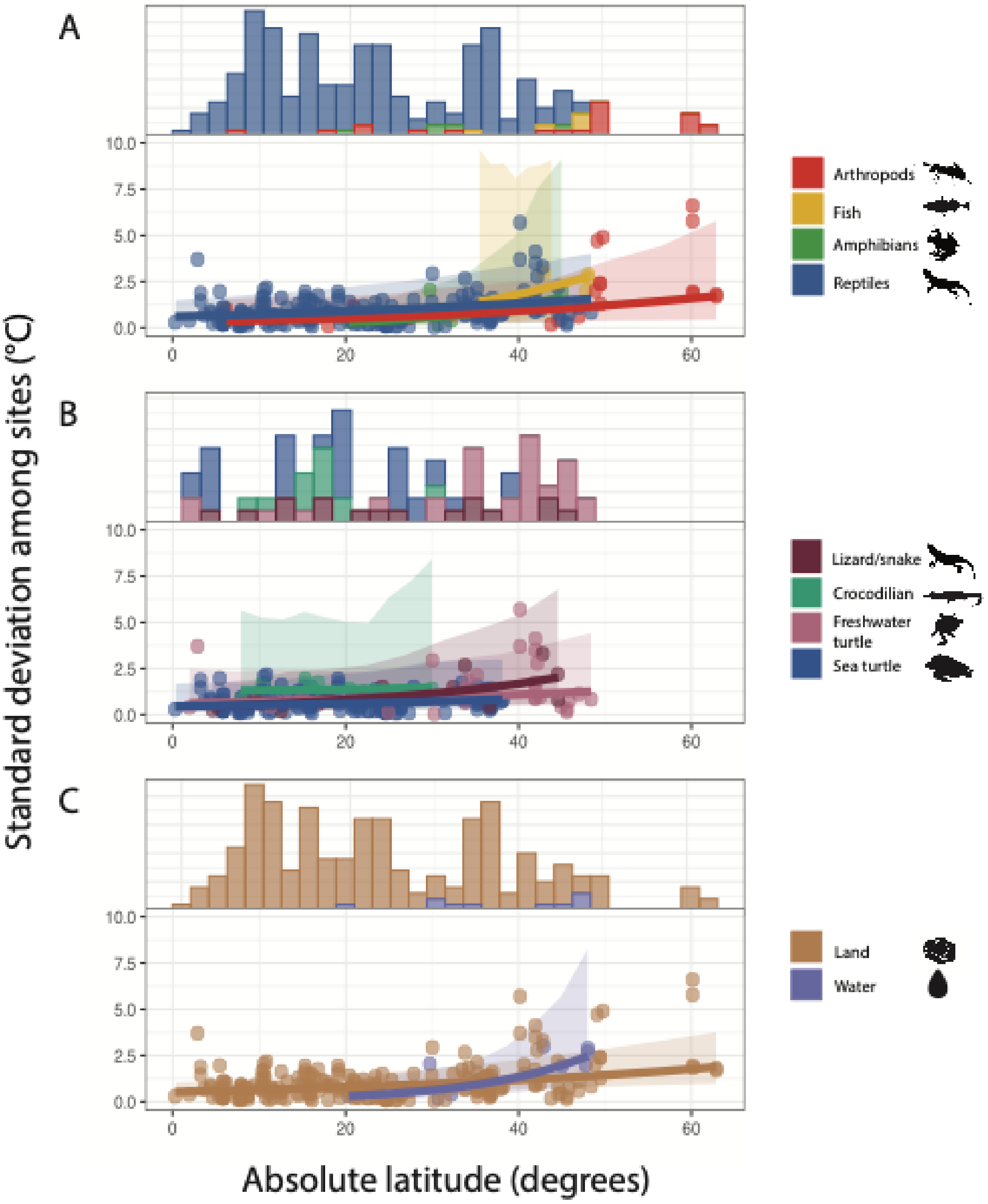

Figure 6. Standard deviation of temperatures among oviposition sites within each sample population as a function of absolute latitude of A) major ectotherm groups (N=255 populations from 237 studies), B) reptile groups (N=218 data points) and C) ectotherms that lay their eggs in the water (n=10) or on land (n=245). Freshwater turtles include tortoises (N=4 data points). Trend lines and shaded error bars (Highest Posterior Density (HPD) intervals) were predicted from Bayesian linear mixed models, back-transformed from natural log. Histograms reflect the number of data points for each category across latitude. Silhouette images obtained from PhyloPic (https://www.phylopic.org).

Meta-analysis

We used a meta-analytic approach to quantify the extent to which mean natural oviposition temperatures impact offspring outcome in ectotherms. Due to restrictions on the data available within the literature, only reptiles (n = 46 studies, n = 19 species) and amphibians (n = 2 studies, n = 2 species) were included in the meta-analysis. We found a large ($|r| > 0.5$, (Cohen, 1988)) and significant association between increasing natural oviposition temperature and decreasing incubation duration (Table 2; Figure 7). We also found a small ($r \sim 0.1$, (Cohen, 1988)) but significant association between increasing natural oviposition site temperature and decreased hatching success (Table 2; Figure 7). By conventional measures, overall heterogeneity in the data was high (hatching success; I^2=87.5%, incubation duration; I^2= 87.8%, Table 3)(Senior et al., 2016). The variance in the data for incubation duration can be explained by phylogenetic relatedness and differences between effect sizes (within-species or within-study variation), with negligible variance explained by differences between species (Table 2). The majority of the variance in the data for hatching success can be explained by differences between effect sizes (within-species or within-study variation), with negligible variance explained by differences between species and phylogenetic relatedness (Table 2).

Table 2. Effect of correlations between nest temperature and phenotypic outcomes on reptiles and amphibians. The table shows parameter estimates with 95% confidence intervals (CI) and 95% prediction intervals (PI) from the multi-level meta-analysis (MLMA). I^2 represents the percentage of heterogeneity, N_e represents the number of effect sizes, N_{st} represents the number of studies and N_{sp} represents the number of species for each dataset.

Trait	N_e	N_{st}	N_{sp}	*Overall* $I^2(\%)$	*Random effects* I^2 *(%)*	*Coefficients*	P value
Incubation duration	38	35	15	86.8	Total = 87.8 Phylogeny = 45.3 Species = 0 Data ID = 42.4	Zr = -0.580, CI = -1.071, -0.089, PI = -1.945, 0.785	P = 0.021
Hatching success	32	27	14	87.5	Total = 87.0 Phylogeny = 0 Species = 0 Data ID = 87.0	Zr = -0.076, CI =-0.367, -0.076, PI = -0.926, 0.483	P = 0.003

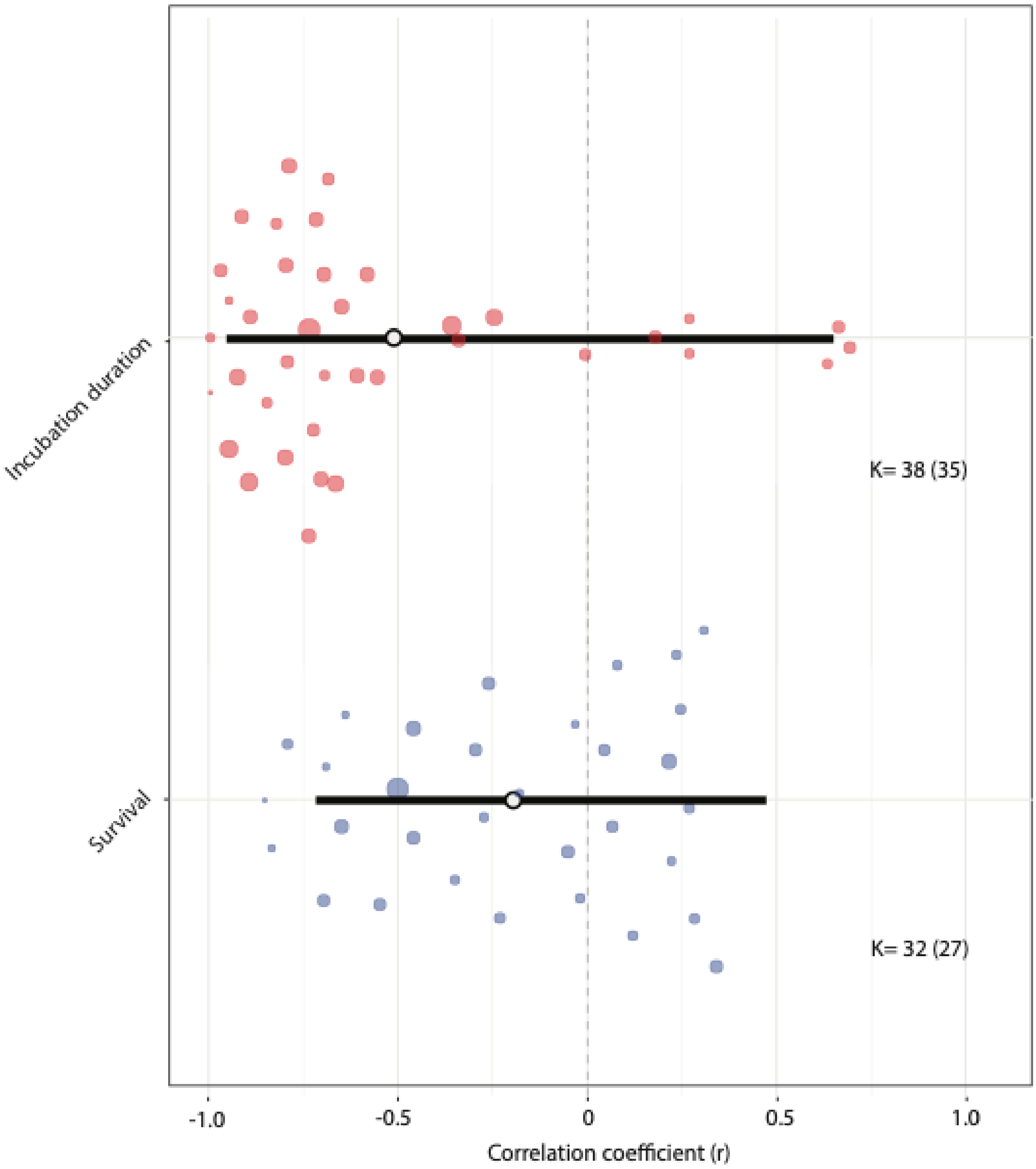

Figure 7. The distribution of effect sizes, back-transformed from Zr effect sizes to correlation coefficient (r), representing the relationship between mean oviposition site temperature and offspring phenotypes of incubation duration and hatching success (modelled separately). Middle points are mean estimates, thick bars represent confidence intervals (CI), thin bars represent prediction intervals (PI), points are individual effect sizes scaled by precision (1/standard error), k is the number of effect sizes, number in brackets is number of studies.

Discussion

In this study, we provide the first synthesis of over 60 years of research on natural thermal variation experienced by ectotherms during embryonic development. This synthesis is timely given the explosion of studies in the past 25 years and the urgency of increasing climate change. We examined patterns across latitude, environment type, and taxa, and analysed whether thermal variation within a population impacts ectotherm phenotype. Firstly, we found that there is an inherent taxonomic bias in the literature towards reptile species, likely influenced by technological availability and biases in areas of research. Secondly, we found little support for an association between mean oviposition site temperatures and latitude, but variation in temperatures among oviposition sites within a population was higher at higher latitudes. Lastly, our meta-analysis demonstrated an association between natural oviposition site temperature and offspring phenotype, with small-to-large negative correlations between mean oviposition site temperatures, incubation duration, and hatching success. Below, we first discuss the implications of the meta-analysis results, followed by considering them in light of the macroecological findings. We end by considering both sets of findings in the context of the history of the field, and what future avenues of research would help advance the field.

Meta-analysis

Our findings that incubation duration and hatching success both decrease with increasing oviposition site temperature are consistent with the effects of developmental temperatures on reptile hatchling phenotypes reported under laboratory conditions (e.g. Noble et al., 2018). Notably, Noble et al. (2018) found that the relationship between temperature and hatching success in the lab was not linear, peaking at intermediate temperatures and declining at both colder and hotter temperatures (see also Du and Shine 2015; Noble et al. 2021). Therefore, the negative correlation we found between developmental temperatures and hatching success suggests that the warmest oviposition sites within natural populations are similar to the warmer end of temperatures investigated in the laboratory. Such lethally-warm oviposition sites in nature suggests that some of the variation in temperatures among sites (e.g. among nests) is non-adaptive or shaped by competing ecological factors (e.g. competition or predation). Moreover, fluctuations around hot temperatures during development are known to decrease reptile hatching success in the lab (compared with constant temperatures; Raynal et al. 2022 but see Stocker et al., 2024), suggesting that any increase in within-site fluctuations in natural oviposition sites will likely reduce hatching success. Our finding that the effect of natural developmental temperatures on incubation duration was more than seven times as large as the effect on hatching success is also consistent with the same meta-analytic comparisons of laboratory incubation studies using reptiles (Noble et al., 2018; Raynal et al., 2022). While we did not recover sufficient data on phenotypes such as morphology, behaviour, or performance to include them in our analyses, extending findings from laboratory studies suggests that these phenotypes will also be affected by natural temperatures, though to a lesser magnitude than are hatching success and incubation duration (Elphick & Shine, 1998; Hall & Warner, 2020; Raynal et al., 2022).

While hot constant temperatures and fluctuations in temperature have both been shown to negatively impact offspring phenotype in the lab, temperature fluctuations in natural oviposition sites could also reduce the impact of increasing mean temperature (Bowden et al., 2014). Indeed, in laboratory studies, phenotypic differences arising from changing the mean developmental temperature become less pronounced under fluctuating developmental temperatures (Bowden et al., 2014; Noble et al., 2018). Accordingly, one might predict that changes in mean oviposition site temperatures in nature (where temperature fluctuate) would have only a weak impact on offspring. Thus, our findings that incubation duration and hatching success decline with mean oviposition site temperature even in a natural setting is significant contrary evidence. However, it is worth noting that, in our study, most correlations between mean oviposition temperature and offspring phenotype originated from sea turtles, whose deep nests experience relatively minor temperatures fluctuations during the developmental period (Booth & Astill, 2001). Thus, it remains possible that changes in mean temperature in natural oviposition sites has comparatively smaller impact in species where eggs experience substantial temperature fluctuation (e.g. terrestrial arthropods or reptiles with shallow nests). In addition, other uncontrolled natural variables may be exacerbating the observed reduction in hatching success with temperature (e.g., concomitant changes in soil moisture; Bell et al., 2025).

Most of the variance in our meta-analysis is explained by differences in phylogenetic relatedness and between effect sizes, with zero variance explained by differences between species. This indicates that our results are likely generalisable across species (at least reptiles). However, it must be noted that studies on two sea turtle species make up a large proportion of the effect sizes in our dataset (green sea turtles, 21.4%, and loggerhead sea turtles, 31.4%). As only four studies contributed more than one effect sizes to our dataset, the variance between effect sizes likely represents differences between studies and populations. Studies in this dataset range considerably in the types of technology used, research question (and therefore their methodological approach) and how many times temperatures were measured within an oviposition site. These factors also likely contribute to the overall high heterogeneity in the data, which is common in meta-analyses of multiple species with different ecologies (Senior et al., 2016).

Through results from laboratory experiments, we know that the phenotype of arthropods, fishes, and amphibians can be strongly influenced by temperature (reviewed in Colinet et al., 2015; Massey and Hutchings, 2020). However, our systematic search retrieved only 9 studies (3 arthropod, 4 fish and 2 amphibian) that measured an offspring phenotype alongside natural oviposition site temperature in these taxa (Figure S1). Collecting data on the association between natural developmental temperatures and offspring phenotype across a greater diversity of taxa is imperative to generalise our findings across ectotherms.

Macroecological patterns

Surprisingly, we found little evidence for a relationship between oviposition site temperature and latitude. Given the large differences in air temperatures across this range of latitudes (-43° (south) – 63° (north) latitude), our findings suggest that maternal behaviour is important for maintaining oviposition site temperatures near a standard, presumably optimal, temperature regardless of the local climate (Refsnider and Janzen 2010).

The importance of maternal oviposition site selection has been explored in many ectothermic species, though commonly in contexts other than site temperature (Refsnider & Janzen, 2010). In reptiles where multiple species and populations have been investigated, nest temperatures are similar across latitude largely owing to among-population differences in the nest microhabitat or timing of oviposition (Blouin-Demers et al., 2004; Bodensteiner et al., 2023; Kolbe & Janzen, 2002; Mitchell et al., 2013; Pike et al., 2012; Shine, 2004; Shine & Harlow, 1996; Warner & Shine, 2008). In the current dataset, populations of sea turtles and crocodilians have notably flat mean oviposition site temperatures across latitude (Figure 5A). For crocodilians, among-population similarity in temperature is most likely due maternal nest attendance to regulate nest temperature (Hénaut and Charruau, 2012). Similarly, the few studies that have investigated the role of temperature in oviposition site selection in arthropods found that thermal microclimate plays a large role in oviposition site location (Pike et al., 2012; Potter et al., 2009; Sousa et al., 2022; Wilson et al., 2020). However, nest-site selection in relation to temperature is comparatively understudied in arthropods, fish and amphibians, with no studies found using fish and only one using amphibians (Luza et al., 2015). Overall, maternal oviposition site selection has long been considered crucial in reproductive ecology, such that the near-complete lack of latitudinal trends in site temperature is striking and provides impetus for greater geographical comparisons of maternal behaviour.

Variation we observed in oviposition site temperatures suggests that maternal behaviour is less effective at selecting optimal oviposition site temperatures at high latitudes. In particular, at latitudes greater than 30-35 degrees, there was an apparent increase in variation in mean oviposition temperatures among populations (i.e. scatter in Figure 5), and a large increase in standard deviation within populations (Table 1, Figure 6). In many wild populations, variation in oviposition site temperatures is driven by variation in vegetation cover above the oviposition site and the time of year when eggs were oviposited (Schwanz and Janzen 2008, Schwanz et al., 2010; Bennett et al., 2015; Kolbe & Janzen, 2002; Pincebourde et al., 2016; Refsnider & Janzen, 2010; Telemeco et al., 2009). Thus, the increased variation above 30° latitude could reflect reduced choice of microhabitat temperatures (thus, more sub-optimal site temperatures) given that habitats at these latitudes are often arid or open-woodland (Georges, 1992; Jackson & Forster, 2010). In addition, if high-latitude, short-season populations are more constrained in their phenology, ovipositing individuals may accept sub-optimal temperatures to ensure developmental completion prior to winter. Moreover, we could not account for altitude in our models as most studies did not report it. Altitudinal variation could be contributing to some of the temperature variation at high latitudes, particularly within the arthropod group (Figure 6A). Regardless of the drivers, the increase in temperature variation within populations at higher latitudes could lead to suboptimal phenotypic outcomes (e.g. embryonic death).

Alternatively, increased variation in oviposition site temperatures at high latitudes may also indicate that populations at higher latitudes have specific adaptations (e.g. broader thermal performance curves, diapause) that allow success despite a broader range of possible developmental temperatures. Embryonic adaptations for dealing with cooler or more variable oviposition site temperatures could reduce fitness costs associated with temperatures that are detrimental in other populations as well as reduce the selective pressure on maternal oviposition behaviour (Bale & Hayward, 2010; Danks, 2010; Wourms, 1972).

Variable sampling effort across latitude, taxa and studies led to challenges in interpreting our findings. There was substantial variation among studies in the numbers of oviposition sites sampled within each population and the number of temperature records per oviposition sites. However, the number of oviposition sites surveyed was not always clearly reported, so we could not account for the sampling variation in our statistical analyses. Small sample sizes can lead to inaccurate estimates of mean or among-site variation in developmental temperatures, thus it is critical that future studies report sample sizes. However, the most extreme mean temperatures (high latitude arthropods and amphibians), as well as the population with the greatest variability among sites (high latitude fish and arthropods) did not have conspicuously small sample sizes ($N \geq 5$ oviposition sites). In addition, latitudinal range varied among major taxa. Amphibian populations, in particular, were not sampled across a broad range of latitudes (Figure 5-6). Around 76% of amphibians inhabit tropical rainforests (Pillay et al., 2022), and our dataset only reflect observations from sub-tropical or temperate amphibians (>30 degrees of latitude), which likely partly explains why some frog studies recorded extremely low oviposition site temperatures (Frisbie et al., 2000; Mitchell and Seymour, 2000).

Many studies that appeared in our initial search assumed oviposition site temperatures using weather station data, or nearby ground temperatures. However, these proxies are often not accurate (Nowakowski et al., 2018; Woods et al., 2015). Indeed, we found significant variation in temperatures among oviposition sites within the same population, indicating that even climatic data with small spatial resolution are not sufficient to capture relevant variation in the temperatures experienced by embryos (Bodensteiner et al., 2023; Pincebourde et al., 2016). For example, in tobacco hornworms (*Manduca sexta*), eggs are laid on leaves, and oviposition site temperatures depend on the size of the leaf (Potter et al., 2009). In fact, most habitats experience large spatial variation in temperature across microhabitats (Barber, 2013; Nowakowski et al., 2018; Potter et al., 2013; Pincebourde & Casas, 2019). Therefore, coarse climatic data is unlikely to capture the cryptic microclimatic variation experienced by embryos during their development (Pincebourde et al., 2016).

Systematic map

Our systematic map showed that a combination of technology availability and research question focus has contributed to a large taxonomic bias towards reptile species in oviposition site temperature research. We found that most of the arthropod, amphibian and fish species uncovered in our systematic search construct nests for oviposition. The construction of nests makes eggs much easier to locate and often easier to monitor with miniature dataloggers. For example, eusocial insects dominate the arthropod group in our dataset, and often construct very large, conspicuous nests. While there were very few species of fish (N = 7 species) and amphibians (N = 8 species) included in our study; all fish, and 63% of amphibians in our study construct nests. This likely reflects the technical difficulties in finding and measuring the temperature of eggs deposited in inconspicuous locations in nature, or with inconspicuous oviposition behaviours. Interestingly, fish and arthropods make up most of the studies in the first 20 years of studies retrieved in our search (Greenwood, 1958; Jay and Frankson, 1972; Josens, 1971; Lévieux, 1972; Omo, 1977; Siefert, 1968), yet these taxa did not see increased interest in the 1980s and 1990s. A possible explanation for the lack of increased interest is that advances in laboratory technology (and decreasing prices) made laboratory experiments more feasible than studying the animals in nature. In many model amphibians, arthropods and fish, laboratory experiments have provided a large body of knowledge on thermal tolerance and developmental biology that could be bolstered by insights from natural oviposition site temperature data (Bull and Shepherd, 2003; Pottier et al., 2022b).

Additional potential explanations for the taxonomic bias are that many fish, arthropods, and amphibians have challenging reproductive biology, short embryonic development times and complex lifecycles where developmental forms go through several morphological and habitat modifications before reaching adulthood (Moran, 1994). Not only are complex life-cycles difficult to study in the field, but temperatures experienced during the short embryonic phase may have a transient or limited effect on phenotype compared with temperatures experienced during the juvenile or adult stage (but see, e.g., Pottier et al., 2022a). Additionally, many invertebrate and fish species have inconspicuous reproductive strategies, including a small number of eggs, very small eggs, planktonic eggs, highly cryptic broods, or scattered eggs (Barber, 2013; Colinet et al., 2015). These eggs may be difficult to locate or simply do not have a singular, fixed ‘site’ at which to measure temperature. Even when oviposition sites can be identified, substantial technological challenges remain for measuring temperature in small, aquatic, or agglutinated egg masses. Indeed, the miniaturization of dataloggers (~1-3cm size) that was a boon for terrestrial nests of at least 10cm diameter provided no improvement over smaller-tip thermocouple probes (~1-2m) for oviposition sites of many ectotherms. This means that only a portion of these taxa may be suitable model species for studying how oviposition site temperatures in particular impact offspring phenotype.

It is unfortunate that many of the insights gained from the most frequent taxa in our systematic search – sea turtles – are not directly applicable to other ectotherms, and likely not even other reptiles, due to their deep nests relative to other species. The taxonomic bias towards sea turtles is likely driven by their charismatic nature, conspicuous nesting behaviours, temperature-dependent sex determination, and populations being at high risk of anthropogenic impacts such as climate change (Miguel et al., 2022). These factors together likely make funding easier to obtain and make studies easier to publish and more likely to reach a wider audience (Hayer et al., 2013).

There is significant pressure for scientists to produce novel research with impactful outcomes, with an emphasis on fashionable topics or species (Hayer et al., 2013; Møller & Jennions, 2001; Sutton, 2009). Funding and time constraints facilitate using well-studied model species with established protocols, equipment, and reliability (Peirson et al., 2017). However, choosing understudied model species to research ecology and evolution topics can clarify concepts that remain elusive in their generality (Jenner & Wills, 2007). For example, from relatively extensive research using reptile model species, we still do not have an evolutionary explanation for the occurrence of temperature-dependent sex determination (Schwanz & Georges, 2021). However, there are many unstudied species of reptiles, fishes, anurans, and arthropods that exhibit forms of temperature-dependent sex determination and live in habitats that will be impacted by future climate change projections (Conover, 1984; IPCC, 2014; Korpelainen, 1990; Ruiz-García et al., 2021). Studying evolutionary transitions across taxa and species would offer a comparative view that is currently missing by using well-studied model species. Additionally, such data may be important for the conservation of understudied and endangered species and may in-turn enhance our conservation efforts across taxa in the face of climate change (Culumber et al., 2019).

Recommendations

There are many challenges to recording natural oviposition site temperatures. However, our systematic review paints a compelling picture of the taxa, habitats and latitudes where data are markedly lacking. Through our systematic review, we discovered that technological advances and the motivating questions underpinning research have resulted in a major reptilian bias in the data available on oviposition site temperatures and their influence on ectotherm phenotypes. Furthermore, a restricted geographical (i.e. latitudinal) range of studies on non-reptilian taxa limit our power to test ecological and evolutionary hypotheses related to oviposition site temperatures. Here we make recommendations to minimise obstacles and obtain data from diverse taxa.

Ecologists are often innovative and creative when it comes to manipulating the technology available to suit their research needs (Lovegrove, 2009; Virens and Cree, 2018). As such, improvements to temperature dataloggers may encourage research in a greater number of natural habitats. While the development of mini-dataloggers in the 1990’s encouraged more research on developmental temperatures in the wild, technological improvements have been relatively slow ever since. Waterproofing and the battery size of dataloggers remain limitations for their deployment in some oviposition sites. Self-contained, programmable dataloggers (e.g., iButtons and Hobo pendants) cannot be deployed in very small or fragile oviposition sites (e.g. spider egg sacs, frog or fish egg masses) because their in-device battery and memory chip currently require too much physical space. Instead, weather- or water-proof dataloggers with small-tip thermocouple probes would be incredibly useful for small eggs and clutches, as the small probes can be inserted into egg masses or affixed to oviposition site surfaces (e.g. underside of a leaf). Currently, dataloggers with probes are expensive and not always waterproof, limiting the number of units that can be deployed, and requiring additional waterproof casings.

In the absence of technological advances, many possible target species construct highly conspicuous nests or egg masses that could be accessed and measured using current technology. Fish are one of the most common model species used in studies investigating the evolution of nest construction (second only to birds; Barber, 2013). For example, salmon (Buxton et al., 2015), sticklebacks (Rushbrook et al., 2010), Antarctic icefish (Purser et al., 2022), and chubs (Svensson & Kvarnemo, 2023) build complex nests that can host a datalogger. While eusocial insects make some of the most impressive and conspicuous nests from the arthropod group, several other arthropod taxa have conspicuous oviposition behaviours which could be leveraged to locate eggs. For example, many species of spiders and beetles make visible nests (silk egg sacs and brood balls) where thermocouple probes attached to a datalogger could be inserted (Cambefort and Hanski, 1991; Sethy and Ahi, 2022). For arthropod species that do not make nests or lay easily identifiable eggs, some consistently lay eggs in certain substrates, which could aid in locating egg clutches to measure the temperature using thermocouples (Bennett et al., 2015). For example, many butterfly species lay eggs on specific host plant species and some Tephrioidae flies oviposit in fruit and vegetables (Bennett et al., 2015; Díaz-Fleischer et al., 2001). Additionally, many insects lay phenotypically unique eggs, such as stink bugs (Abram et al., 2015), eastern tent caterpillar moth (Koval and Binnie, 1999) and tabanid flies (Graham and Stoffolano, 1983). These are just few examples of taxa that could be used as model species to understand how temperature impacts development in nature.

Due to the ongoing threats faced by amphibians (Luedtke et al., 2023), a greater understanding of their embryonic thermal ecology would not only complement fundamental knowledge but also potentially inform conservation. Moreover, amphibians are an excellent taxon for comparative evolutionary biology, exhibiting a wide range of reproductive modes including aquatic and terrestrial eggs, oviparity and viviparity, and singular nests or communal egg laying (Shepard and Caldwell, 2005; Liedtke et al., 2022). Many amphibians lay terrestrial eggs inside foam nests created by mucous secretions or mud basin nests, or egg masses in aquatic systems (Gould, 2021; Schäfer et al., 2019; Lietdke et al., 2022). The size and location of these nests vary, but many are placed in recognisable locations (e.g., water's edge, attached to tree branches leaning over water) that would be relatively simple to locate (Cooper et al., 2017; Fischer, 2023; Gould, 2021).

Incubation duration and hatching success were almost never measured in studies focused on fish and arthropods. These two offspring outcomes are likely the easiest to measure in the field and are important for understanding population phenology, demography, and fitness. Similarly, other fitness-related traits such as sex ratio, morphology, and behaviour are sensitive to temperatures in the laboratory (Noble et al., 2018) yet rarely studied in the field. While it may be difficult to capture small hatchlings for phenotypic measurements, it is still possible. Hatching success of small terrestrial animals could be measured using motion sensitive camera traps set up at oviposition sites, or by using Malaise or adhesive traps for flying and crawling animals, respectively (Lo et al., 2019; Uhler et al., 2022). Technology used by marine researchers to study population dynamics, such as baited remote underwater video (BRUV), could be adapted to monitor incubation duration and hatching underwater (Lowry et al., 2011). Additionally, artificial intelligence software could be used to take automated morphological or behavioural measurements (da Silva et al., 2023). We are hopeful that combining knowledge from natural history and laboratory experiments with emerging field and computational technologies will offer interesting avenues for understanding the influence of natural developmental environments on ectotherm phenotypes.

Conclusion:

1. Our meta-analysis revealed that increases in mean developmental temperatures are negatively correlated with developmental time and hatching success. This is

consistent with evidence from laboratory studies, attesting to the ecological relevance of laboratory studies.

2. We found no evidence for an association between natural oviposition site temperatures and latitude, suggesting that maternal ovipositing behaviour maintains embryonic development within a narrow thermal range, regardless of local climate. However, maternal ovipositing behaviour is less effective at higher latitudes, as evidenced by larger variation in oviposition site temperatures among nests within populations at higher latitudes compared with lower latitudes.
3. We found large taxonomic biases in the literature, challenging the generalisability of our findings to all ectothermic species. Little data could be obtained from certain latitudes and most of the data came from studies on reptiles.
4. This taxonomic bias is likely explained by a confluence of technology availability and research question focus, which has been amplified over time.
5. Recent technological developments and knowledge of the natural history of ectothermic species provides compelling opportunities to increase taxonomic breadth.

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*denotes inclusion in the macroecological analysis, +denotes inclusion in the meta-analysis

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