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Patterns of developmental plasticity in response to incubation temperature in reptiles

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Abstract

Early life environments shape phenotypic development in important ways that can lead to long-lasting effects on phenotype and fitness. In reptiles, one aspect of the early environment that impacts development is temperature (termed 'thermal developmental plasticity'). Indeed, the thermal environment during incubation is known to influence morphological, physiological, and behavioral traits, some of which have important consequences for many ecological and evolutionary processes. Despite this, few studies have attempted to synthesize and collate data from this expansive and important body of research. Here, we systematically review research into thermal developmental plasticity across reptiles, structured around the key papers and findings that have shaped the field over the past 50 years. From these papers, we introduce a large database (the 'Reptile Development Database') consisting of 9,773 trait means across 300 studies examining thermal developmental plasticity. This dataset encompasses data on a range of phenotypes, including morphological, physiological, behavioral, and performance traits along with growth rate, incubation duration, sex ratio, and survival (e.g., hatching success) across all major reptile clades. Finally, from our literature synthesis and data exploration, we identify key research themes associated with thermal developmental plasticity, important gaps in empirical research, and demonstrate how future progress can be made through targeted empirical, meta-analytic, and comparative work.

KEYWORDS

crocodiles, environment, lizards, phenotypic plasticity, Reptile Development Database, snakes, thermal plasticity, tortoises, tuatara, turtles

1 | INTRODUCTION

The environment experienced by individuals can have significant effects on their phenotype and ultimately fitness. While plastic responses can occur across all life-history stages (Mousseau & Fox, 1998), they are often most pervasive early in life when an organism undergoes most of its growth and development (West-Eberhard, 2003). Such developmental plasticity is partly unavoidable, for example, as a by-product of physical or physiological limits on biological systems. However, the extent and form of plasticity is also shaped by natural selection such that developmental responses are fine-tuned to particular environmental conditions (Schlichting & Pigliucci, 1998; West-Eberhard, 2003). In either case, developmental plasticity is a major source of phenotypic variation that mediates how organisms respond to environmental change at both local and global scales.

Reptiles have been widely used in developmental plasticity research for a number of reasons (by "reptiles" we refer to extant non-avian clades). Reptiles are ectothermic and most species are oviparous with embryos developing outside the mother's body. Thus, reptile embryos are exposed to a wide range of (sometimes unpredictable) biotic (e.g., nutrition, competition, and predation) and abiotic (e.g., moisture, photoperiod, and temperature) environmental conditions (Ackerman & Lott 2004; Andrews, 2002; Warner, Lovern, & Shine, 2007, 2009). Even viviparous reptiles, which have a greater capacity to buffer external conditions throughout development via maternal effects (Qualls & Andrews 1999; Shine 1999; Shine & Downes 1999), have been widely studied in this respect, with conditions experienced by the mother before and throughout gestation having a significant effect on offspring phenotype (Itonaga, Jones, & Wapstra, 2012; Wang, Zeng, Li, Bi, & Du, 2016).

The environmental factor that has been best studied in the context of developmental plasticity in reptiles is temperature (hereafter referred to as "thermal developmental plasticity"). Most reptile embryos do not successfully develop when incubated at constant temperatures lower than 20°C or higher than 35°C, with divergent optimal developmental temperatures for the different major lineages (Du & Shine 2015; Warner, Radder, & Shine, 2009). Within this range, developmental processes appear to be further optimized at particular temperatures, which are consistent with the general pattern of thermal adaptation (Angilletta, 2009). Even though females can mediate the developmental environment of their eggs via maternal nest site choice (Li et al., 2018; Pezaro, Doody, & Thompson, 2017; Refsnider & Janzen 2010; Schwanz, Spencer, Bowden, & Janzen, 2010b), reptile nests still vary considerably in both temperature and moisture content (Brown & Shine, 2005, 2006; Elphick & Shine 1998; Robbins & Warner 2010; Shine, Elphick, & Harlow, 1997; Warner et al. 2010). For example, nest temperatures often fall within a range from below 10°C to well above 40°C (Warner & Shine 2008a). Such variation is not just prevalent between nests but also within nests, with diel thermal fluctuations in some nests greater than the divergence in mean thermal values among nests (Shine & Harlow 1996; Shine, Elphick, & Barrott, 2003).

Given the above, it is perhaps unsurprising that there is a large and growing empirical literature testing the effects of the thermal environment during incubation on the development of a range of traits across all the major reptile taxa (Deeming, 2004; Deeming & Ferguson 1991; Noble, Stenhouse, & Schwanz, 2018b). This includes incubation duration (e.g., While et al., 2015), developmental processes (e.g., gene expression; Feiner, Rago, While, & Uller, 2018a), morphology (e.g., body size, growth rate; Andrews, Mathies, Warner, & Mathies, 2009; Du et al., 2009, 2010; Monasterio, Shoo, Salvador, Iraeta, & Díaz, 2013), behavior (e.g., antipredator behavior; Burger, 1990; Downes & Shine 1999), performance (e.g., sprint speed; Elphick & Shine 1998), physiology (e.g., hormones, metabolic activity, energy, and nutrient content; Crews, Coomber, Baldwin, Azad, & Gonzalez-Lima, 1996, 1997; Du, Shou, & Liu, 2003; Ji & Braña 1999), cognition (Amiel & Shine 2012; Clark, Amiel, Shine, Noble, & Whiting, 2014; Dayananda & Webb 2017), and, in many species, sex (Valenzuela & Lance 2004). The phenotypic variation generated in response to the thermal environment has been shown to have fitness consequences in both the short-term (e.g., via increased post-hatching growth and survival; Andrews et al., 2009) and the long-term (e.g., future reproductive success; Warner & Shine 2008b).

As a result of the above, research in thermal developmental plasticity in reptiles has made important contributions to our understanding of key evolutionary and ecological processes (Boyle, Hone, Schwanz, & Georges, 2014; Schwanz et al., 2010b). For example, it has featured prominently in adaptive (and non-adaptive) explanations of variation in sex-determining mechanisms (i.e., genotypic or temperature dependent; Pen et al., 2010; Pezaro et al., 2017; Schwanz, 2016; Schwanz, Cordero, Charnov, & Janzen, 2016; Shine, 1999), maternal effects (Shine, 2004; Uller et al., 2011), the early evolution of parental care (e.g., maternal nesting behavior; Refsnider & Janzen 2010; Schwanz & Janzen 2008; Warner & Shine 2008b), and life history evolution (e.g., the evolution of viviparity; Schwarzkopf & Andrews 2012; Shine,

1995). Furthermore, because of their developmental sensitivity to temperature, reptiles are increasingly used as indicator species for assessing the potential impacts of projected climate change (Boyle, Schwanz, Hone, & Georges, 2016; Dillon, Wang, & Huey, 2010; Hawkes, Broderick, Godfrey, & Godley, 2007; Huey et al., 2012; Janzen, 1994; Mitchell, Kearney, Nelson, & Porter, 2008).

Despite our understanding of the range of ways in which temperature can influence phenotypic variation in reptiles, our ability to generalize about the underlying causes of this variation and its consequences has been limited. First, by both necessity and design, temperature is predicted to impact phenotypic development in a myriad of context-dependent ways. This makes broad generalizations across species difficult per se (Noble et al., 2018b). Indeed, individual traits are often sensitive to temperature in different ways with unpredictable links to fitness (Deeming, 2004; Noble et al., 2018b). Furthermore, relationships between temperature and development are often nonlinear (Georges, Beggs, Young, & Doody, 2005), which can make predictions regarding how the thermal environment should mediate phenotypic development difficult if reaction norms are not fully characterized. Second, there have been few attempts to synthesize the literature in ways that describe widespread patterns in either a qualitative or quantitative way. This is important if we want to propose mechanistic or evolutionary explanations that apply across taxa. Furthermore, by identifying gaps and limitations in the literature, we can build a foundation from which future empirical work could target new and promising research directions. Ultimately this will enable us to comprehend the nature of the organism–environment relationship early in development, and through this, understand how phenotypes vary and how and why they evolve.

The aim for this paper is to address the second of these shortcomings, that is, to provide a synthesis of the literature on thermal developmental plasticity and identify gaps and limitations. First, we provide a systematic review of research into thermal developmental plasticity across reptiles, structured around the key papers and findings that have shaped the field over the past 50 years. Second, we present a large database of studies examining thermal developmental plasticity. This database encompasses a range of phenotypes, including morphological, physiological, behavioral, and performance traits along with growth rate, incubation duration, sex ratio, and survival (e.g., hatching success). Third, we use the above information to provide a brief qualitative overview of the key research themes associated with thermal developmental plasticity in reptiles, with the goal being to demonstrate how future progress can be made through targeted empirical, meta-analytic, and comparative work. Throughout we provide fruitful avenues for empirical and comparative research in core research areas of thermal developmental plasticity.

2 | LITERATURE SYNTHESIS OF THERMAL DEVELOPMENTAL PLASTICITY IN REPTILES

We searched for published literature (1967–2016) describing experiments that manipulated incubation temperature in reptiles in Web of

Science (v5.13.2) using the following 'title' or 'abstract' search terms: temperature* AND incubat*, along with one of the following: reptil*, lizard*, squamat*, snake*, turtle*, chelon*, testudin*, crocodil*, alligator*, tuatara*, and sphenodon*. In addition, we considered all citations in three major reviews of the topic, and included any additional papers from these sources not identified in our searches. From these initial searches, we surveyed publication and citation patterns in the field using the *bibliometrix* (Aria & Cuccurullo, 2017) package in R (v3.4.2; R Core Team, 2017). This package allowed us to extract data on the most influential papers in the field of thermal developmental plasticity in reptiles as well as data on publication trends (i.e., total number of papers published across years), the countries publishing the most papers, and the most prolific authors. This was used to construct a co-authorship network of researchers who have worked on thermal developmental plasticity in reptiles, and thus identify links between the major subject and research groups in the field. For full information on our search and bibliographic protocols, please refer to the Supporting Information.

The 1,306 articles identified in the initial searches spanned a total of 314 journal sources and included 2,376 authors. Articles examining thermal developmental plasticity in reptiles have increased over the past 50 years with an annual increase of 11% (Figure 1a). Overall, these publications have been well cited with a total of >32,000 citations or an average of 25 citations per article. The major sources of research into thermal developmental plasticity include the Journal of Experimental Zoology (publishing *n* = 66 papers), Journal of Herpetology (*n* = 47), General and Comparative Endocrinology (*n* = 43), Physiological and Biochemical Zoology (*n* = 39), and the Journal of Thermal Biology (*n* = 38).

Major countries contributing to thermal developmental plasticity in reptiles include the United States, Australia, China, Brazil, and Canada (Figure 1b). Perhaps unsurprisingly, the major researchers in the field also hail from these areas. Specifically, Richard Shine (Australia, 102 articles), David Crews (United States of America, 73 articles), Wei-Guo Du (China, 43 articles), Fredric Janzen (United States of America, 43 articles), Xiang Ji (China, 37 articles), David Booth (Australia, 34 articles), Thane Wibbels (United States of America, 29 articles), Daniel Warner (United States of America, 26 articles), Arthur Georges (Australia, 25 articles), and Turk Rhen (United States of America, 25 articles) represent the 10 most prolific authors (See also Figure 2 for a full set of main 20 authors). These authors also contribute significantly to the most highly cited works in the area (Table 1). Major publications in the field include several significant reviews (Ewert, Jackson, & Nelson, 1994; Janzen & Paukstis 1991; Lang & Andrews 1994; Sarre, Georges, & Quinn, 2004; Shine, 2005) often covering the topic of sex determination, discussing both its evolutionary and ecological relevance (Janzen, 1994; Lang & Andrews 1994; Sarre et al., 2004; Shine, 1999). However, one review focuses on the consequences of thermal environments for life-history evolution (Shine, 2005). Accordingly, the most highly cited empirical papers are those that focus on the impact of thermal environments for sex-determination as well as phenotypic development more generally (Elphick & Shine 1998; Shine & Harlow 1996; Van Damme, Bauwens, Braña, & Verheyen, 1992; Warner & Shine 2008b).

A weighted authorship network of the field shows a tightly connected network with most major research groups connected via co-authorship of papers (Figure 2). However, substantial structuring within the network suggests multiple, relatively independent, research nodes. These nodes focus, broadly, on different topics within the overall theme of thermal developmental plasticity. For example, sub-network C ("turquoise circles" in Figure 2c) includes authors who have primarily published on the role of incubation temperature on sex determination (TSD) and the physiological mechanisms responsible for patterns of TSD. In contrast, sub-network D ("purple circles" in Figure 2d), while not totally independent, contains authors who have published primarily on the evolutionary causes and consequences of TSD as well as phenotypic effects of the developmental environment more generally. In contrast, some nodes appear to have a more taxonomic focus. For example, node B is comprised of researchers that primarily focus on thermal developmental plasticity in sea turtles (Figure 2b). Overall, an examination of the major nodes suggests that they are related to both major research groups as well as major themes within the overall research area.

3 | MAJOR TRENDS AND GAPS IN THE DATA

We carefully screened the 1,306 papers that made up our initial data set to find studies with suitable experimental designs for the construction of a thermal developmental plasticity database on reptiles (named the "Reptile Development Database" or RepDevo database; the technical details of which are presented in Noble et al., 2018a). The database was produced by systematically identifying relevant articles from our initial searches above, based on a number of key criteria. Specifically, we included studies in the final database that had the following attributes: (1) included research on an oviparous reptile (Class Reptilia; excluding birds); (2) employed an experimental manipulation of incubation temperature of eggs; (3) presented data on hatching success, incubation duration, or post-hatching phenotypes; (4) consisted of eggs that did not receive exogenous hormone application and yolk removal; and (5) for which there was not a substantial delay between oviposition and experimental manipulation (e.g., >48-hr). This resulted in a final data set of 300 publications from which we extracted complete or partial data on embryonic responses to different developmental temperatures as well data on study and experimental attributes including: (1) the authors of the study, (2) the year of publication, (3) taxonomic and locality information on the focal species, (4) type of incubation experiment, (5) whether temperatures were constant or fluctuating (and the extent of fluctuations), (6) age of individuals measured in the sample, (7) sex of individuals in the sample, and (8) whether the experiment also included a manipulation of water potential. Access to the full database, meta-data, and citation details for the empirical papers that were included in this database can be found at https://www.repdevo.com/.

In total, the RepDevo database consists of 9,773 trait means across 300 studies. Studies in the database are spread across each of the four major taxonomic groups (Crocodilia, Rhycocephalia, Squamata, and Testudines; Figure 3), with a total of 155 reptile species
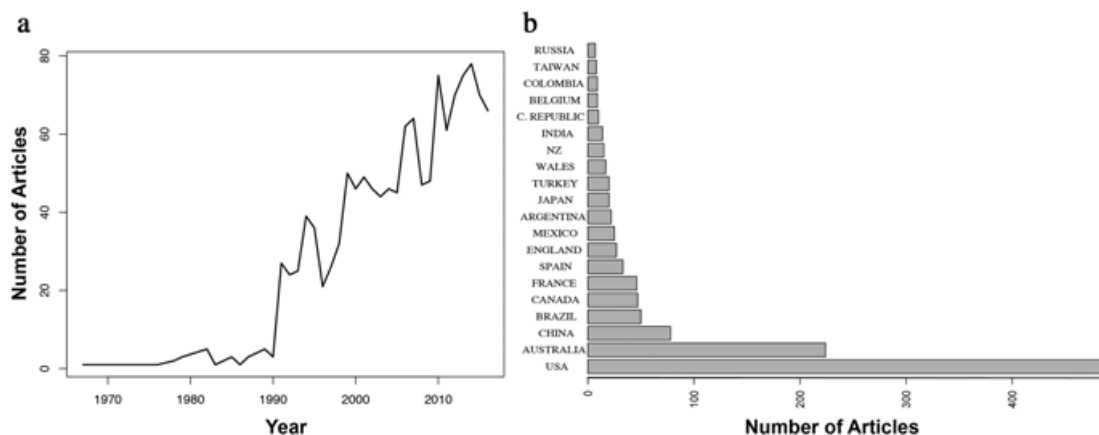
FIGURE 1 (a) The total number of papers on thermal developmental plasticity published each year between 1967 and 2016. (b) The total number of papers on thermal developmental plasticity published by country. Country represents the location of the researchers, which does not always correspond to the native country of the species studied. Only the top 20 countries of authors are shown
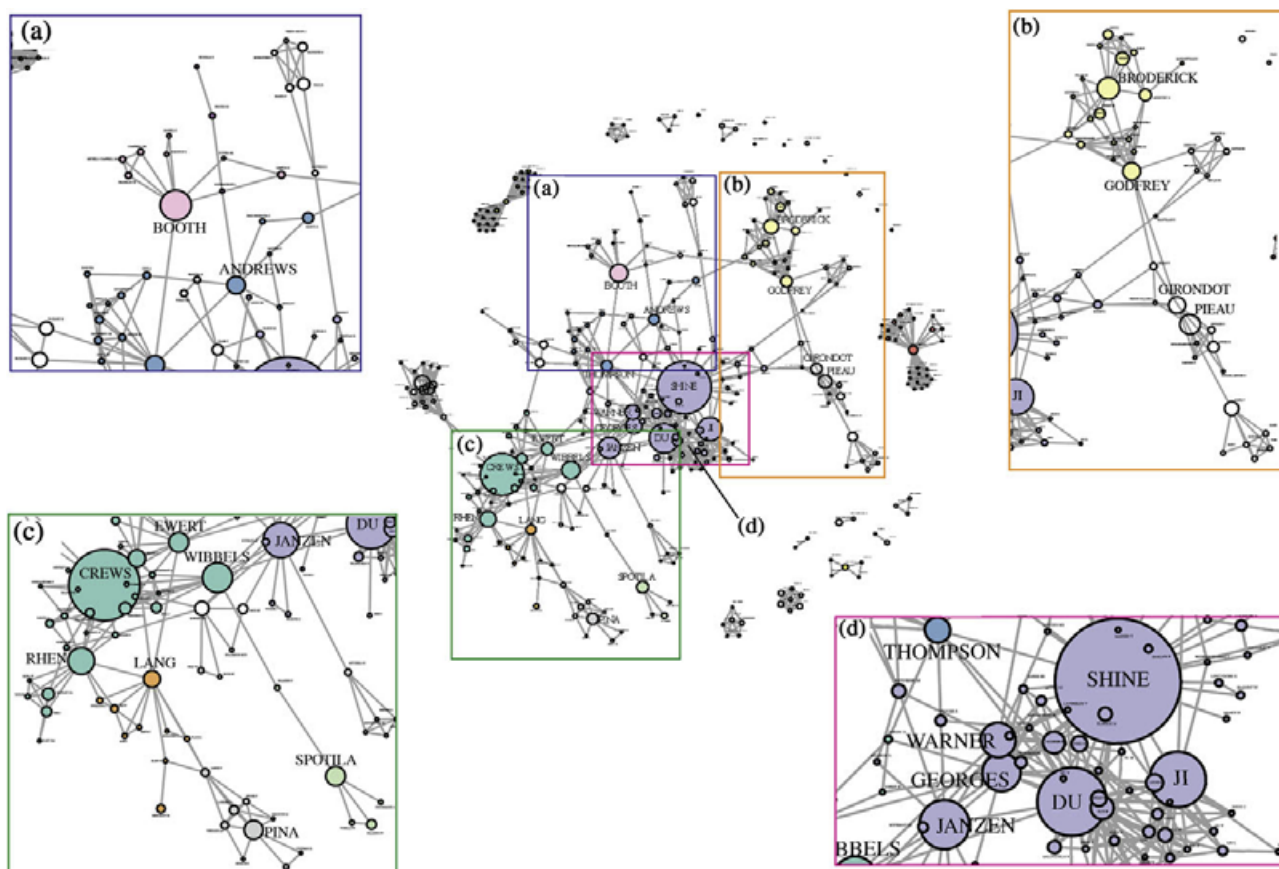

FIGURE 2 Author collaboration network. The overall network containing the most relevant 300 papers is positioned centrally to provide an overview of the overall network structure. The top 20 authors are named and the size of their "bubble" indicates a greater number of papers and connections within the network. (a–d) are zoomed into parts of the main network so that authors and their collaborative networks can be more readily discerned. Like colors signify sub-networks with a high degree of connectedness. We provide the raw figure in the supplement should readers like to zoom in on aspects of the network [Color figure can be viewed at wileyonlinelibrary.com]

studied to date. Despite this broad taxonomic range, a number of taxa contribute disproportionately. Specifically, a large number of studies (32% of the total number of studies) have focused on six key species; *Chelydra serpentina* (*n* = 24), *Bassiana duperreyi* (*n* = 19), *Chrysemys picta* (*n* = 15 papers), *Eublepharis macularius* (*n* = 15), *Trachemys scripta* (*n* = 14), and *Sceloporus undulatus* (*n* = 10) (Figure 3).

In addition to the broad taxonomic coverage, research into thermal developmental plasticity has covered a broad geographic range (Figure 4). However, this coverage is highly heterogeneous. While species from North America (*n* = 3,331 phenotypic means from 121 studies), Asia (*n* = 3,144 phenotypic means from 73 studies), Australia (*n* = 1,949 phenotypic means from 71 studies), and Europe (*n* = 1,109

TABLE 1 Top 20 most highly cited papers

Paper	TC	TCY	Article Type
Janzen & Paukstis, 1991[a]	319	12.27	Review
Ferguson & Joanen, 1982[a]	244	6.97	Empirical
Janzen, 1994[a]	242	10.52	Empirical
Ewert & Nelson, 1991[a]	225	8.65	Empirical
Lang & Andrews, 1994[a]	222	9.65	Review/Empirical
Shine & Harlow, 1996	218	10.38	Empirical
Shine, 2005	207	17.25	Review
Ewert et al., 1994[a]	186	8.09	Review/Empirical
Van Damme et al., 1992	178	7.12	Empirical
Kettlewell, Raymond, & Zarkower, 2000[a]	177	10.41	Empirical
Shine et al., 1997	161	8.05	Empirical
Yntema, 1976[a]	161	3.93	Empirical
Elphick & Shine, 1998	152	8.00	Empirical
Shine, 1995	150	6.82	Empirical
Hawkes et al., 2007*	147	14.70	Empirical
Sarre et al., 2004[a]	146	11.23	Review
Warner & Shine 2008b[a]	146	16.22	Empirical
Wibbels, Bull, & Crews, 1991[a]	142	5.46	Empirical
Bowden, Ewert, & Nelson, 2000[a]	135	7.94	Empirical
Wibbels & Crews, 1994[a]	134	5.83	Empirical

TC, total citations; TCY, average total citations per year. Citations are relevant up to December 19, 2017. Full citation details are provided in the reference section. [a]Indicates studies on sex determination.

phenotypic means from 24 studies) have contributed extensively to the literature on developmental plasticity, there have been relatively few studies on South American ($n = 164$ phenotypic means from 12 studies) and African species ($n = 76$ phenotypic means from five studies). Within each region, there is also substantial variation in taxonomic coverage (Figure 4; See also Figure 1). South America had no studies on thermal developmental plasticity in squamates, and most research focuses on turtles and crocodilians. In contrast, in North America there has been almost an equal focus on testudines and squamates with fewer studies on their two species of crocodilians (Figure 4). Trait diversity also varies geographically. Studies in Africa and South America have quantified fewer traits compared to North America, Europe, and Australia, but this also varied with taxonomic group (Figure 4).

3.1 | Traits studied

Thermal developmental plasticity studies cover a wide range of traits across each of the major trait types (performance, physiology, behavior, morphology, sex, survival, and development). By far, most data have been collected on morphology (~40% of the data; 3,895 trait means), followed by physiology (12%; 1,213 trait means), sex ratios (~10%; 964 sex ratio proportions), and incubation duration (~9%; 910 means). Our word clouds indicate that within each trait category a number of key traits have been focused on across studies (Figure 5). These include easily measured traits such as mass, snout-vent length (SVL),

tail length, growth rates (generally mass and SVL), hatching success of eggs, but also sprint and swimming speed (Figure 5). Within trait categories, plasticity has been studied across a range of developmental temperatures. Specifically, the average minimum and maximum temperatures ranged from 22.9°C to 31.1°C across traits with the lowest temperature within a study being 6°C and a maximum temperature 40°C (Figure 6). Notably, the highest ranges in both maximum and minimum temperatures were for studies examining morphology, survival, sex, and incubation duration (Figure 6).

Our word clouds also identify a number of phenotypic traits that are underrepresented in the database. These include traits such as metabolic rate, activity levels, foraging, and antipredator behavior, and thermal preferences like CT_{max} and CT_{min}. These traits may be closely linked to fitness or are important traits conceptually because they are embedded in general theoretical frameworks in ecology and evolution (e.g., metabolic rate; Dynamic Energy Budget and Pace-of-Life Theory; Kooijman, 2009; Reale et al., 2010; Ricklefs & WIlkelski 2002). Furthermore, the majority of data center on the effects of the thermal developmental environment on early life history with a noticeable lack of studies that examine the effects on key components of adult life history (e.g., age at maturity, longevity, and reproduction; Mitchell, Janzen, & Warner, 2018). This is an important omission given that early life experiences, via their effects on adult life history, can mediate key ecological and evolutionary processes (e.g., the evolutionary dynamics of sex determining systems; Pen et al., 2010).

3.2 | Experimental designs and thermal treatments

Experiments on thermal developmental plasticity incorporate a broad range of experimental approaches. By far the most common approach is to incubate eggs at two temperatures in a split clutch design with multiple eggs from a single clutch often being incubated in each of the temperatures (74% of the data set included experiments of this kind). In contrast, studies that characterize developmental plasticity across a range of temperatures are still relatively rare, despite the fact that this provides researchers with the greatest power to accurately describe thermal reaction norms (Figure 7). There are clearly logistical reasons for limiting the number of temperature treatments within studies. Clutch sizes for many reptile groups (e.g., geckos, anoles) are highly conserved and splitting eggs across many temperatures is often impossible. However, there are a number of species of sea turtles, large lizards, snakes, and crocodilians where females often lay large clutches of eggs. This makes it quite feasible to characterize the entire thermal reaction norm more effectively. Reducing the number of eggs from a single clutch within an experimental treatment and spreading these eggs across a wider range of temperatures would go a long way to establishing representative thermal reaction norms across populations and species. Many studies for many species we have the capacity to do such experiments—given enough incubators—as the vast majority of studies utilize experimental designs (65%) with (at times) large numbers of eggs from the same clutch in the same thermal treatment. A full characterization of thermal reaction norms will facilitate a greater understanding of optimal developmental temperatures (T_{opt}) across
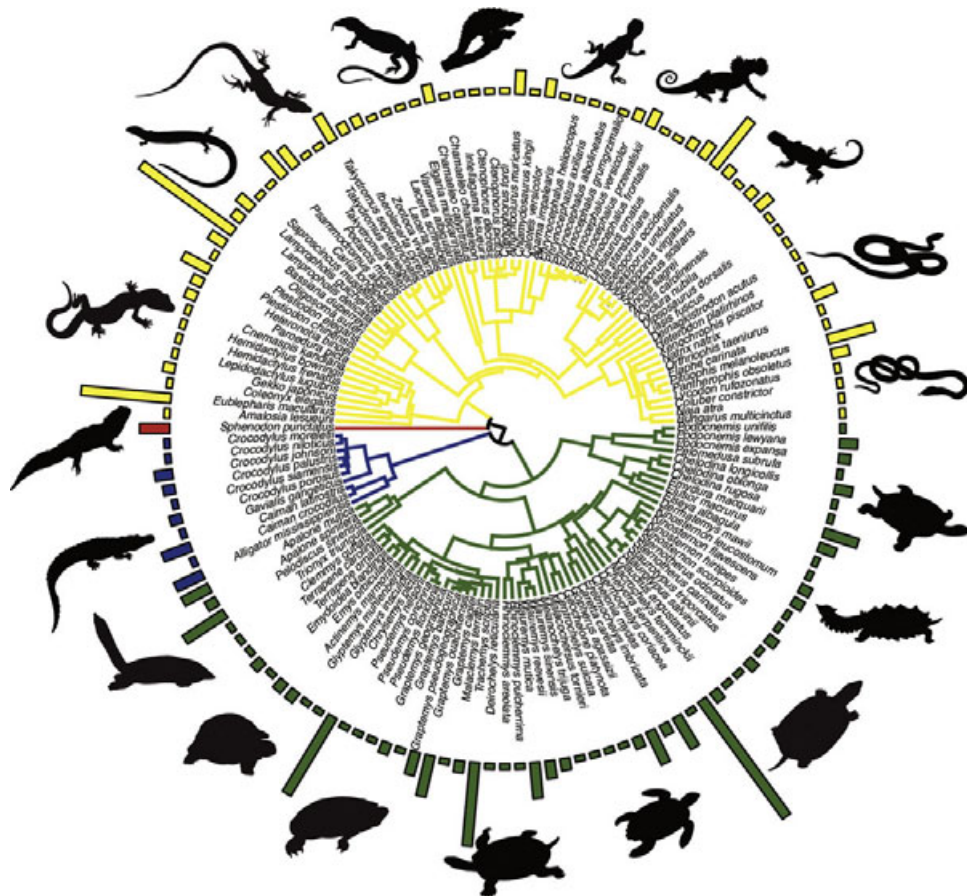
FIGURE 3 Phylogenetic tree (derived from TimeTree.org; Hedges, Dudley, & Kumar, 2006; Kumar, Stecher, Suleski, & Hedges, 2017) of 140 taxa present within the RepDevo database (15 taxa were excluded because of ambiguity surrounding their taxonomic position–see below). Each of the four major orders are represented in the database ("blue", Crocodilia; "red", Tuatara; "yellow", Squamata; and "green", Testudines). Bars above taxa indicate the number of studies (scaled by a factor of 10) for each species. The 15 taxa not identified in TimeTree.org were as follows: *Sceloporus aneus*; *Tropidonophis mairii*; *Chelodina expansa*; *Gopherus polyphemus*; *Heosemys grandis*; *Graptemys versa*; *Scincella modesta*; *Ptyas dhumnades*; *Nannoscincus maccoyi/Anepischetosia maccoyi*; *Malayemys macrocephala*; *Pelusios castaneus*; *Kinosternon subrubrum*; *Sternotherus minor*; and *Graptemys nigrinoda* [Color figure can be viewed at wileyonlinelibrary.com]

species to ascertain if T_{opt} is phylogenetically conserved, and how and what environmental variables drive differences across species.

In addition to manipulations of mean temperatures within studies, particular thought should also be given to temperature fluctuations. Most studies so far have incubated eggs under constant temperatures ($< \pm 1°C$; 84%), whereas a smaller number (28%) incubated eggs at temperatures that fluctuated in some way that mimic more natural incubation conditions. A few studies incubated eggs at both constant and fluctuating temperatures. The phenotypic effects of thermal fluctuations during incubation and their ecological significance have been widely discussed (see, for example, Bowden, Carter, & Paitz, 2014), but the relative frequency of studies that use thermal fluctuations has not substantially changed relative to those using constant incubation conditions (Figure 8). When reptile nests can be located in the wild, which is not a trivial task for many species, implementing natural variation in incubation temperatures can be achieved using iButton data loggers (to measure nest or ground temperatures in the field) and programmable incubators that have the capability to mimic thermal environments in the field (Pearson & Warner, 2016). This technology enables researchers to assess the effect of irregular thermal fluctua-

tions that are common in nature, as well as season- or habitat-specific thermal profiles (Pearson & Warner 2016).

4 | ADVANCING THE STUDY OF THERMAL DEVELOPMENTAL PLASTICITY

Our qualitative synthesis makes it clear that thermal developmental plasticity in reptiles has had a long and diverse history and our bibliometric analysis shows that the field is highly collaborative. Nevertheless, it is also evident that the field has been heavily influenced by a few major authorities contributing substantial empirical, theoretical, and applied insights that have stimulated growth of the field. The reasons for the interest in plasticity are many and varied, including attempts to understand developmental mechanisms, evolutionary adaptation and diversification, ecological interactions, and individual and population level responses to environmental change. Below we discuss the major research themes that have emerged from the literature and identify promising new research directions where we believe thermal developmental plasticity will make important advances to our understanding
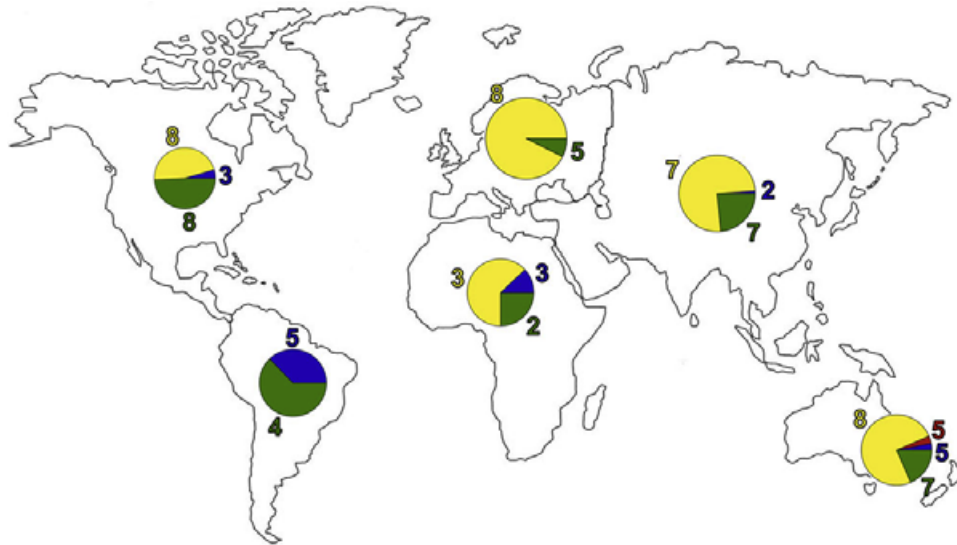
FIGURE 4 The global distribution of reptile incubation effects contained in our database. Each pie chart summarizes the number of effects for each continent (North America, South America, Africa, Europe, and Australia) by reptile order (Sphenodon in red, Crocodilia in blue, Squamata in yellow, and Testudines in green). The numbers beside each slice of pie (color corresponds to the appropriate pie slice) represent the number of trait categories out of eight possible categories (i.e., incubation, development, morphology, etc.) that are represented. Note that effects are categorized by study species' distributional range. In some instances, captive colonies of species from different continents were studied. In these cases, the species was grouped into the continent of their native distributional range. Some studies contained species from multiple continents and these studies contributed data to each location [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 Word clouds summarizing the most frequently quantified traits within studies for six of the eight trait categories. The "Sex" and "Incubation" categories are not presented because they include a single trait (sex ratio and incubation duration, respectively). The size of the word indicates a higher relative frequency in the RepDevo database [Color figure can be viewed at wileyonlinelibrary.com]
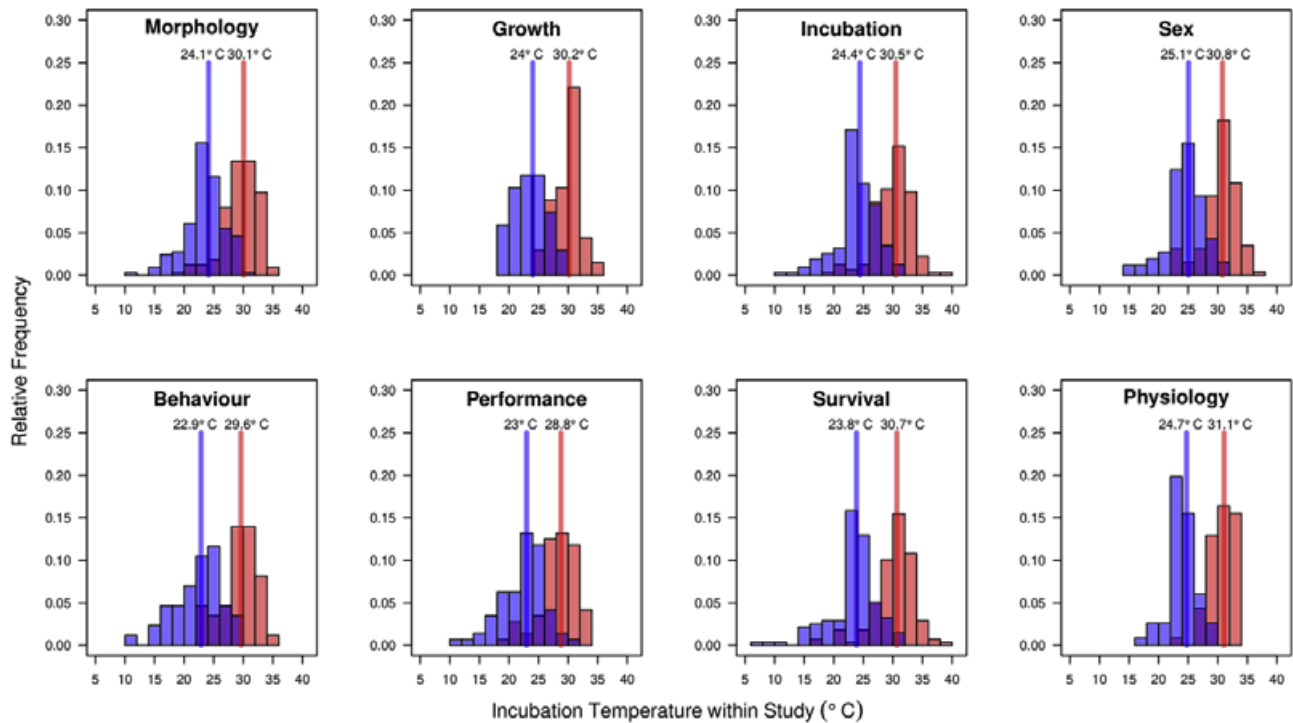
FIGURE 6 Relative frequency (i.e., proportion) of the minimum (blue) and maximum (red) incubation temperatures experimentally manipulated within papers for each trait category. Vertical lines ("red" and "blue"), and numbers above lines, signify the mean minimum and maximum temperature within a study for each trait category. Temperature values above the histograms are the average minimum and maximum for each trait category [Color figure can be viewed at wileyonlinelibrary.com]
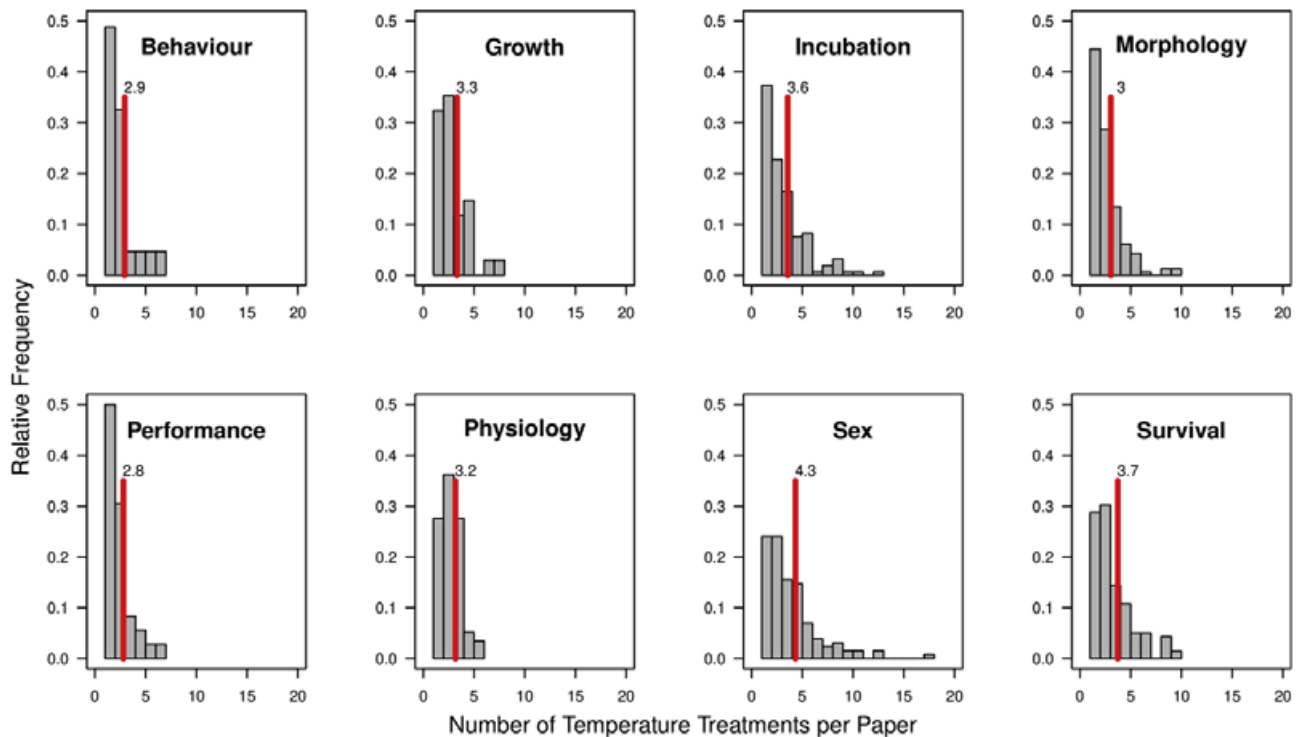

FIGURE 7 Relative frequency (i.e., proportion) of the number of incubation temperatures experimentally manipulated within papers for each trait category. Red lines, and numbers above lines, signify the mean number of temperatures for each trait category [Color figure can be viewed at wileyonlinelibrary.com]
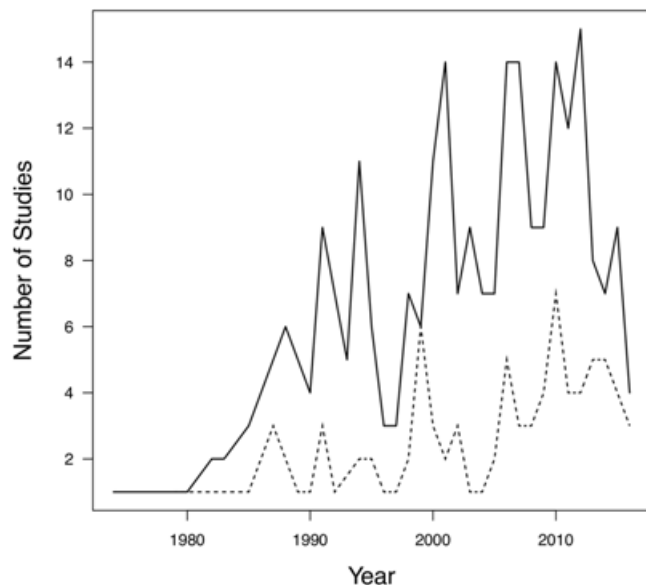
FIGURE 8 Number of studies using constant incubation temperatures (solid line) versus those using more natural fluctuations around a mean incubation temperature (dashed line)

of ecological and evolutionary processes more generally. In the process, we reiterate how the current gaps in our knowledge limit our ability to address these questions and provide suggestions for how future work can resolve these gaps.

4.1 | Mechanisms underpinning thermal developmental plasticity

Given the well-established evidence for thermal developmental plasticity in reptiles, it is perhaps surprising how little is known about the underlying mechanisms generating and maintaining different developmental outcomes in response to thermal environments (Aubin-Horth & Renn 2009). This includes elucidating the hormonal, cell signaling, and epigenetic modifications that influence gene expression leading to alternative developmental outcomes (Aubin-Horth & Renn 2009; Dufty, Clobert, & Møller, 2002; Feiner et al., 2018b; O'Dea, Noble, Johnson, Hesselson, & Nakagawa, 2016; Paredes et al. 2016). Additionally, we argue that early developmental responses must consider the complex milieu of parental (especially maternal) environmental effects that can have substantial impact on offspring development (Mousseau & Fox 1998; Uller, 2012). Studies of thermal developmental plasticity that are integrated with manipulations of parental effects may provide insights into the ways that multiple aspects of the developmental environment interact and may help explain complex effects observed across species (Noble et al., 2018b).

Of the research that has been carried out on the mechanisms of thermal developmental plasticity, most has involved studies aiming to understand temperature-dependent sex determination (TSD) (see below). In contrast, few studies have attempted to elucidate the underlying mechanisms of organism-wide thermal developmental responses. However, there are a growing number of exceptions. For example, one study of thermal developmental plasticity in wall lizards (*Podar-*

cis muralis) identified suites of genes that are up- or downregulated at low temperatures (Feiner et al., 2018a). Transcripts with the most extreme changes in expression profiles were associated with transcriptional and translational regulation and chromatin remodeling, suggesting possible epigenetic mechanisms underlying acclimation of early embryos to cool temperature. This is consistent with another study showing that the DNA in the brain of cool-incubated lizards is hypo-methylated (Paredes, Radersma, Cannell, While, & Uller, 2016). Changes in gene expression in this species is also associated with rapid evolutionary responses to cope with cool developmental environments following the introduction of the species to England (Feiner, Rago, While, & Uller, 2018b). Specifically, genes with thermal responsive expression in the native populations were particularly likely to show a selective shift in expression following introduction, with some evidence for functional convergence in lizards originating from different source locations.

Incubation temperature has also been shown to impact gene expression and enzyme activity in a number of other species. Work in Loggerhead sea turtles has also shown a host of genes involved in cell proliferation, development, and biogenesis to be differentially regulated in response to early embryonic heat stress, with heat shock proteins being strongly upregulated in response to acute temperature extremes that embryos encounter (Bentley, Haas, Tedeschi, & Berry, 2017; Tedeschi et al., 2015). Interestingly, these responses have a strong maternal and additive genetic basis (Tedeschi et al., 2016). Embryos of *Pelodiscus sinensis* exposed to high incubation temperatures have also been shown to have enhanced mitochondrial respiration rates and significantly increased metabolic enzyme activity (Sun, Li, Gao, Ma, & Du, 2015), providing mechanisms explaining the faster development times observed across reptilian taxa at higher temperatures (Noble et al., 2018b). At the moment, however, it is possible that changes observed at the molecular level do not translate to the effects observed on phenotypic traits that are most commonly targeted, such as morphology or physiological performance. The developmental biology of thermal plasticity in reptilian embryos remains almost entirely a black box and studies integrating multiple levels of biological organization will provide substantial insights.

4.2 | Adaptive significance of thermal developmental plasticity

Phenotypic plasticity in response to the thermal developmental environment is predicted to be advantageous when it enables individuals to match their phenotype to their environment. Plastic responses are favored when populations are exposed to variable environments, when selection favors different phenotypes under different environmental conditions and when no phenotype has superior fitness across all environmental conditions (Bradshaw, 1965; Ghalambor, McKay, Carroll, & Reznick, 2007; Schlichting & Pigliucci 1998). Although there are many known cases of adaptive plasticity, not all responsiveness to the environment is beneficial. This is particularly true of developmental plasticity as it can have organizational effects on phenotypes that can be long lasting and potentially constrain phenotypic development later in life (Dufty et al., 2002; Noble et al., 2018b).

In reptiles, the adaptive significance of thermal developmental plasticity remains unclear. Even the adaptive significance of TSD is poorly understood (see below). This situation is partly because trait integration can be complex and adaptive phenotypic responses early in development may not be reflective of an optimal "phenotype–fitness" match later in life. It is clear from meta-analytic work that phenotypic effects in response to early thermal environments can have long-lasting effects (Noble et al., 2018b), and so, long-term studies directly accessing the covariance between traits and fitness are needed. However, such studies are still rare (Andrews et al., 2009; Dayananda, Gray, Pike, & Webb, 2016; Fordham, Georges, & Corey, 2007; Freedberg, Ewert, & Nelson, 2002; Janzen, 1995; Joanen, McNease, & Ferguson, 1987; Lewis-Winokur & Winokur, 1995; Monasterio et al., 2013; Nelson, Thompson, Pledger, Keall, & Daugherty, 2004; Parker & Andrews, 2007; Peet-Pare & Blouin-Demers, 2012; Qualls & Andrews, 1999; Verdú-Ricoy, Iraeta, Salvador, & Díaz, 2014; Webb & Cooperpreston, 1989). In addition, it has been surprisingly difficult to establish natural variation in exposure to temperature and how it relates to ecological conditions that cause differences in fitness between individuals. This requires the natural history of the species to be reasonably well understood.

With clearly defined hypotheses, it should be possible to generate fitness measures of animals developing under different thermal environments to test whether or not the resulting phenotypes result in higher fitness under conditions predicted by incubation temperature. Comparative studies that contrast populations or species for which the fitness benefits of incubation temperature should differ are particularly useful to avoid adaptive story telling. For example, one study contrasting cool and warm adapted populations of a viviparous skink suggested that thermal effects on offspring size is due to weak selection against plasticity rather than adaptation (Uller et al., 2011). Comparative data on trait means and sample variance could also be used to explore maladaptive responses of higher temperatures through increased developmental stress—lack of a change in the trait mean but a change in its variance would give precedence to the idea that higher temperatures lead to developmental instability.

4.3 | Temperature dependent sex determination

A large proportion of research into thermal developmental plasticity in reptiles has been in the field of sex determination. Out of the 20 top cited papers, 13 focus specifically on some aspect of sex determination. Indeed, TSD is the one area of research in which both the mechanisms and the adaptive significance of thermal developmental plasticity have been relatively well studied. Bias toward research on TSD is a result of many factors. First, TSD is a clear example of a polyphenism in reptiles, where the phenotypic outcomes of incubation temperature are consistently discrete categories (i.e., male or female) and are irreversible. Polyphenisms such as these are of general interest and convenient target phenotypes for any study of developmental plasticity (e.g., Snell-Rood et al., 2011). Second, the sex of an individual has major consequences on its physiology, behavior, life history, and fitness. In addition, changes in sex ratios have numerous consequences at the population level (e.g., Janzen, 1994). Third, theoretical models for the adaptive

significance of TSD are well established and testable (Charnov & Bull 1977; Pen et al., 2010; Schwanz et al., 2016; Shine, 1999), making TSD a convenient form of plasticity to assess its adaptive value. Furthermore, sex determination systems in reptiles vary considerably at macro scales, specifically in the context of phylogeny (Gamble, 2010; Valenzuela & Lance 2004). Fourth, physiological and molecular mechanisms of sex determination have been studied for decades across diverse taxa (Beukeboom & Perrin 2014; Pifferer, 2013; Rhen & Schroeder 2010; Solari, 1994), and many pathways are conserved among species with TSD and genotypic sex determination (Beukeboom & Perrin 2014; Czerwinski, Natarajan, Barske, Looger, & Capel, 2016; Marshall Graves & Peichel 2010). Due to these factors (and others), TSD is a unique topic within the field of thermal developmental plasticity that has generated considerable interest among both reptile and nonreptile biologists.

Despite the long and continued interest in TSD, there are still many open questions relating to patterns of sex determination in reptiles. We identify four major areas where research on this topic would be most fruitful.

First, given that sex-determining mechanisms have been identified in <5% of known taxa, our general understanding of the phylogenetic history of TSD and evolutionary transitions among sex-determining mechanisms remains limited. Thus, descriptive incubation studies of sex-determining mechanisms in underrepresented reptile clades would be particularly useful. Moreover, mechanisms of transitions between sex-determining systems are unclear, though recent theoretical and empirical work is shedding light in this area (Holleley et al., 2015; Pen et al., 2010; Quinn, Sarre, Ezaz, Marshall Graves, & Georges, 2011; Schwanz, Ezaz, Gruber, & Georges, 2013; Uller & Helanterä 2011).

Second, the physiological and molecular mechanistic basis for TSD is also an active area of research and recent studies have proposed a variety of ways in which temperature during development may influence sex determination (Czerwinski et al., 2016; Deveson et al., 2017; Navarro-Martin et al., 2011; Radhakrishnan et al. 2017; Yatsu et al. 2016). Indeed, there appears to be many pathways by which temperature is converted to a sex-determining signal. Exploring how intermediate temperatures produce both sexes may be one particularly fruitful avenue of research within this context. Deeming and Ferguson (1989) highlight the importance of understanding the extent to which natural variation in sensitivity to temperature and to variability in thermal sensitive periods can produce sexes at one temperature, but this has seldom been addressed in the literature. Nonetheless, it is difficult to generate a mechanistic understanding of natural variation in sex ratio as studies of gene expression and gene regulation during sex determination typically disrupt further development

Third, the ecology and adaptive significance of TSD are still poorly understood, despite some experimental demonstrations of its influence on fitness (Holleley et al., 2015; Janzen, 1995; Warner & Shine 2008b). Given the multiple origins of TSD across reptiles with diverse ecologies and life histories, a single explanation for the evolution of TSD is unlikely. Yet, we know next to nothing about the fitness consequences of incubation temperature in nearly all taxa (particularly the effects of natural fluctuating incubation temperatures, as most

studies of TSD use constant temperature incubation), which leaves this area wide open for future exploration.

Lastly, while TSD reaction norms have been described in numerous studies, taxonomic coverage is biased toward turtles. Hence, we know very little about the shape of the TSD reaction norm for the majority of taxa. The shape of the TSD reaction norm, as described by the pivotal temperature(s) and the range of temperatures that produce both sexes, plays a crucial role in the evolution, ecology, and conservation of species, and can be described through laboratory incubation experiments (Girondot, 1999; Hulin, Delmas, Girondot, Godfrey, & Guillon, 2009). The shape of the reaction norm may reflect local selective pressures based on ecology and life history (Carter, Bowden, & Paitz, 2017; Ewert, Lang, & Nelson, 2005; Schwanz & Proulx 2008; Schwanz, Janzen, & Proulx, 2010a). In turn, this influences clutch and population sex ratios (Hulin et al., 2009; Schwanz et al., 2010b) and is thought to predict evolutionary response under directional climate change (Hulin et al., 2009). More studies are therefore required that describe the reaction norm across taxa if we are to address these questions adequately.

4.4 | Patterns of thermal developmental plasticity at macroecological scales

The broad taxonomic and geographic distribution of the studies on thermal developmental plasticity suggests that there is substantial scope to explore how responses to the thermal environment vary at a macro-ecological scale. Theory predicts that populations and/or species from more thermally variable environments should be selected to have greater plasticity compared to those from more thermally stable environments because the benefits of maintaining plastic responses outweigh the costs (Angilletta, 2009). Because thermal microclimatic profiles might be predicted to be more variable at high elevation and high latitude, species in these regions may be better able to cope with thermal fluctuation (Shah, Funk, & Ghalambor, 2017). An obvious caveat is that it is unclear to what extent plasticity in, for example, morphology is adaptive or nonadaptive (Uller et al., 2011). It will therefore be important to carefully select traits for which fitness is unlikely to be thermally dependent or to understand the adaptive significance of plasticity. Empirical studies to date suggest that the extent of thermal developmental plasticity is quite variable between populations and species living in different climates, and at least sometimes this appears consistent with how climate should influence natural selection (e.g., Uller et al., 2011; While et al., 2015).

Comparative data on how developmental timing and hatching success may be affected by early thermal conditions can also be usefully integrated into species distribution models (when combined with microclimatic data on soil temperatures) to better predict how plastic responses with respect to temperature (or other environmental variables, such as moisture) might influence predictions regarding population extinction and species distributional changes through time (e.g., Dayananda et al., 2016; Monasterio et al., 2013; While et al., 2015). Thermal plasticity differences among species may themselves be related to the distributional range of a species, with more

"generalist" species showing higher levels of plasticity in some traits compared to more restricted, "specialist", species (Sultan, 2000).

Advancing our understanding in these areas is also likely to have substantial implications for our ability to address major contemporary ecological challenges. For example, understanding how development responds to changes in the thermal environment will be particularly important in the context of global climate change, particularly as plasticity is often championed as a potential mechanism that will allow organisms to adjust physiological processes to cope with a changing climate (Chevin, Lande, & Mace, 2010; Gunderson & Stillman 2015; Seebacher et al. 2015). Furthermore, given that climatic similarity can be a good predictor of colonization or invasion success in ectotherms (e.g., Rago, While, & Uller, 2012), mechanistic models that include the effects of incubation temperature on hatching date and offspring phenotype may also prove useful to understand why some species are highly successful invaders. Expanding the geographic and taxonomic breadth of thermal developmental plasticity research with these questions in mind could provide particularly useful insights into the processes underlying macro-ecological patterns.

5 | CONCLUSIONS AND SUMMARY

Despite the long and productive history of thermal developmental plasticity research in reptiles, it is clear that new and exciting avenues remain to be explored at both the micro- and macro-ecological level. Reptile thermal developmental plasticity represents an extremely well-studied area of experimental ecology with over 300 studies containing important data that can be used in a comparative context. As a result, the insights garnered from our qualitative synthesis not only provide new and stimulating directions for empirical research, but elucidate promising research directions that can utilize the power of large comparative datasets. Global scale comparative data is becoming even more important for tackling questions related to invasive species and climate change, but also fundamental research questions related to life-history evolution and the adaptive significance of plasticity, including TSD. Such comparative data provide a unique opportunity to test the generality of theory and to reveal gaps in our current state of knowledge. Working to fill in the empirical gaps we have identified, and taking strides to collate and synthesize existing empirical research, will ensure that important ecological, evolutionary, and conservation related questions can be tackled effectively from different angles and ultimately improve our understanding of pressing fundamental and applied research questions.

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SUPPORTING INFORMATION