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REVIEW

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Introduction to the special issue—Developmental plasticity in reptiles: Physiological mechanisms and ecological consequences

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1 | INTRODUCTION

The environment is a major contributor to phenotypic variation within natural populations. Almost every organism has some aspect of its phenotype that is influenced by the environment it encounters. Thus, plastic responses are ubiquitous and are of broad interest to biologists spanning many disciplines (e.g., genetics, development, physiology, behavior, ecology, evolution, and medical sciences). Plasticity generally refers to phenotypic sensitivity to the environment, and more specifically is defined as the capacity of a genotype to produce multiple phenotypes across different environments. Plasticity is often quantified as a reaction norm (a function describing the relationship between the environment and a phenotype), which can vary considerably among species, populations, and among individuals within a population (DeWitt & Scheiner, 2004). Given this variation, plasticity can have major consequences on ecological and evolutionary processes (e.g., either hindering or facilitating evolutionary change; Chevin, Lande, & Mace, 2010; Lande, 2009; Price, Qvarnstrom, & Irwin, 2003). Moreover, plasticity itself can have a heritable basis and can evolve like any trait that exhibits additive genetic variation (Thompson, 1991). For example, natural selection can shape plastic responses to environments in adaptive directions, which often enables phenotypes to optimally match the environment in which an organism lives. Theory predicts that plasticity should evolve in heterogeneous, but predictable, environments because it enables phenotypes to develop that are suited for current environmental conditions or future conditions that have been experienced before in the organism's evolutionary history (DeWitt & Scheiner, 2004). Although many empirical studies support this prediction (Green, 1989; Van Buskirk, 2017), plasticity can also arise in nonadaptive ways owing to physiological or physical constraints (Ghalambor, McKay, Carroll, & Reznick, 2007; Ghalambor et al., 2015), and plasticity can sometimes be maladaptive, particularly in rapidly changing environments (Zimova, Mills, & Nowak, 2016).

Plasticity can occur at any life stage, from embryonic, to neonatal, to adult stages. Conditions during embryonic development are of particular interest because phenotypes are sensitive and labile during this early stage while organ systems are still very malleable (West-Eberhard, 2003) and because adult phenotypes are often directed by phenotypic variation during development. Thus, environmental conditions experienced during embryonic development can have long-lasting consequences throughout an individual's life (Uller, 2008; West-Eberhard, 2003). These early-life responses to embryonic or neonatal environments are referred to as developmental plasticity. Scientific interest in developmental plasticity is far-reaching, as it encompasses many important subdisciplines in biology (e.g., maternal effects, sex allocation, and sex determination) and has implications for research on life-history evolution (evolution of viviparity, environmental sex determination; Shine, 1995; Warner & Shine 2008), cognition (Amiel & Shine 2012; Siviter et al., 2017), species distributions (Carlo, Riddell, Levy, & Sears, 2018), and conservation or global change biology (e.g., climate change, urbanization: Mitchell, Kearney, Nelson, & Porter, 2008; Tiatragul, Kurniawan, Kolbe, & Warner, 2017).

Our understanding of developmental plasticity comes from research across a diversity of model and nonmodel organisms. Importantly, no single model has all the ideal attributes for addressing the major questions in this field. Reptiles, however, have many characteristics that make them outstanding organisms for research on this topic (Warner, 2014). First, reptile embryos experience considerable environmental variation (whether inside the nest in oviparous species, or in utero in viviparous species) that influences the development of phenotypes. For example, aspects of maternal nutrition or body temperature in viviparous species or thermal and hydric environments during egg incubation shape variation in a suite of morphological, physiological, and behavioral traits of offspring (Noble, Stenhouse, & Schwanz, 2018a; Warner, Lovern, & Shine, 2007) in ways that affect fitness. Importantly, reptiles display considerable ecological, physiological, and behavioral diversity, and thus the effects of developmental conditions can vary considerably among taxa, particularly across major clades (Noble et al., 2018a). Second, many reptiles are highly fecund and produce large clutch sizes, which is convenient for experimental studies. Moreover, the presence of oviparity and the low occurrence of parental care facilitate manipulative studies that decouple the effects of the environment from those of maternal identity (Rhen & Lang, 1998; Warner & Andrews, 2002). Third, husbandry and incubation protocols are well established for many species (e.g., Sanger, Hime, Johnson, Diani, & Losos, 2004). Although some species are difficult to maintain and breed in captivity (owing to, for example, body size, specific husbandry requirements, or because they are venomous), many are relatively small and can be housed in large numbers. Finally, many species occur in relatively high densities in the field, which facilitates collection for laboratory experiments, locating nest sites for field measurements of nest conditions for some species, and conducting capture-mark-recapture studies for quantifying how selection operates on environmentally induced phenotypic variation (Brown & Shine, 2004; Webb, Shine, & Christian, 2006; Pearson & Warner, 2018). As a consequence of these attributes (and others), research on reptiles has been particularly influential in our understanding of developmental plasticity from both mechanistic and eco-evolutionary perspectives.

Research on developmental plasticity in reptiles has also provided insights into general conceptual areas of interest to ecologists and evolutionary biologists. For example, reptile models have been subjects of landmark studies that have identified key mechanisms underlying environmental sex determination (Bachvarova et al., 2009; Deveson et al., 2017; Ge et al., 2018; Georges & Holleley, 2018; Matsumoto, Buemio, Chu, Vafaee, & Crews, 2013; Radhakrishnan, Literman, Neuwald, Severin, & Valenzuela, 2017; Schroeder, Metzger, Miller, & Rhen, 2016; Shoemaker-Daly, Jackson, Yatsu, Matsumoto, & Crews, 2010), as well as models for robust empirical tests of the adaptive significance of this peculiar form of developmental plasticity (Holleley et al., 2015; Pen et al., 2010; Shine, 1999; Warner & Shine, 2008). Studies of maternal effects in viviparous squamates, such as the thermal environment during pregnancy, provide insights into the evolution of viviparity in vertebrates (Shine, 1995; Webb et al., 2006). Moreover, the 100+ independent origins of viviparity (in squamates) and multiple origins of temperature-dependent sex determination (TSD) make reptiles ideal for studies on these topics (Blackburn, 2015; Gamble et al., 2015). Characteristics of reptiles have facilitated unique tests of the environmental matching hypothesis to better understand the adaptive significance of plastic responses to incubation and maternal environments (Pearson & Warner, 2018; Wang, Li, Zeng, Liang, & Du, 2017; Warner, Buckelew, Pearson, & Dhawan, 2015). We now have a better understanding of how the complex thermal environment in utero and in nests influences phenotypes in the field—both average and thermal variability can be independently influential—in ways that can be predicted from controlled laboratory experiments (Du, Shou, Shen, & Lu, 2005; Georges, Doody, Beggs, & Young, 2004; Georges, Limpus, & Stoutjesdijk, 1994; Shen, Pei, Lin, & Ji., 2017). Studies of thermally sensitive gene expression and steroid activity in reptiles provide a novel understanding of the mechanisms underlying responses to developmental environments (Pallotta et al., 2017; Tang, Mu, Valenzuela, & Du, 2017) and their potential to span generations (Paredes, Radersma, Cannell, While, & Uller, 2016). Research on reptiles has also been critical in sex allocation theory, whereby mothers differentially invest into sons versus daughters in response to current or future conditions, often in directions predicted by theory (Olsson & Shine, 2001; Uller, Massot, Richard, Lecomte, & Clobert, 2004; Wapstra & Warner, 2010). Lastly, studies of reptile developmental plasticity have provided important forecasts of how organisms might deal with global change (Carlo et al., 2018; Jensen et al., 2018; Mitchell et al., 2008). However, despite the major role that reptiles have played in the development of this field, there is still much to learn from studies focused on this taxonomic group.

2 | BRIEF HISTORY OF THE FIELD

Research on reptilian development has a long history (reviewed by Andrews & Mathies, 2000; Billett, Gans, & Maderson, 1985; Yntema, 1964). To our knowledge, early experimental studies date back to the 1930s (Pasteels, 1937; Nakeo, 1939), but those that demonstrate clear effects of incubation environments on offspring development and phenotypes were mostly conducted in the 1950s and 1960s (some reports are earlier—Cunningham, 1922; Fox, 1948). This was a time when many researchers were developing methods for incubating reptile eggs for studies of embryology (Holder & Bellairs, 1962; Maderson & Bellairs, 1962; Panigel, 1956; Raynaud, 1959; Zweifel, 1961) whereby observational and experimental reports of the effects of developmental environments on egg survival and offspring phenotypes were accumulating (Fitch & Fitch, 1967; Licht & Moberly, 1965). Several studies demonstrated that incubation temperature and moisture induce abnormalities in turtles (Lynn & Ulbrich, 1950; Yntema, 1960) and snakes (Fox, Gordon, & Fox, 1961). Some of the first demonstrations of developmental plasticity in reptiles were on the effects of incubation temperature on scalation in *Thamnophis elegans* (Fox, 1948), on the effects of drying egg environments on the size of hatchling *Anolis carolinensis* (Gordon, 1960), and on the effect of incubation temperature on sex ratio in *Agama agama* (Charnier, 1966).

Throughout the 1970s and 1980s, research on reptile egg incubation developed as an important area in the fields of herpetology and physiological ecology. During this time, skepticism about TSD in reptiles faded as laboratory and field studies clearly demonstrated this sex-determining mechanism in many turtles and crocodilians (Bull, 2004; Bull & Vogt, 1979; Ferguson & Joanen, 1982; Pieau, 1974). Research on TSD has since been the most prominent area of focus in reptilian developmental plasticity (see While et al., 2018). Further detailed work (Ackerman, 1980; Packard & Packard, 1988; Prange & Ackerman, 1974) firmly established the roles of hydric conditions and gas exchange during egg incubation in shaping physiological and morphological phenotypes of hatchling reptiles. Research on viviparous squamates (Guillette, Jones, Fitzgerald, & Smith, 1980; Packard, Tracy, & Roth, 1977; Shine & Bull, 1979) also advanced our understanding of the evolution of viviparity. By the mid-late 1980s, experimental manipulations of exogenous steroids (Bull, Gutzke, & Crews, 1988; Gutzke & Bull, 1986) demonstrated the role of these hormones in sexual differentiation, which has been further established by Crews (1996), and others (Dorizzi, Richard-Mercier, Desvages, Girondot, & Pieau, 1994) over the subsequent decades.

Owing to the wealth of research on reptilian incubation, a symposium was held at the University of Manchester in 1989. This symposium, entitled "Physical Influences on Embryonic Development in Birds and Reptiles", advanced this field by bringing together scientists who specialize in incubation and physiology of avian and nonavian reptile eggs. This symposium led to an important edited volume that synthesized many, but not all, aspects of the field at this time (Deeming & Ferguson, 1991). Interest in reptile developmental plasticity continued and expanded. Studies that integrated laboratory and field work were becoming more common and provided new insights into the fitness consequences of developmental environments in nature (Sinervo, Zamudio, Doughty, & Huey, 1991; Janzen, 1993, 1995; Andrews, Mathies, & Warner, 2000). Laboratory incubation experiments combined with mark-release-recapture efforts in the field continue to provide critical insights into the adaptive significance of developmental plasticity (see Mitchell, Janzen, & Warner, 2018).

In 2004, two important books were published; these were Deeming's edited volume entitled "Reptilian Incubation: Environment, Evolution and Behavior", and Valenzuela & Lance's edited volume entitled "Temperature-Dependent Sex Determination in Vertebrates" (Valenzuela & Lance, 2004). These two books provide broad overviews of the field at that time. Several other important reviews have since been published (Booth, 2006; Du & Shine, 2015; Du, Ji, & Shine, 2013; Kohler, 2005; Noble et al., 2018a; Radder, 2007; Warner, 2011), but no recent review has fully captured the current state of this very broad and active field of reptile biology. One major hindrance to this challenge is that the field has grown extensively, and developmental plasticity involves much more than what was encapsulated in previous syntheses. For example, earlier syntheses focus almost exclusively on studies of egg incubation, yet developmental plasticity is clearly not confined to oviparous species. Any comprehensive review must include discussion on embryonic environments in utero prior to oviposition or parturition (Shine, 1995; Wapstra, 2000). Indeed, parental effects are a form of developmental plasticity transmitted through the parents, and can occur via several pathways, such as maternal resource allocation, epigenetic modification that alter gene expression in response to environment, behavioral thermoregulation, and nest-site selection. In addition, recent advances in molecular technology over the past 10–15 years has led to a wealth of studies on the underlying molecular mechanisms of developmental plasticity in relation to TSD (Bachvarova et al., 2009; Deveson et al., 2017; Ge et al., 2018; Matsumoto & Crews, 2017; Matsumoto et al., 2013; Matsumoto, Hannigan, & Crews, 2016; Radhakrishnan et al., 2017; Shoemaker-Daly et al., 2010). Another limitation of many previous syntheses involves taxonomic bias. Such bias is largely a function of the knowledge available for different taxonomic groups. There are far more studies on relatively short-lived squamates than on long-lived chelonians or crocodilians (e.g., While et al., 2018). Moreover, reviews of reptile developmental plasticity often exclude research on birds (DuRant, Hopkins, Hepp, & Walters, 2013), despite the fact that birds fall within the reptilian clade and exhibit many similar developmental responses to the environment as nonavian reptiles.

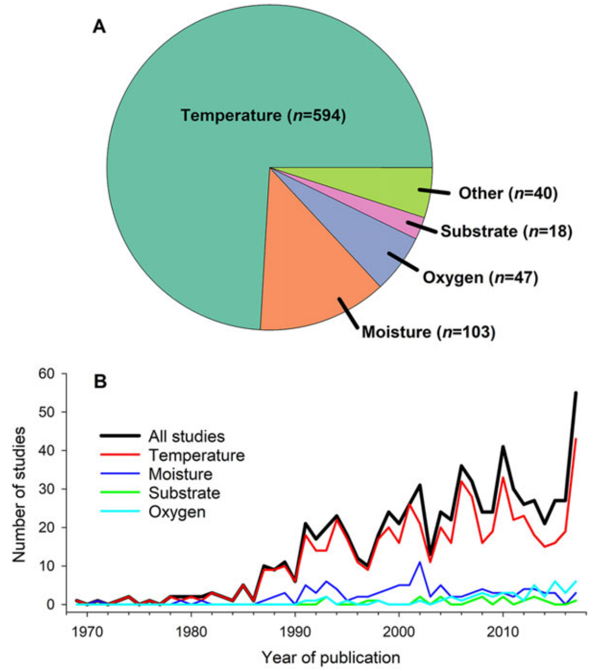

FIGURE 1 General publication trends for studies that examine the effect of different environmental variables on embryo development and offspring phenotypes in reptiles. (a) Proportion of studies that examine the effects of egg incubation temperature, moisture, oxygen, and substrate. The category "other" includes studies that examine the effects of egg aggregation ($n = 11$), inundation ($n = 5$), microbes ($n = 1$), substrate pH ($n = 1$), substrate salinity ($n = 1$), light environment ($n = 3$), contaminants ($n = 13$), and general nest effects ($n = 5$). (b) Annual variation in egg incubation studies from 1969 to 2017. The "All studies" line represents the number of publications on this topic in each year, but lines that illustrate trends for each incubation variable are not always from independent studies (e.g., for a study that examines temperature × moisture interactions, this publication was counted once for the temperature category and once again for the moisture category). Only the commonly used environmental variables of egg incubation studies were assessed, and thus the large body of literature on maternal effects are not included. Data were gathered from Web of Science searches and the Reptile Development Database. More details are provided in the online Supporting Information [Color figure can be viewed at wileyonlinelibrary.com]

Parental effects in avian and nonavian reptiles have received considerable research attention over many decades.

The number of published papers on reptile developmental plasticity has continued to increase since Deeming's (2004) volume (Figure 1). Moreover, the complexity of this field is becoming more apparent with studies that focus on different aspects of the developmental environment. The vast majority of studies in this field (~75%) has focused on the phenotypic effects of developmental temperature, followed by studies of incubation moisture conditions (Figure 1A). Other important environmental factors have also been studied, such as incubation medium and embryo hypoxia, but research on these variables continue to receive less attention than developmental temperature (Figure 1B). Moreover, several maternal factors (e.g., nutrition, basking behavior, nesting behavior, and reproductive allocation) have major developmental consequences, but the literature in this area has yet to be synthesized. Importantly, the vast literature on this topic and

FIGURE 2 The Reptile Development Database (www.repdevo.com) was made available in 2018. This database is freely accessible and provides a resource for researchers interested in reptile developmental plasticity. This database currently compiles results of studies on reptile thermal developmental plasticity, and can be used for a variety of purposes (e.g., examining trends in the literature, identifying gaps in current knowledge, and performing meta-analyses). This database will be updated annually as papers are continually published in the field, and there are plans to expand the database beyond studies of incubation temperature (e.g., to include studies of incubation moisture, maternal effects, etc.). See Noble et al. (2018b) for details [Color figure can be viewed at wileyonlinelibrary.com]

steady increase in publications over the past decades have made it difficult to draw overarching conclusions about the field's current state.

Thus, the synthesis of the current state of reptilian developmental plasticity in this special issue is very timely. The long history of papers on this topic published in the *Journal of Experimental Zoology* (see While et al., 2018) makes this journal a very appropriate outlet. This special issue was inspired by a symposium held at the Eighth World Congress of Herpetology in 2016 in Tonglu in Hangzhou, China. The symposium, entitled "Physiological mechanisms and ecological consequences of developmental plasticity in reptile embryos", was attended by many leaders in this field, many of whom are contributors to this issue. The goals of this symposium were to bring together scientists from around the world to review and synthesize the current state of the field, discuss gaps in knowledge, and identify ways to advance this area of reptile biology. This symposium was highly successful, which enabled a consolidation of research efforts to produce The Reptile Development Database, which is a new resource for researchers in this field (Noble et al., 2018b; Figure 2). This freely accessible database provides a means to address broad questions about reptile developmental plasticity and evaluate overarching patterns using meta-analytic approaches. In addition, discussions at that symposium identified several current challenges and knowledge gaps, which form the foundation for the collection of papers in this special issue.

3 | GOALS AND OVERVIEW OF THIS SPECIAL ISSUE

The focus of this special issue is to highlight the important contributions that reptile biologists have made in advancing our understanding of developmental plasticity. This issue emphasizes a variety of ecological and evolutionary perspectives, examines several experimental and observational approaches, integrates physiological and molecular mechanisms underlying developmental plasticity, and emphasizes the importance of this field in conservation and global change biology. The goal for this special issue is to summarize the current state of the field, share new and exciting findings and methods, and to identify gaps in knowledge as well as productive avenues that will further advance our understanding of this fascinating topic in reptile biology.

To achieve these goals, we have compiled 22 papers from leaders in the field of reptile and avian developmental plasticity. The formats of these contributions include reviews of specific topics, perspectives on controversial areas, original research, and qualitative meta-analyses. Due to strong enthusiasm, the number of contributions exceeds what can be accommodated in a single issue of the *Journal of Experimental Zoology A*. Thus, the papers have been divided between two issues that fall into five general themes. The first issue includes papers that focus on (1) phenotypic effects of incubation temperature, (2) fitness consequences and adaptive significance, and (3) global change biology and conservation. The second issue includes papers that focus on (4) maternal effects and their interaction with developmental conditions, and (5) mechanisms of developmental plasticity. Importantly, we recognize that several papers have considerable overlap among these themes, that this special issue does not cover all aspects of reptile developmental plasticity, and original research papers on some taxonomic groups are under-represented (e.g., archosaurs). Nevertheless, we hope that the information here will add to the foundation of this field and stimulate continued interest in this important topic. We provide an overview of the papers in each of these themes below.

3.1 | Phenotypic effects of incubation temperature

Temperature is the most frequently studied aspect of the developmental environment in reptiles (Figure 1a), and thus the literature on thermal developmental plasticity is vast. The first four papers in this issue synthesize the literature on this topic with several reviews and original research. While et al. (2018) used the Reptile Development Database (Figure 2) to provide a qualitative synthesis of the effects of egg incubation temperature on phenotypes to identify influential papers and collaborative networks in the field, and to examine major research trends and draw attention to geographic and taxonomic biases in current research. Complementary to this review, Bowden and Paitz (2018) discussed the importance of integrating natural conditions into laboratory experiments (e.g., fluctuating temperature and natural variation in yolk estrogens) that examine TSD. The third and fourth papers in this theme describe original research that quantifies the potential role of incubation temperature in shaping sexual size dimorphism in geckos (Kratochvíl, Kubička, Vohralík, & Starostová, 2018) and behavioral traits in birds (Hope, Kennamer, Moore, & Hopkins, 2018). Several other papers in this issue examine the phenotypic consequences of incubation temperature, but address this topic from a mechanistic perspective or in the context of maternal effects and global change (see below).

3.2 | Fitness consequences and adaptive significance

How embryos respond to developmental environments can have important impacts on fitness, and natural selection could shape those responses in adaptive directions. Little is known about the fitness consequences of environmentally induced phenotypes, owing largely to the difficulty of measuring long-term fitness in the wild. Nevertheless, significant advances have been made in this area. Mitchell et al. (2018) reviewed key papers that have demonstrated long-term effects of developmental environments on adult phenotypes and fitness, and examine the advantages, disadvantages, and challenges of different experimental designs that researchers have used to address this important area of plasticity. Shine and Du (2018) provided a perspective on behavioral thermoregulation of reptile embryos, which is a topic that may have profound implications for the field of developmental plasticity, as embryos may be capable of adaptively adjusting their own phenotypic development. Brown and Shine (2018) provided new results that demonstrate how hydric conditions during egg incubation affect immune function in keelback snakes, and its link to growth and survival in the field.

3.3 | Global change biology and conservation

Environmental change at a global scale will undoubtedly impact the developmental conditions that embryos experience, and in turn have dramatic effects on offspring phenotypes and fitness in ways that will impact populations and communities. The impact of environmental change on embryo development and population persistence has been an active focus of research in recent years, and knowledge of the potential effects of global change (climate change, urbanization, habitat modification and fragmentation, and pollution) is critical for effective conservation plans and any action that follows. This section contains four original research papers that examine the potential consequences of warming temperatures and pollutants on development of reptile embryos. First, Thompson et al. (2018) demonstrated that snapping turtle embryos are negatively affected by shaded conditions in agricultural fields, as well as by mercury pollution at these sites. Sanger, Kyrkos, Lachance, Czesney, and Stroud (2018) demonstrated that increasing temperatures negatively affect embryo survival during the stages of morphogenesis in brown anoles, and suggest that climate change will likely negatively affect egg survival given that nests in the field are currently at the thermal limits. Ma et al. (2018) exposed embryos of two sympatric lizard species (that occupy different microhabitats) to climate warming scenarios and show that the impact of climate warming on these species is dependent upon preferred microhabitats. Lastly, Cunningham, Fitzpatrick, While, and Wapstra (2018) examined the consequences of thermal conditions at the margins of the population's temperature range in a viviparous skink, and suggest that advancing birth dates due to warming climates could have positive effects for their montane population. All of these studies have important implications for making predictions about the impacts of environmental change at global and regional scales.

3.4 | Maternal effects and their interaction with developmental conditions

Maternal effects occur when an individual's phenotype is influenced by the phenotype or environment of its mother. For example, maternal effects often involve the maternal environment (e.g., nutrition, social interactions), maternal behavior (e.g., basking, nesting), and reproductive allocation, and all these factors may interact with post-oviposition or post-parturition developmental conditions. In this section, Van Dyke and Griffith (2018) reviewed how sources of embryonic nutrition (lecithotrophy vs placentotrophy) lead to developmental plasticity of offspring phenotypes and its fitness consequences, highlighting the importance of understanding nutrition-driven developmental plasticity for conservation. Roush and Rhen (2018) reviewed the literature on factors that generate among-clutch variation in sex ratios under TSD (genetic basis vs. maternally derived steroids) and examine experimental approaches needed to assess these factors. Next, several original research papers demonstrate independent effects of maternal environments on offspring phenotypes, as well as interactions among maternal and post-oviposition developmental conditions. For example, Andrews (2018) showed that maternal identity, egg size, and incubation temperature independently and interactively influence offspring phenotypes, such as sex and climbing speed, in chameleons. So and Schwanz (2018) showed that parental and early-life thermal conditions affect offspring thermal preferences and limits, demonstrating transgenerational and within-generation impacts of thermal environments in jacky dragons. Owen, Sheriff, Engler, and Langkilde (2018) experimentally demonstrated that maternal plasma corticosterone has sex-specific effects on offspring body condition in eastern fence lizards, supporting the Trivers-Willard hypothesis that mothers in poor condition invest less in sons. Hoffman, Finger, and Wada (2018) showed that exposure to a mild stressor early and late in life can impact immune function and clutch viability in zebra finches. Nelson, Keall, Refsnider, and Carter (2018) examined how nesting phenology of mothers may influence sex ratios of offspring tuatara.

3.5 | Mechanisms of developmental plasticity

Plastic responses to developmental conditions can arise via many mechanisms, and studies that examine the molecular and biochemical pathways that underlie plastic responses to developmental environments will provide new insights into the evolution of developmental plasticity. Booth (2018) provided a review of the influence of incubation temperature on phenotypes and draws particular attention to the importance of future work aimed at understanding the cellular and physiological basis for thermal developmental plasticity and its fitness consequences. Feiner, Rago, While, and Uller (2018) examined gene expression profiles in wall lizard embryos that experience stressfully low temperatures and show that transcripts are differentially expressed between different egg incubation temperature regimes. McGlashin, Thompson, Janzen, and Spencer (2018) examined potential physiological mechanisms underlying synchronous hatching in painted turtles, and demonstrate that less advanced embryos hatch early through metabolic compensation and premature hatching. Lastly, Deeming (2018) used a phylogenetically controlled analysis to examine factors that may have led to variation in shell types (rigid or pliable) in turtles. His results have implications for how nesting environments may have driven the evolution of increased egg shell calcification, which in turn can affect clutch size and mechanisms underlying embryo plasticity.

4 | CONCLUSIONS

Research on developmental plasticity in reptiles has a long history, and our knowledge of this topic has advanced considerably over the years. As with many active fields in science, the increased interest in reptile developmental plasticity has led to increased complexity and difficulty in synthesizing the vast literature on this topic. Although this special issue summarizes much of our current knowledge in this field, it is still far from comprehensive, and many challenges remain to be addressed. This issue highlights many of those challenges and provides numerous examples of studies and approaches that tackle those challenges. From our perspective, some of the major needs for advancing this field are as follows.

1. Enhanced ecological relevance of laboratory experiments and better characterization of the environment as it manifests in natural nests and in oviducts. This will provide a better understanding of the occurrence and relevance of developmental plasticity in nature.
2. Detailed characterizations of reaction norms at genotype and population levels, as well as studies that investigate heritability of reaction norms. This will provide better predictions of embryo responses to environmental variation, and improve our understanding of the evolutionary potential of plasticity.
3. Long-term research programs that follow individuals to maturity and quantify fitness as survival and reproductive success in nature. Linking hatchling phenotype and fitness is the key to understand the role of developmental plasticity in adaptation.
4. More studies that investigate the fundamental epigenetic mechanisms by which environmental conditions influence phenotypic development. Many recent technological and methodological advances provide an opportunity to explore proximate mechanisms at molecular, biochemical, and physiological levels.
5. Syntheses of the literature using comparative and meta-analytical approaches. These types of analyses will identify broad overarching patterns and provide insight into the evolution of developmental plasticity.
6. Studies that incorporate plastic responses of embryos to predict population and distributional shifts to changing environments. This will enhance our ability to forecast population changes or species extinctions, and prioritize conservation efforts.

We feel that research programs that target these topics will be critical in advancing this exciting area of reptile biology. Indeed, many researchers are focusing their efforts on these specific topics, as illustrated by the array of papers in this special issue. The increasing interest in using reptiles as models for studies of developmental plasticity illustrates that this is an exciting time to be involved in this dynamic and integrative field.

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