Developmental plasticity of thermal ecology traits in reptiles: Trends, potential benefits, and research needs

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A B S T R A C T

A variety of phenotypic traits in reptiles are affected by conditions during embryonic development, a phenomenon known as developmental plasticity. In particular, many traits in which expression changes with temperature, such as locomotor performance or growth rates, are also developmentally plastic. However, much less is known about the extent to which traits associated with thermal ecology, such as thermal tolerance and behavioral thermoregulation, are developmentally plastic. Here, we review the literature on developmental plasticity in physiological and behavioral traits associated with thermal ecology in reptiles. Most studies on developmental plasticity of thermal traits have assessed plasticity in behavioral traits, such as selected temperature or time spent basking, and these studies have found mixed support for the presence of developmental plasticity in behavioral thermal traits. In contrast, very few studies have assessed developmental plasticity in physiological traits, yet these studies generally support a developmentally plastic basis for thermal tolerance. Most studies have only tested for developmental plasticity in thermal ecology traits at the hatchling stage, which limits our understanding of the benefits of developmental plasticity to individuals, or the adaptive significance of developmental plasticity in populations. We recommend that research on developmental plasticity in reptile thermal ecology be expanded to include incubation conditions other than mean temperature, consider traits associated with cold-tolerance, and endeavor to understand how developmental plasticity in thermal ecology traits is beneficial. In particular, determining how long differences persist over ontogeny, and testing for benefits of developmental plasticity across multiple life stages, are crucial first steps towards understanding the adaptive significance of developmental plasticity in thermal ecology traits.

1. Introduction

Ectotherms are profoundly influenced by the thermal landscape. Many of their phenotypic traits, such as digestion rate, running or swimming speed, and color, are thermally dependent and often change substantially based on an individual's body temperature (e.g., Hertz et al., 1982; Van Damme et al., 1992; Walton and Bennett, 1993; Elsworth et al., 2003). Other phenotypic traits, such as thermal tolerance and thermoregulatory behavior, directly relate to an individual's thermal biology. These thermal ecology traits, including upper and lower thermal tolerances, preferred body temperature, thermal performance breadth, and measures associated with thermoregulatory behaviors, govern an individual's habitat use, activity in time and space, and behavior in the context of the thermal landscape.

In many ectotherms, variation in thermal ecology is the result of developmental plasticity, whereby conditions during embryonic development affect phenotypes in subsequent life stages. For example,

Drosophila were more cold-tolerant as adults if they had experienced low development temperatures as embryos (Gilbert and Huey, 2001). In amphibians, incubation temperature during the larval stage affects thermal performance curves of later life stages in the striped marsh frog (*Limnodynastes peronii*; Seebacher and Grigaltchik, 2014). Similarly, in wood frogs (*Rana sylvatica*), interactive effects of the temperatures experienced during early development affected swimming performance during the subsequent larval period (Watkins and Vraspir, 2006). In general, and as predicted by the environment-matching hypothesis, developmental plasticity is likely to be beneficial when conditions during early embryonic development match phenotypic values with the environmental conditions likely to be experienced by an individual in the future (e.g., Seebacher and Grigaltchik, 2014). That is, by setting an individual along a trajectory that is likely to optimize a phenotype in its environment, developmental plasticity during early life stages has the potential to ensure that the individual has the best possible "fit" to the environment in which it will find itself during later life stages. By

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Table 1

Standardized names, synonyms, symbols, and definitions for commonly measured thermal ecology traits.

Trait name, synonyms, and standardized symbols	Definition
Critical thermal maximum (CT_{max}, T_C, or T_{Crit})	The upper thermal limit on performance (as in Sinclair et al., 2016)
Critical thermal minimum (CT_{min}, T_C, or T_{Crit})	The lower thermal limit on performance (as in Sinclair et al., 2016)
Preferred temperature (T_p or T_{pref})	The temperature selected by an organism placed in a laboratory thermal gradient
Selected temperature (T_{sel})	
Thermal preferenda	
Thermal breadth	The width of the thermal performance curve (often CT_{max} - CT_{min})
Thermal performance optimum (T_{opt})	The temperature at which performance is maximized
Thermoregulatory precision ($T_b$precision)	The variance of mean selected temperatures

extension, when developmental plasticity results in phenotypes that are in the same direction as those favored by natural selection, such plasticity can be considered adaptive at the population level (Ghalambor et al., 2007). Alternatively, the environment experienced by later life stages may not be predictable based on the environment experienced during embryonic development. In such a case, developmental plasticity permanently matching an individual to the environment in which it developed as an embryo is likely to be maladaptive.

Reptiles have long been a model taxon for understanding how conditions during embryonic development affect phenotypes in subsequent life stages. The relative ease with which reptilian eggs can be incubated under controlled laboratory conditions has allowed researchers to empirically test the effects of temperature and hydric conditions on a diverse array of phenotypes across reptile taxa (Qualls and Shine, 1998). We now know that incubation conditions experienced by developing reptile embryos affect numerous traits including size, growth rate, morphology, locomotor performance, sex, immune functioning, behavior, and cognition in hatchlings and later life stages (e.g., Bull, 1980; Elphick and Shine, 1998; Freedberg et al., 2008; Les et al., 2009; Telemeco et al., 2010; Amiel and Shine, 2012; Ballen et al., 2015; Noble et al., 2018); furthermore, developmental plasticity in at least some of these traits has been observed across all four orders of extant reptiles. Much less research has focused on developmental plasticity in thermal ecology traits in reptiles. However, the fact that thermal ecology traits are developmentally plastic across widespread ectothermic taxa suggests that thermal ecology is likely developmentally plastic in at least some reptiles as well.

Here, we review the literature on developmental plasticity in thermal ecology traits in reptiles. We searched the published literature for experimental studies in which reptile eggs were incubated, or gravid females were housed, under different temperature or moisture regimes, and in which thermal ecology phenotypes were subsequently quantified in offspring. We used Google Scholar and Web of Science with the following search terms: temperature* AND incubat*, or development* AND plastic*, combined with one of the following: reptil*, squamat*, lizard*, snake*, chelon*, testudin*, turtle*, crocodil*, alligator*, sphenodon*, and tuatara*. Plasticity in thermally dependent traits (i.e., traits in which phenotypic values differ among individuals from different developmental temperatures because of the direct effects of temperature on those traits' developmental pathways) is reviewed extensively elsewhere (Deeming, 2004; Clusella-Trullas and Chown, 2014; Noble et al., 2018; Booth, 2018; While et al., 2018). Therefore, we focus exclusively on thermal ecology traits that are direct measures of an individual's thermal biology. We focus specifically on developmental plasticity, in which environmental conditions during early life stages (in reptiles, typically the egg or very early juvenile stages) shape an individual's subsequent thermal ecology phenotype. Our discussion includes instances where developmental plasticity may be irreversible (also known as developmental acclimation, as in Angilletta et al., 2006) or reversible (also known as reversible phenotypic plasticity, phenotypic flexibility, or phenotypic modulation; Smith-Gill, 1983; Wilson and Franklin, 2002; Seebacher, 2005). We summarize trends regarding which thermal ecology traits are developmentally plastic, in which

reptile taxa, and for how long developmentally plastic differences persist following hatching or birth. We also discuss the potential benefits of developmental plasticity in thermal ecology traits to individuals and populations. Finally, we suggest a variety of avenues for future research into the developmental plasticity of thermal ecology traits in reptiles.

1.1. Developmental plasticity in physiological and behavioral traits in reptiles

In reptiles, the traits associated with thermal ecology can be broadly divided into two categories. Physiological traits include measures such as an individual's thermal tolerance (i.e., critical thermal maximum [CT_{max}] and critical thermal minimum [CT_{min}]), thermal performance optima (T_{opt}), and thermal breadth. Behavioral traits include thermal ecology traits associated with thermoregulation (as in Gvoždík, 2018), such as preferred (T_{pref}) or selected (T_{sel}) body temperature (considered by some authors to be physiological traits), thermoregulatory precision (T_b precision), and time spent basking (see Table 1 for definitions).

Very few studies have investigated whether thermal ecology traits associated with physiology are developmentally plastic in reptiles (Table 2). Limited empirical evidence supports the presence of developmental plasticity in several physiological traits across reptile taxa. In particular, Chinese three-keeled pond turtle (*Chinemys reevessii*) hatchlings from eggs incubated at higher temperatures had higher critical thermal minimum temperatures (CT_{min}) than hatchlings from eggs incubated at cooler temperatures (Du et al., 2006). Similarly, rainforest sunskink (*Lamphropholis coggeri*) hatchlings from eggs incubated at cooler temperatures had lower CT_{min} than hatchlings from eggs incubated at warmer temperatures, but CT_{max} was unaffected by egg incubation temperature (Llewelyn et al., 2018). The opposite pattern was found in velvet geckos (*Amalosia lesueurii*), where hatchlings from eggs incubated at high temperature had lower CT_{max} but higher CT_{min} than hatchlings from eggs incubated at cooler temperatures (Dayananda et al., 2017). In the latter study, the relationship between egg incubation conditions and subsequent thermal tolerance seems to be mediated by hatching date: cooler-incubated eggs hatched later than warmer-incubated eggs, and therefore hatchlings from cooler incubation conditions encountered less thermally stressful environments than their warmer incubation counterparts (Dayananda et al., 2017).

In comparison to the number of studies on physiological traits in reptiles, considerably more research has assessed whether behavioral traits associated with thermal ecology are developmentally plastic (Table 2). To our knowledge, all such studies have involved traits associated with thermoregulatory behavior, such as selected or preferred temperature, or time spent basking. In addition, the experimental designs of all such studies included incubating eggs under controlled laboratory conditions at several different temperatures or humidity levels, and subsequently assessing thermoregulatory behavior of offspring in thermal gradients. In a few viviparous species, gravid females were maintained under controlled laboratory conditions and thermoregulatory behavior of their offspring was assessed after birth (Arnold et al., 1995; Blouin-Demers et al., 2000).

Table 2
Studies testing for developmental plasticity in physiological and behavioral thermal ecology traits in reptiles, whether developmental plasticity was detected, and if so, the age to which plastic differences persisted.

Trait	Order	Species	Developmentally plastic?	If plastic, persistence length	Reference
Physiological					
CT_{max}	Squamata	velvet gecko, *Amalosia lesueurii*	yes	only assessed in hatchlings	Dayananda et al. (2017)
CT_{max}	Squamata	rainforest sunskink, *Lamphropholis coggeri*	no	not plastic (tested hatchlings)	Llewelyn et al. (2018)
CT_{min}	Squamata	velvet gecko, *Amalosia lesueurii*	yes	only assessed in hatchlings	Dayananda et al. (2017)
CT_{min}	Squamata	rainforest sunskink, *Lamphropholis coggeri*	yes	plasticity disappeared in adults	Llewelyn et al. (2018)
CT_{min}	Testudinata	Chinese three-keeled pond turtle, *Chinemys reevessi*	yes	only assessed in hatchlings	Du et al. (2006)
Behavioral					
T_{pref}	Squamata	tiger snake, *Notechis scutatus*	yes	plastic at14 mo; unable to adjust at 15–16 mo	Aubret and Shine (2010)
T_{pref}	Squamata	northern watersnake, *Nerodia sipedon*	yes	only assessed in hatchlings	Blouin-Demers et al. (2000)
T_{pref}	Squamata	black rat snake, *Elaphe obsoleta*	no	not plastic (tested hatchlings)	Blouin-Demers et al. (2000)
T_{pref}	Squamata	garter snake, *Thamnophis elegans*	no	not plastic (tested hatchlings)	Arnold et al. (1995)
T_{pref}	Squamata	Cuban rock iguana, *Cyclura nubila*	no	not plastic (tested up to 16 mo)	Alberts et al. (1997)
T_{pref}	Squamata	western fence lizard, *Sceloporus occidentalis*	no	not plastic (tested up to 7 wk)	Buckley et al. (2007)
T_{pref}	Squamata	eastern fence lizard, *Sceloporus undulatus*	no	not plastic (tested hatchlings)	Warner and Andrews (2002)
T_{pref}	Squamata	jacky dragon, *Amphibolurus muricatus*	yes	only assessed in hatchlings	Esquerre et al. (2014)
$T_bprecision$	Squamata	western fence lizard, *Sceloporus occidentalis*	yes	plastic up to 7 wk	Buckley et al. (2007)
$T_bprecision$	Squamata	striped plateau lizard, *Sceloporus virgatus*	yes	only assessed in hatchlings	Qualls and Andrews (1999)
T_{set}	Squamata	three-lined skink, *Bassiana duperreyi*	no	not plastic (tested up to 90 d)	Du et al. (2010)
T_{set}	Squamata	veiled chameleon, *Chamaeleo calyptratus*	no	not plastic (tested hatchlings)	Andrews (2008)
T_{set}	Squamata	Bynoe's gecko, *Heteronotia binoei*	no	not plastic (tested hatchlings)	Andrewartha et al. (2010)
T_{set}	Squamata	*Anolis carolinensis*	yes	plasticity disappeared after 3 wk	Goodman and Walguarnergy (2007)
T_{set}	Squamata	Madagascar ground gecko, *Paroedura pictus*	yes	plastic at 3 wk	Blumberg et al. (2002)
T_{set}	Squamata	striped plateau lizard, *Sceloporus virgatus*	yes	only assessed in hatchlings	Qualls and Andrews (1999)
T_{set}	Testudinata	snapping turtle, *Chelydra serpentina*	yes	plastic at 6 mo	O'Steen (1998)
T_{set}	Testudinata	painted turtle, *Chrysemys picta*	yes	plastic at 10–11 mo	Tamplin et al. (2011)
T_{set}	Testudinata	desert tortoise, *Gopherus agassizii*	no	not plastic (tested at 40 d)	Spotila et al. (1994)
T_{set}	Crocodilia	Siamese crocodile, *Crocodylus siamensis*	no	not plastic (tested hatchlings)	Lang (1987)
T_{set}	Rhynchocephalia	tuatara, *Sphenodon punctatus*	no	not plastic (tested at 3 mo)	Nelson et al. (2017)
Time spent basking	Squamata	three-lined skink, *Bassiana duperreyi*	yes	only assessed in hatchlings	Shine (1995)
Time spent basking	Squamata	three-lined skink, *Bassiana duperreyi*	yes	only assessed in hatchlings	Shine and Harlow (1996)
Time spent basking	Testudinata	snapping turtle, *Chelydra serpentina*	yes	plastic at 6 mo	Rhen and Lang (1999)

In the lepidosaur lineage (i.e., snakes, lizards, and tuatara), there is mixed support regarding whether selected temperature is developmentally plastic. Most studies on the effects of egg incubation temperature or humidity on thermoregulatory behavior in lizards found that selected temperature was not developmentally plastic in the resulting hatchlings (Alberts et al., 1997; Warner and Andrews, 2002; Buckley et al., 2007; Andrews, 2008; Andrewartha et al., 2010; Du et al., 2010). However, a few studies observed developmentally plastic differences in selected temperatures in hatchlings up to three weeks old (e.g., Blumberg et al., 2002). For example, lizards incubated at cooler temperatures selected higher temperatures in a laboratory gradient than lizards incubated at warmer temperatures in some studies (Qualls and Andrews, 1999; Goodman and Walguarnery, 2007). In contrast, jacky dragon (*Amphibolurus muricatus*) hatchlings from eggs incubated at intermediate temperatures had cooler and more stable temperature selection than hatchlings from eggs incubated at cooler or warmer temperatures (Esquerré et al., 2014). Additionally, time spent basking was developmentally plastic in the three-lined skink (*Bassiana duperreyi*), in that hatchlings from cooler incubation conditions spent more time basking than those from warmer incubation conditions (Shine, 1995; Shine and Harlow, 1996). Interestingly, a study on western fence lizards (*Sceloporus occidentalis*) found that selected temperature was not affected by egg incubation temperature, but that thermoregulatory precision (i.e., how closely an individual is able to maintain its body temperature to its preferred temperature) was developmentally plastic because warm-incubated juveniles thermoregulated more precisely than cool-incubated juveniles (Buckley et al., 2007). Thermoregulatory precision was also found to be developmentally plastic in the congener *S. virgatus* (Qualls and Andrews, 1999). Fewer studies have been conducted in snakes, but these again provide mixed support for developmental plasticity in behavioral traits associated with thermal ecology. Preferred body temperatures were affected by egg incubation temperature, and therefore developmentally plastic, in neonates of the viviparous tiger snake (*Notechis scutatus*; Aubret and Shine, 2010) and northern watersnake (*Nerodia sipedon*; Blouin-Demers et al., 2000). However, preferred body temperatures were not affected by egg incubation temperature in a viviparous garter snake (*Thamnophis elegans*; Arnold et al., 1995) or the oviparous black rat snake (*Elaphe obsoleta*; Blouin-Demers et al., 2000). Finally, in tuatara (*Sphenodon punctatus*), temperature selection by hatchlings was not developmentally plastic (Nelson et al., 2017).

Few studies have assessed developmental plasticity in behavioral traits in turtles or crocodilians. Temperature selection by hatchling painted (*Chrysemys picta*; Tamplin and Cyr, 2011) and snapping (*Chelydra serpentina*; O'Steen, 1998) turtles was negatively correlated with egg incubation temperature, as was time spent basking by hatchling snapping turtles (Rhen and Lang, 1999). In contrast, neither incubation temperature nor humidity affected temperature selection by hatchling desert tortoises (*Gopherus agassizii*; Spotila et al., 1994). We are aware of only one study on effects of egg incubation conditions on thermoregulatory behavior in crocodilians, but because sex and temperature were confounded in this study of a species with temperature-dependent sex determination, observed differences in temperature selection may be due to sex differences in preferred body temperature rather than plasticity in behavioral thermoregulation itself (Lang, 1987).

1.2. How long do plastic differences persist?

Effects of incubation conditions on offspring phenotypes in reptiles are often studied at the hatchling stage, as individual hatchlings can be tied directly to the controlled laboratory conditions in which they incubated as an egg. However, studies that continue to follow individuals over time into later life stages are particularly valuable because they provide insight regarding how long throughout ontogeny differences in developmentally plastic traits persist. Furthermore, such study designs allow us to test whether developmental plasticity is beneficial to an

individual later in life. Riska (1991) hypothesized that maternal effects, such as incubation environment, should be strongest early in life and then fade over time. Although such a pattern is sometimes observed (Buckley et al., 2007; Goodman and Walguarnery, 2007), developmentally induced phenotypic differences in reptiles may persist for months or even years (e.g., Tousignant and Crews, 1995; Elphick and Shine, 1998), or differences may become apparent later in ontogeny that were not present at hatching (Goodman, 2008).

The majority of studies on developmental plasticity in thermal traits in reptiles have assessed the presence of plasticity only during the early hatchling stage (e.g., Arnold et al., 1995; Du et al., 2006; Buckley et al., 2007; Nelson et al., 2017). However, a few studies have tested for developmental plasticity later in ontogeny, and most of these studies found that plasticity in thermal traits persists into life stages beyond that of the neonate. In turtles, developmental plasticity in temperature selection may be evident months after hatching. For example, differences in temperature selection by hatchling snapping turtles incubated at different temperatures were evident following the first overwintering period at six months of age (O'Steen, 1998). Similarly, painted turtle hatchlings incubated at different temperatures selected different water temperatures at 10–11 months of age (Tamplin and Cyr, 2011). Because temperature selection by hatchling turtles affects growth rate (e.g., Rhen and Lang, 1999), these studies suggest that egg incubation temperature can mediate hatchling growth rate via its effects on hatchling temperature selection. In squamates, developmentally induced differences in thermal ecology traits vary in their persistence past the neonate stage. Aubret and Shine (2010) found that juvenile tiger snakes exhibited developmental plasticity in thermoregulatory behavior at 14 months of age. In contrast, differences in CT_{min} resulting from different egg incubation temperatures were apparent in rainforest sunskink hatchlings at one month of age, but had disappeared when the same individuals were re-assessed for CT_{min} as adults (Llewelyn et al., 2018).

1.3. How might developmental plasticity in thermal tolerance be beneficial?

Generally, phenotypic plasticity is thought to benefit individuals by producing the phenotype that optimizes the individual's performance, survival, and/or fitness in the environment in which it finds itself (West-Eberhard, 1989). In the case of developmental plasticity specifically, if environmental conditions during early embryonic development are predictive of the environmental conditions likely to be experienced later in life, then it would make sense for specific environmental cues during early development to induce a particular phenotype that would benefit the individual later in life, as predicted by the environment-matching hypothesis (Seebacher and Grigaltchik, 2014). Currently, studies on the potential benefits of developmental plasticity in thermal ecology traits in reptiles are sparse.

Most studies testing for developmental plasticity in thermal traits in reptiles have only examined very early life stages, which precludes conclusions on whether developmental plasticity in thermal traits increases an individual's survival and/or reproductive output relative to other individuals. One study found indirect evidence suggesting that developmental plasticity in a thermal trait may be beneficial later in life. In the viviparous tiger snake, juvenile snakes raised from the neonate stage under different temperature treatments adjusted their thermoregulatory behavior appropriately to maintain similar body temperatures regardless of rearing condition at 14 months of age (Aubret and Shine, 2010). However, the snakes were unable to adjust their thermoregulatory behavior appropriately at 16 months of age following a sudden switch to more variable temperatures, suggesting that a mismatch between environmental conditions during early development and the environment experienced later in life can be detrimental if thermoregulatory behaviors are "programmed" by conditions experienced during early development (Aubret and Shine, 2010).

Phenotypic plasticity may be beneficial at the population level by facilitating adaptation to local conditions. For example, if a particular

environment induces a plastic change in a phenotype in the same direction as that favored by natural selection in that environment, then the plastic response could be considered adaptive and may be the first step towards adaptive evolution in the population (e.g. West-Eberhard, 2003; Ghalambor et al., 2007). However, recent empirical evidence suggests that it is actually non-adaptive phenotypic plasticity, rather than adaptive plasticity, that potentiates evolution because non-adaptive plasticity increases the strength of directional selection (Ghalambor et al., 2015). Therefore, plastic responses in an individual's phenotype in response to environmental conditions may benefit the individual over the short term, but may actually constrain adaptive evolution in the population across generations and over longer timescales (Ghalambor et al., 2015). The potential benefits of developmental plasticity in thermal preferences and tolerances to individuals and across generations were recently tested in jacky dragons (*Amphibolurus muricatus*). Adult lizards were maintained under two different thermal regimes differing in availability of basking opportunities, and subsequently offspring from each parental environment were maintained under each of the two thermal regimes, allowing the effects on offspring thermal ecology phenotypes due to parental environment vs. early developmental environment to be parsed (So and Schwanz, 2018). Juveniles whose parents had greater basking opportunities preferred higher body temperatures but did not exhibit greater thermal tolerance, while individuals who themselves were raised with greater basking opportunities demonstrated higher thermal tolerance (So and Schwanz, 2018). This study demonstrates that thermal ecology traits of individual lizards are determined by the thermal environment experienced by their parents, as well as during their own early development, which extends the environment-matching hypothesis for developmental plasticity trans-generationally (So and Schwanz, 2018). Clearly, far more research is needed on the potential benefits to individuals, and the role in adaptive evolution, of developmental plasticity in thermal ecology traits in reptiles.

2. Discussion

Phenotypic plasticity is a mechanism by which an individual can express the most advantageous phenotype, given its genotype, in the environment in which it finds itself. Developmental plasticity is a specific form of phenotypic plasticity that occurs when conditions experienced during early development affect an individual's phenotype, and is hypothesized to be a mechanism by which individuals' phenotypes later in life are "matched" to their environment. Reptiles in particular are well-known for having a wide variety of developmentally plastic traits, including traits associated with behavior, morphology, performance, and even sex (e.g., Bull, 1980; Elphick and Shine, 1998; Ballen et al., 2015; While et al., 2018). Yet, relatively little is known about the extent to which traits associated with thermal ecology are developmentally plastic in reptiles.

There is mixed support for whether behavioral traits associated with thermal ecology, and particularly preferred or selected temperature, are developmentally plastic in the lepidosaur lineage. Several potential explanations could account for the inconsistent patterns across lizards and snakes. First, preferred temperatures may not be the most appropriate behavioral trait to measure. Most studies that have assessed effects of conditions during development on subsequent thermal ecology use thermal gradients to quantify temperature selection. Thermal gradients may not provide a sufficient range of environmental conditions to adequately measure fine-scale variation in thermal ecology traits, and preferred body temperatures or selected environmental temperatures may be affected by environmental factors that are difficult to control for experimentally. Instead, traits such as thermal tolerance, optimum performance temperature, and/or thermal breadth may vary more with conditions during development than preferred temperature per se. In particular, studies that assessed the behavioral trait of time spent basking, rather than preferred body temperature, detected

developmental plasticity in basking behavior (Shine, 1995; Rhen and Lang, 1999). Proportion of time spent basking is known to be a behaviorally plastic trait in lizards (Refsnider et al., 2018), and therefore may provide more insight into developmental plasticity of thermal ecology than preferred or selected temperature.

An alternate explanation for why temperature selection is not consistently developmentally plastic in lepidosaurs is that preferred temperature may have become canalized in some species and therefore is no longer related to conditions during embryonic development. Stabilizing selection should result in the evolution of developmental processes that robustly produce a given phenotype regardless of incubation temperature. Although there are too few studies to make any strong inference, one existing study appears to suggest that behavioral thermoregulation is more canalized than is thermal physiology (e.g., Du et al., 2006). This is perhaps surprising, as plasticity in behavior is expected to evolve more easily than plasticity in physiology (West-Eberhard, 1989), but could indicate that canalization of behavior reduces the variance in thermal regimes under which physiological functions need to be maintained. It is possible that detecting developmental plasticity in thermal ecology traits associated with behavior is particularly difficult because other thermally dependent traits, such as growth rate or size, are also dependent on thermal conditions during incubation, and these traits confound subsequent thermoregulatory behaviors, which are the target of many of the studies reviewed here. Finally, variation in preferred temperature may simply be tied to overall genetic variation among populations, and may reflect local adaptation rather than developmental plasticity. More research is clearly needed on thermal ecology traits in lepidosaurs to better understand the conditions that predict developmental plasticity vs. canalization in behavioral and physiological traits.

Even in species where thermal ecology traits are developmentally plastic, we know very little about the role played by plasticity throughout the lifespan of an individual, and even less about the adaptive significance (or lack thereof) of developmental plasticity. Theory predicts that developmentally plastic differences in phenotypes resulting from different environmental conditions during embryonic development should disappear relatively early in ontogeny as subsequent developmental systems become impacted more by the current environment than that experienced during embryonic development (Riska, 1991; Deeming, 2004), and such a pattern was recently demonstrated empirically in another ectotherm, the common frog (*Rana temporaria*; Enriquez-Urzelai et al., 2019). This fading over time of incubation-environment effects might be more pronounced in reptiles characterized by a slow pace-of-life (i.e., later maturity, longer lifespan) because early-life effects on phenotypes may be offset by development later in ontogeny (Noble et al., 2018). In thermal ecology traits in reptiles, this prediction is sometimes supported, but developmentally plastic differences may also persist for long periods, and occasionally even into adulthood. Impacts of incubation temperature persisted at least one year post-hatching in traits not related to thermal ecology, suggesting that incubation temperature has the potential to affect an individual's survival later in life by mediating traits such as behavior, physiology, morphology, and performance (Noble et al., 2018). Moreover, selection for thermal ecology traits such as thermal tolerance may differ across life stages (Law, 1991; Lockwood et al., 2018), such that developmental plasticity optimizes an individual's mean lifetime phenotype at the expense of failing to perfectly match phenotype with environment during a particular life stage. The occasional observation of developmental plasticity persisting late into an individual's lifespan suggests that in such instances, environmental conditions during embryonic development play a profound role in an individual's developmental trajectory, and likely impact the individual's survival and reproductive fitness. Critically, however, we cannot assess whether developmental plasticity is adaptive if we only test for developmental plasticity in thermal ecology traits at the hatchling stage.

2.1. Future research directions

We are only just beginning to understand how conditions early in embryonic development affect thermal ecology traits associated with physiology and behavior. Reptiles are excellent organisms for such research because of the relative ease with which eggs can be maintained under controlled laboratory settings, and due to the wide variety of phenotypic traits influenced by incubation conditions in ectotherms. Here, we suggest several avenues for future research that will advance our understanding of developmental plasticity in reptilian thermal ecology. These avenues can be categorized under three broad headings: considering a broader range of developmental conditions, examining traits associated with cold-tolerance, and assessing the benefits of developmental plasticity at the individual and population scales.

2.1.1. Expansion of developmental conditions studied

First, we need to broaden what we consider under the heading of "developmental conditions." We know that, like mean incubation temperatures, variance in incubation temperature is important in determining a variety of phenotypes in reptiles (e.g., Warner and Shine, 2011), which has implications for extrapolating results of controlled laboratory incubation experiments to natural nests that likely experience substantially more fluctuation in environmental conditions. We also know that, in non-thermal ecology traits, the effect of warmer incubation temperatures depends on both the overall magnitude of temperature increase, as well as the starting temperature (Noble et al., 2018). However, almost nothing is known about the effects of temperature variance during early development on subsequent thermal ecology traits in reptiles. For example, how does temperature variance during egg incubation affect the magnitude or persistence length of developmental plasticity in thermal traits? Do the benefits of developmental plasticity to an individual later in life correlate with the magnitude of temperature variance experienced during early development, for example by widening the thermal tolerance breadth of individuals that developed in a highly variable environment? Furthermore, temperature variance tends to be much greater in temperate compared to tropical environments, and thermal tolerances tend to be broader in ectotherms from more variable or extreme environments compared to conspecifics from environments that are stable and thermally moderate (Gilbert and Huey, 2001; Schaefer and Ryan, 2006). Therefore, the relative impacts of an increase in magnitude of incubation temperature variance, particularly in the context of climate change, could differ substantially for tropical compared to temperate ectotherms (Kearney and Porter, 2009; Logan et al., 2015; While et al., 2018).

To date, most studies on developmental plasticity in reptiles have focused on oviparous species because eggs can easily be incubated under controlled laboratory conditions, whereas environmental conditions during embryonic development are more difficult to control in viviparous species where they are confounded by maternal behavior. Nevertheless, there is some evidence that developmental plasticity in thermal traits occurs in viviparous reptiles as well as oviparous taxa (Blouin-Demers et al., 2000; Aubret and Shine, 2010). Given that females of some viviparous species manipulate the thermal environment experienced by their developing offspring during pregnancy in ways that enhance the fitness of their offspring (e.g., Shine, 1995; Webb et al., 2006) - a clear demonstration of developmental plasticity in thermally-dependent traits - it seems likely that such maternal manipulation would also affect thermal ecology traits. Finally, the studies reviewed here focused almost exclusively on the effects of environmental conditions experienced during the egg stage. Can conditions experienced during the neonate or early hatchling stage also affect the trajectory of an individual's future thermal ecology? That is, can developmental plasticity be induced by conditions during early ontogeny exclusive of embryonic development? So and Schwanz (2018) study on thermal tolerance of juvenile jacky dragons provides some evidence that it can.

2.1.2. Consideration of cold-tolerance

We also need to expand our research on thermal traits to include traits associated with cold-tolerance, as well as heat-tolerance. Cold-tolerance is rarely considered in studies of reptile thermal ecology, likely because the majority of reptile thermal ecology studies have been conducted in tropical species that spend most of their time in climates with temperatures near their CT_{max}, and rarely if ever experience cold temperatures (e.g., Kearney and Porter, 2009; Sinervo et al., 2010; Logan et al., 2015). However, cold-tolerance is important in determining species' range limits in temperate species in general and montane species in particular (StClair and Gregory, 1990; Mitchell et al., 2017). Furthermore, cold-tolerance is critically important in the context of climate change because, although climate change is predicted to increase temperatures globally, in many areas winters are predicted, paradoxically, to become colder and drier (Jylhä et al., 2008; Logan et al., 2014). Colder winter conditions combined with less snow-cover will likely pose a substantial risk to hibernating species that depend on the insulative properties of a thick snowpack for overwinter survival (Brown and DeGaetano, 2011; Pauli et al., 2013). Therefore, developmental plasticity for traits associated with cold-tolerance would be beneficial if it successfully matched an individual's cold-tolerance to its environment later in life.

We know that in at least one turtle and two lizards, CT_{min} is developmentally plastic (Du et al., 2006; Dayananda et al., 2017; Llewelyn et al., 2018). Other studies are now beginning to show that cold-tolerance and CT_{min} should actually evolve faster than CT_{max}, possibly because behavioral thermoregulation can buffer ectotherms against selection on heat-tolerance but is less effective at buffering against selection on cold-tolerance (e.g., Kolbe et al., 2014; Muñoz et al., 2014). Therefore, it seems likely that traits associated with cold-tolerance are affected by environmental conditions during development, and should exhibit developmental plasticity. Furthermore, traits associated with cold-tolerance might exhibit a greater magnitude of developmental plasticity in viviparous compared to oviparous reptiles (as in Webb et al., 2006), and in species from temperate compared to tropical climates (Kearney and Porter, 2009; Logan et al., 2015).

2.1.3. Assessment of adaptive significance

Finally, there is a critical need to assess the benefits of developmental plasticity in thermal ecology traits at the individual scale, and its adaptive significance at the population scale, in reptiles (also see While et al., 2018). To address this question, we need to understand the environmental conditions most likely to select for developmental plasticity in physiological or behavioral traits. It is possible that incubation conditions experienced during embryonic development "set" an individual's thermal tolerance for life, which should be beneficial when incubation conditions are also predictive of environmental conditions that would subsequently be experienced by later life stages (e.g., Weisrock and Janzen, 1999). Environments where incubation conditions reliably predict conditions experienced later in ontogeny may be more likely in, for example, tropical rather than temperate regions, or in species that tend to be habitat specialists rather than generalists (Kassen, 2002; Kearney and Porter, 2009; Logan et al., 2015; Lockwood et al., 2018). Importantly, these scenarios assume that, when developmental plasticity is adaptive, it improves the reproductive success of plastic individuals. However, it is possible that the fitness benefits of adaptive plasticity may be expressed for only a brief period during ontogeny, rather than manifested as a relative increase in lifetime reproductive success (e.g., Van Buskirk, 2002). If developmental plasticity is beneficial during a particular "window" but not necessarily over an individual's entire lifetime, this would require identification and fitness testing of developmental plasticity during that specific period for the species and trait of interest.

Alternatively, there are several situations under which developmental plasticity in physiological or behavioral traits may not be beneficial. First, if incubation conditions "set" an individual's thermal

tolerance later in ontogeny, but do not reliably predict the subsequent environment experienced by an individual, then developmental plasticity for thermal tolerance is unlikely to be advantageous and may, in fact, be maladaptive (e.g., Aubret and Shine, 2010). Second, phylogenetic history and selection pressures acting in a taxon's recent evolutionary past may affect the magnitude of developmental plasticity for physiological or behavioral traits that can be expressed at present (e.g., Caldwell et al., 2017); however, because phylogenetic effects likely differ substantially across traits (Losos, 2011), tests for phylogenetic effects may be necessary for each trait under consideration. Finally, developmental plasticity for some physiological or behavioral traits may not be under selection at all, but instead could simply be a versatile response mounted by individuals triggered by a particular environmental cue.

2.1.4. Study design considerations

Addressing the question of how developmental plasticity in thermal ecology traits is beneficial in reptiles requires study designs that are more complex than controlled egg incubation experiments followed by measurements of hatchling phenotypes. For example, controlled egg-incubation experiments using common-garden or reciprocal transplant designs could be followed by an extended period where offspring are released either into mesocosms or back into the wild (as in Andrews et al., 2000). Such a design would allow for subsequent recapture of marked individuals to determine whether individuals from different incubation regimes continue to exhibit differences in thermal ecology traits. Furthermore, this design would allow researchers to detect and quantify the magnitude of natural selection acting on developmental plasticity in thermal traits. Several studies have recently used a similar design to quantify selection on thermal traits in wild populations (e.g., Gilbert and Miles, 2017; Refsnider et al., 2018). Study designs that follow individuals from different developmental environments over their lifetimes, and quantify developmentally plastic trait values and reproductive success of those individuals throughout ontogeny, are critical for elucidating both the benefits of developmental plasticity in thermal ecology traits to individuals, and the adaptive significance to populations.

Reptiles have become model study organisms for research on the effects of incubation conditions on hatchling phenotypes because it is relatively straightforward to incubate reptile eggs under controlled laboratory conditions. However, attempts to determine the effects of egg incubation conditions on phenotypes of later life stages have historically been limited by the difficulty of individually marking or tracking most juvenile reptiles. Without some method of following specific individuals throughout ontogeny, it has been almost impossible to determine whether developmental plasticity in thermal ecology traits persists beyond the hatchlings stage, and if so, whether such plasticity is beneficial later in life. Fortunately, advances in marking and tracking methods are now allowing us to overcome these historical limitations. In most cases, juvenile reptiles can now be easily and permanently marked, which allows for future identification of individuals. In addition, innovations in miniature sensor technology, such as decreased battery weight, will allow data loggers and transmitters to be attached to smaller, lighter animals (reviewed in Wilmers et al., 2015). The ability to mark and track small and potentially juvenile animals will facilitate data collection and continuous monitoring of individual animals in the wild, thereby allowing us to follow individuals from known developmental regimes into later life stages and under natural conditions, and to begin to understand the individual benefits and adaptive significance of developmental plasticity.

3. Conclusions

How environmental conditions during embryonic development shape thermal ecology traits is an important area of study in ectotherms in general, and reptiles specifically. Overall, physiological traits seem

more likely to have a developmentally plastic basis than behavioral traits. Where developmentally plastic differences are detected, their persistence length into later life stages differs; however, most studies have only tested for developmental plasticity during the neonate stages, and have not assessed persistence length. Without knowing how long developmentally plastic differences last into ontogeny, our ability to determine whether developmental plasticity is adaptive is limited. Researchers should now endeavor to determine the adaptive significance of developmental plasticity in thermal traits.

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