Thermal adaptation revisited: How conserved are thermal traits of reptiles and amphibians?

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Abstract

Ectothermic animals, such as amphibians and reptiles, are particularly sensitive to rapidly warming global temperatures. One response in these organisms may be to evolve aspects of their thermal physiology. If this response is adaptive and can occur on the appropriate time scale, it may facilitate population or species persistence in the changed environments. However, thermal physiological traits have classically been thought to evolve too slowly to keep pace with environmental change in longer-lived vertebrates. Even as empirical work of the mid-20th century offers mixed support for conservatism in thermal physiological traits, the generalization of low evolutionary potential in thermal traits is commonly invoked. Here, we revisit this hypothesis to better understand the mechanisms guiding the timing and patterns of physiological evolution. Characterizing the potential interactions among evolution, plasticity, behavior, and ontogenetic shifts in thermal physiology is critical for accurate prediction of how organisms will respond to our rapidly warming world. Recent work provides evidence that thermal physiological traits are not as evolutionarily rigid as once believed, with many examples of divergence in several aspects of thermal physiology at multiple phylogenetic scales. However, slow rates of evolution are often still observed, particularly at the warm end of the thermal performance curve. Furthermore, the context-specificity of many responses makes broad generalizations about the potential evolvability of traits tenuous. We outline potential factors and considerations that require closer scrutiny to understand and predict reptile and amphibian evolutionary responses to climate change, particularly regarding the underlying genetic architecture facilitating or limiting thermal evolution.

KEYWORDS
amphibians, climate change, conservatism, evolution, plasticity, reptiles, thermal physiology

1 | INTRODUCTION

Temperature dictates the pace of nearly all biochemical processes, whereas temperature variation is a nearly ubiquitous feature of biological systems (Angilletta, 2009; Hochachka & Somero, 2002).

Yet organisms display a broad array of mechanisms to maintain functionality even as biochemical and biophysical parameters shift across space and time. Ectothermic animals, for example, utilize their external environments to regulate body temperature as they lack sources of internal heat production in the manner of endotherms.

Though reliance on external sources for temperature regulation is generally energetically efficient, it does make ectothermic organisms particularly vulnerable to rapidly warming global temperatures and ongoing environmental change (Deutsch et al., 2008; Huey et al., 2009; Li et al., 2013; Sinervo et al., 2010). Organismal thermal biology reflects the combined, nonadditive interactions of myriad behavioral and physiological processes across different scales of biological organization. Here, we consider the evolution of thermal traits in amphibians and nonavian reptiles (hereafter, reptiles), two vertebrate ectotherm lineages of key concern under climate change (Diele-Viegas & Rocha, 2018; Huey et al., 2009, 2012; Rohr et al., 2008; Whitfield et al., 2007).

The field of evolutionary physiology has a rich conceptual history dating back to the mid-20th century (e.g., Bartholomew, 1964; Bogert, 1949). One of the core questions of this field is the degree to which physiological traits are phylogenetically labile or conserved (Angilletta et al., 2002; Hertz et al., 1983). The classical view, based primarily on work in reptiles, is that thermal traits evolve slowly (i.e., are evolutionarily conserved). This concept emerged from seminal studies showing that lizards in different thermal environments have similar body temperatures due to behavioral thermoregulation (i.e., behavioral plasticity; Bogert, 1949; Cowles & Bogert, 1944). By choosing microclimates that match their ancestral preferences and optimize their physiological functions, species can dampen the strength of natural selection and slow rates of trait evolution (Bogert, 1949; Huey et al., 2003; Hutchison & Dupre, 1992). Several influential studies found little or no divergence in the thermal physiology of closely related taxa from disparate thermal habitats, lending support to the idea that evolution in physiological traits is generally sluggish (e.g., Crowley, 1985; Hertz et al., 1983; van Damme et al., 1990). More recently, evidence consistent with phylogenetic conservatism for some thermal traits (frequently heat tolerance) has come from comparative studies of evolutionary rates at broader macroevolutionary time scales (Araújo et al., 2013; Grigg & Buckley, 2013; Muñoz et al., 2014; Salazar et al., 2019).

Yet many issues related to this idea remain unresolved. On conceptual grounds, it is worth considering what is meant by evolutionary "lability" or "conservatism," terms which have not been defined consistently in the literature. The early, seminal studies in this field pre-date the advent of modern phylogenetics; as such, many early approaches lacked a rigorous comparative framework. "Lability" and "conservatism" represent opposite ends of an evolutionary continuum: testing inferences about these patterns requires an appropriate comparative framework and null hypothesis. Another issue relates to the validity of the concept on empirical grounds. Several studies in the past decade demonstrate evolutionary lability in reptile and amphibian thermal traits (Gilbert & Miles, 2019b; Herrando-Pérez et al., 2020). For example, several species of *Pristimantis* frogs display similar rates of evolutionary change in both CT_{max} and CT_{min} when accounting for microclimatic temperature variations (Pintanel et al., 2019), suggesting that CT_{max} evolution might not be as conserved as previously thought (Araújo et al., 2013; Gunderson et al., 2018; Hoffmann et al., 2013). Lability in thermal traits has also been

identified in other taxa, including newts and numerous lizard species (Clusella-Trullas & Chown, 2014; Domínguez–Guerrero et al., 2020; Gvoždík, 2012). Research in the past few decades has robustly demonstrated that physiological diversity is actually a mosaic of evolutionary patterns and rates; the key question resides in identifying the processes sculpting these differences in the tempo and mode of physiological evolution. Understanding the mechanisms guiding the timing and patterns of physiological evolution is crucial for accurate predictions of how organisms will respond to global change (Catullo et al., 2019; Chown et al., 2010; Hoffmann & Sgro, 2011; Huey et al., 2012; Merilä & Hendry, 2014; Moritz & Agudo, 2013; Muñoz & Moritz, 2016; Urban et al., 2014). In this review, we synthesize our understanding of the evolution of reptile and amphibian thermal traits. The evolutionary patterns we observe reflect a number of key phenomena including behavioral buffering of selection, developmental plasticity and ontogenetic shifts, the underlying genetic architecture of physiological phenotypes, and the ecological context within which thermal physiology does, or does not, evolve. We hope to provide an updated synthesis of recent work that can inform future studies of thermal adaptation in reptiles and amphibians. We argue that the field should continue and expand work directed toward discovering the mechanisms that guide the tempo and mode of physiological evolution at micro- and macroevolutionary scales.

2 | THE ROLE OF THERMOREGULATORY BEHAVIOR

Thermoregulatory behavior is the primary means by which ectotherms control their body temperatures (Cowles & Bogert, 1944; Huey, 1982). To achieve their preferred body temperatures, organisms may strategically shuttle between different microhabitats, alter their activity times, adjust body posture and orientation, or take advantage of retreat sites (e.g., Bakken, 1989; Gunderson & Leal, 2016; Hertz, 1992; Huey et al., 1989; Kearney et al., 2009). By allowing organisms to preferentially seek out thermal conditions to which they are adapted, thermoregulatory behavior has the power to buffer organisms against natural selection. When translated over long time periods, behavioral buffering is predicted to slow the pace of physiological evolution (Bartholomew, 1964; Bogert, 1949; Brandon, 1988; Wake et al., 1983). In homage to Charles Bogert, who pioneered this idea, this phenomenon (a regulatory behavior slowing evolutionary response) has been coined the "Bogert effect" (Huey et al., 2003).

When organisms encounter new selective pressures they are expected to adapt to the extent that traits under selection have sufficient heritable variation and are unconstrained by genetic correlations. Many empirical studies speak to the potential for adaptation to be swift (Hairston et al., 2005; Hendry & Kinnison, 1999). Yet, paradoxically, nature is also rife with examples of long-term niche stasis (Wiens & Graham, 2005; Wiens et al., 2010). The Bogert effect can provide a proximate mechanism for niche conservatism, as buffering behaviors are expected to slow physiological adaptation to

novel or changing environments, resulting in temporal debts in adaptation to climate. For example, plethodontid salamanders from eastern North America exhibit precise behavioral preferences for their ancestral climatic conditions (Farallo et al., 2018). This results in remarkably slow adaptation to climate, incurring a phylogenetic lag (a "slowness" in adaptation) on the scale of millions of years (Farallo et al., 2020). In other words, buffering behaviors can stymie rates of physiological adaptation to novel environmental pressures (e.g., Buckley et al., 2015; Logan et al., 2019; Muñoz & Bodensteiner, 2019).

The Bogert effect is not equally effective across all contexts, however. The efficacy of the Bogert effect depends, in large part, on the microclimatic structure of the environment that organisms occupy during their activity period. For example, diurnal reptiles often encounter thermally heterogeneous daytime environments essential for precise thermoregulation (Kearney et al., 2009; Sears et al., 2016). In general, thermally heterogeneous environments with short shuttle distances between thermal patches facilitate thermoregulation (Huey, 1974; Sears et al., 2016). At night and in cold habitats, however, refuges from selection on lower limits might be restricted, thus limiting thermoregulatory potential and the power of the Bogert effect (Leal & Gunderson, 2012; Muñoz & Bodensteiner, 2019). In other cases, organisms must balance trade-offs inherent in selecting retreat sites that buffer against warm or cold temperatures (Huey et al., 1989; Kearney, 2002; Sabo, 2003). Moreover, in temperate latitudes, many ectotherms become inactive during the winter, meaning that thermoregulatory behavior is limited in its potential to buffer individuals against lethally cold temperatures. This might explain why CT_{min} seems to evolve more quickly than CT_{max} (Moore et al., 2018; Muñoz et al., 2014) and why the geographic ranges of ectotherms may be more limited by minimum temperatures than by maximum temperatures (St. Clair & Gregory, 1990; Sunday et al., 2011).

In addition to the structure of the thermal environment, behavioral thermoregulation imposes costs (Brewster, Sikes, & Gifford, 2013; Huey & Slatkin, 1976; Huey, 1974; Schwanz et al., 2018). These costs, such as greater exposure to predation, can determine the efficacy and the strength of the Bogert effect. For example, Caribbean anoles are well-known for their rapid radiation into distinct structural niches: release from predators (i.e., ecological opportunity) is thought to have facilitated such rapid and prolific morphological diversification (Losos, 2009; Mahler et al., 2010). Release from predators, however, also lowers the costs of thermoregulation. The Bogert effect is stronger in island anoles than in their mainland counterparts; specifically, island lizards are more effective thermoregulators and, correspondingly, exhibit slower rates of physiological evolution, than their mainland counterparts (Salazar et al., 2019). We note, however, that habitat structure (in addition to predation pressure) may also differ among mainland and island environments, which may also contribute to the different costs of thermoregulation. Finally, the Bogert effect, while serving to slow evolution, might require behavioral shifts in habitat use that impel evolution in other traits. For example, effective thermoregulation at

high elevation in anoles requires a switch in microhabitat use from trees to boulders. This shift concomitantly results in morphological evolution and shifts in display behavior, demonstrating that any shift to compensate for the thermal environment likely has cascading selective consequences on other aspects of the phenotype. Correspondingly, the benefits of physiological buffering are counterbalanced against potential selective pressures on other aspects of the phenotype (Boronow et al., 2018; Muñoz & Losos, 2018). Overall, existing evidence suggests that thermoregulatory behavior is a plastic trait that can be immediately adjusted based on prevailing environmental conditions (e.g., Caldwell et al., 2017; Domínguez–Guerrero et al., 2019; Ortega et al., 2016a; Refsnider et al., 2018). Nonetheless, behavioral plasticity can be confounded by a number of variables, such as season, life stage, hydric environment, reproductive condition, or health status (A. E. Conover et al., 2015; Gatten, 1974; Isaac & Gregory, 2004; Rozen-Rechels et al., 2019; Ryan et al., 2016; Sannolo et al., 2019; van Damme et al., 1987).

Females can also exert behavioral control over the thermal conditions to which their offspring are exposed during incubation and through strategic nest-site choice (Arnold & Peterson, 2002; Aubret & Shine, 2010; Blouin-Demers et al., 2000; reviewed in Refsnider & Janzen, 2010), which, in turn, affects all thermally dependent processes in offspring (e.g., Buckley, 2008; Madsen & Shine, 1999). In this way, maternal behavioral plasticity in one generation can influence the selective thermal environment experienced by developing embryos in the next generation. For example, nest sites chosen by eastern three-lined skinks (*Bassiana* [=*Acritoscincus*] *duperreyi*)[1] were warmer than unused sites (Shine & Harlow, 1996), whereas nest-site choice in painted turtles (*Chrysemys picta*; Mitchell, Maciel, & Janzen, 2013) and oviposition-site selection in wood frogs (*Rana* [=*Lithobates*] *sylvatica*; Freidenburg, 2017) suggest females actively seek out particular thermal environments. The overall power of female behavior to mitigate thermal selection on embryos, however, is unclear. For example, some studies have found a little adaptive divergence in aspects of nest-site choice that would influence the thermal conditions of incubating reptile nests (McGaugh et al., 2010; Refsnider & Janzen, 2016). Similarly, females often do not alter nest site choice based on air temperatures during egg development (Telemeco, Fletcher, et al., 2017a), or do so insufficiently to buffer against a warming climate (Telemeco et al., 2009). More work is required to identify the environmental cues by which females choose oviposition sites, limitations of nest-site choice, and how habitat structure might limit nesting options.

3 | QUANTITATIVE GENETICS

In addition to behavioral buffering, thermal evolution will be shaped by patterns of genetic variation and covariation of the traits in question (Angilletta, 2009; S. J. Arnold, 1987). According to the

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[1]In the first mention of taxa for which nomenclature has been revised within the studies discussed here, we present both names to orient readers to taxonomic synonymy.

breeder's equation, an evolutionary response requires selection on a heritable trait (Lynch & Walsh, 1998). Unfortunately, few studies have estimated quantitative genetic parameters like genetic variances and covariances on thermal physiological traits in reptiles or amphibians. Accurate estimates of heritability are notoriously difficult to attain because they require complex experimental designs and intensive data collection. Nonetheless, some work has found familial differences in traits suggesting broad-sense heritability, although few studies estimate narrow-sense heritability directly. For example, studies of captive-born offspring have found significant among-family variation in thermal preferences (T_{pref}) consistent with a heritable basis for these traits in western terrestrial garter snakes (*Thamnophis elegans*; Arnold et al., 1995), western fence lizards (*Sceloporus occidentalis*; Sinervo, 1990), and European common lizards (*Zootoca* [=*Lacerta*] *vivipara*; Bestion et al., 2015), though these estimates may be confounded with maternal effects. A study of side-blotched lizards (*Uta stansburiana*) attributes the variation among families in the preferred body temperatures of lab-born offspring to transgenerational effects associated with the thermal environment experienced by mothers, rather than additive genetic variance (Paranjpe et al., 2013). Logan et al. (2018) found little narrow-sense heritability (estimates explaining less than 15% of variation and not significantly different from zero) in different aspects of the thermal performance curves for sprint speed among populations of brown anoles (*Anolis sagrei*). Martins et al. (2019) found similarly low heritability estimates in a number of physiological traits related to thermal biology, with the exception of maximum sprint performance. The only strong association was a positive genetic correlation between individual growth rate and critical thermal maximum (CT_{max}). Work to date has found little support for narrow-sense heritability of thermal traits or genetic covariance of thermal traits in reptiles and amphibians, but this is potentially due to limited sample sizes in published studies and the small number of controlled breeding studies. Even so, thermal traits may share pathways and perhaps genetic underpinnings with life-history traits such as growth (Bronikowski, 2000; Refsnider et al., 2019; Sinervo, 1990; Taylor et al., 2020). A variety of factors can lead to phenotypic covariance of thermal or life-history traits within individuals, but determining the adaptive significance of such constraints is challenging (reviewed in Bennett, 1997). For example, consistent patterns of within-individual covariation of thermal physiology and behaviors suggest a syndrome in which traits related to energy flux covary along a "hot–cold" continuum (Goulet, Thompson, & Chapple, 2017; Goulet, Thompson, Michelangeli, Wong, et al., 2017; Michelangeli et al., 2018). Such patterns of covariation within individuals are likely to affect species responses to climate change. For example, common lizards (*Zootoca vivipara*) with lower preferred temperatures dispersed more readily from warm habitats, whereas those with higher preferred temperatures were more likely to leave habitats representing cooler climates (Bestion et al., 2015). How widespread and potentially adaptive these patterns are across reptile and amphibian taxa have yet to be explored.

Although direct evidence for heritability in thermal traits remains scant, evidence for selection on thermal traits is robust.

In four-eyed frogs (*Pleurodema thaul*), individuals with greater CT_{min} exhibited higher survivorship when cold-acclimated, though little evidence was found for selection on several other thermal traits (Bacigalupe et al., 2018). In *Zootoca vivipara*, under seminatural conditions, there was evidence of stabilizing selection on preferred body temperature, but little evidence for correlated selection on the thermal sensitivity of sprint performance, thermoregulatory behavior, and resting metabolic rate (Artacho et al., 2015). In contrast, *Anolis sagrei* experimentally transplanted to a novel warmer thermal environment experienced rapid and strong selection on the optimal temperature and a wider performance breadth for sprint performance (Logan, Cox, & Calsbeek, 2014). Similarly, male ornate tree lizards (*Urosaurus ornatus*) with higher thermal preferences and faster sprint performance at the optimal temperature exhibited greater survivorship than slower lizards with lower thermal preferences (Gilbert & Miles, 2017).

Other recent work links thermally driven natural selection to rapid physiological evolution. Following a polar vortex, green anoles (*Anolis carolinensis*) exhibited rapid shifts in critical thermal minimum (CT_{min}), the liver transcriptome, and in genes related to synapse function (Campbell-Staton et al., 2017). More evidence comes from studies showing apparent rapid local adaptation in the thermal biology of species in novel conditions (*e.g*, Campbell-Staton et al., 2020; Kolbe et al., 2012; Litmer & Murray, 2019; McCann et al., 2018; Winwood-Smith et al., 2015). For example, crested anoles (*Anolis cristatellus*) introduced to Miami, Florida from Puerto Rico exhibited divergences in CT_{min} after only approximately 35 generations, implying that selection has the potential to rapidly change aspects of the thermal biology of invasive lizards (Leal & Gunderson, 2012). On a similar time scale, larval *Rana sylvatica* evolved greater CT_{max} in ponds that had been reinvaded by beavers, which opened canopy cover and thus increased water temperatures (Skelly & Freidenburg, 2000). These studies provide evidence that selection on thermal traits clearly occurs and can lead to rapid evolutionary change. However, more studies quantifying heritability are needed to draw conclusions about the specific contexts and traits where we should expect selection to lead to an evolutionary response.

4 | EVOLUTIONARY PATTERNS ACROSS SPACE AND TIME

By far, most available data on the evolvability of reptile and amphibian thermal traits come from comparative studies of trait divergence within natural habitats over geological time scales. One of the general findings to emerge from these macroevolutionary studies is that different features of the thermal performance curve (defined in Box 1) can evolve independently from each other (Gvoždík, 2015; Huey & Kingsolver, 1993; Muñoz & Bodensteiner, 2019). The most striking pattern is that CT_{min} evolution is often decoupled from CT_{max} evolution (Araújo et al., 2013; Cruz et al., 2005; Sunday et al., 2011). Rates of CT_{max} evolution can be substantially slower than those of CT_{min} (Muñoz et al., 2014) and CT_{max} often exhibits a stronger signal

of phylogenetic inertia (Araújo et al., 2013; Grigg & Buckley, 2013; Labra et al., 2009). Differences in the rate of CT_{max} and CT_{min} evolution may arise because these traits respond to different environmental features, rooted in the different potential for thermoregulation to buffer organisms from hot versus cold temperatures (see above; Araújo et al., 2013; Clusella-Trullas et al., 2011). Specifically, the evolution of CT_{max} appears to respond, at least in part, to behavioral differences in thermal microhabitat partitioning (Gunderson et al., 2018; Hertz, 1979; Muñoz et al., 2016), whereas CT_{min} appears to track thermal macrohabitat, as supported by strong correlations between cold tolerance and key macrohabitat proxies (namely latitude and altitude) (Arajúo et al., 2013; Sunday et al., 2011). Nonetheless, not all aspects of the thermal performance curve may evolve independently (Bauwens et al., 1995). Some thermal traits diverge in tandem as organisms adapt to new thermal environments, ensuring that organisms maintain beneficial body temperatures in the field (Bauwens et al., 1995; Huey & Bennett, 1987; Martin & Huey, 2008; van Berkum, 1986). As a general rule, features at the upper end of the thermal performance curve, like the optimal temperature, the preferred body temperature, and the CT_{max}, tend to be co-adapted (Huey & Kingsolver, 1993; Huey et al., 2012). This is not universally true, however. In Australian rainforest skinks (Lygosominae), for example, the optimal sprinting temperature, the performance breadth (B95: the range of temperatures in which an organism performs at 95% of its maximal performance), and CT_{min} are tightly correlated with local thermal environment; CT_{max} in contrast, responds strongly to basking behavior and relative shade use, but not thermal macrohabitat (Muñoz et al., 2016). Similarly, two closely related Puerto Rican anoles (*Anolis cristatellus* and *Anolis cooki*) have diverged in optimal sprinting temperature without correlated shifts in CT_{max} (Gunderson et al., 2018). Another example is provided by northern and southern alligator lizards in North America (*Elgaria coerulea* and *E. multicarinata*, respectively). These two species do not

performance curve reflects a mosaic of macroevolutionary rates, patterns, and potential trade-offs. For example, specialist-generalist trade-offs or thermodynamic effects (such that organisms with higher optimal temperatures will exhibit higher maximum fitness) can restrain evolution of the shape of thermal performance curves (Angilletta et al., 2003, 2010). The causal mechanisms underlying this variation likely vary across lineages and environmental contexts (Angilletta et al., 2003).

Box 1 A hypothetical thermal performance curve (TPC) (A) illustrating the relationship between body temperature (*x*-axis) on some aspect of organismal performance (*y*-axis). In ectothermic animals, the ability to perform a task, such as sprinting, is contingent on body temperature. This performance is maximized at a certain temperature (T_{opt}) and remains relatively high over a certain range of temperatures. The breadth of the temperature range over which performance exceeds a threshold of 80% or 95% of maximum performance (P_{max}) is defined as B80 or B95, respectively. Performance drops at higher and lower temperatures until the animal is immobilized (CT_{max} and CT_{min}, respectively). TPCs typically exhibit strong left-skew, meaning that performance drops off much more rapidly at higher body temperatures than at lower body temperatures. The lethal limits are usually a few degrees above and below CT_{max} and CT_{min} (Angilletta 2009; Huey 1982). For the sake of this review, we discuss thermal traits as a parameter extracted from a thermal performance curve (e.g., T_{opt} and CT_{max}), whereas thermally dependent traits are anything that could be measured on the *y*-axis.

(a) ... (b) (c) (d) (e) (f) (g)
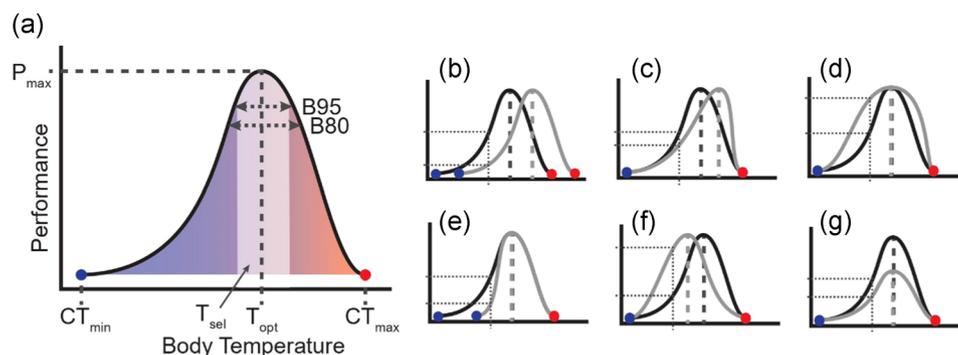
differ in their CT_{max}, but heat stress induces metabolomic shifts in the northern species that are not seen in the southern species, indicating independent responses in heat challenge among different traits (Telemeco, Gangloff, et al., 2017b). In short, the thermal

The panel figures (B–G) demonstrate various ways that TPCs can diverge between two populations (black and grey). The small dotted lines represent the difference in the population-mean performance of a given thermally dependent trait measured at a

single temperature, as is common in many experiments. Though heritable difference in performance for a thermally dependent trait at a single temperature is sufficient evidence for evolutionary divergence, it provides no information about how the shape of the TPCs has diverged. Similarly, measuring a single thermal trait is insufficient to characterize the shape of the TPC. For instance, CT_{max} is identical for all but one panel (B), despite divergence in TPCs. In two panels (D and G), CT_{max}, CT_{min}, and T_{opt} are identical despite divergence in TPC shape. Ideally, performance should be measured at five or more points to characterize differences in TPCs (see Taylor et al., 2020).

Another pattern to emerge is that local adaptation in physiology can occur across microgeographic scales (i.e., within a population's dispersal neighborhood; Richardson et al., 2014), particularly in amphibians and turtles. Microgeographic divergence has been shown extensively in common-garden or transplant experiments on pond-breeding anurans with respect to thermal preference (Freidenburg & Skelly, 2004), embryonic developmental rates (Skelly, 2004), larval developmental rates (Ligon & Skelly, 2009; Orizaola & Laurila, 2009), larval growth rates (Orizaola & Laurila, 2009), and thermal locomotor performance associated with habitat temperature (Navas, 1997; Richter-Boix et al., 2015). Fine-scale divergence also occurs in turtles with respect to embryonic development rates (Tucker & Warner, 1999) and embryonic thermal tolerances (Weber et al., 2012). Temporal variation in habitat temperature also appears to drive divergence in thermal traits at fine-grained spatial scales. For example, populations of Rocky Mountain tailed frogs (*Ascaphus montanus*) from streams with greater variance in temperature acclimated to a wider range of temperatures than adjacent populations (Hossack et al., 2013). Similarly, species of frogs in the genus *Pristimantis* inhabiting thermally variable open habitats had higher CT_{max} than species restricted to more thermally constant microclimates inside the forest, and this trend was consistent along an elevational gradient (Pintanel et al., 2019). Fine-scale heterogeneity in thermal habitat may be an important driver of microevolution. Studies that do not consider fine-scale divergence in assessing range-wide variation may draw spurious conclusions about the direction and magnitude of adaptation, such as confusing microgeographic adaptation with plasticity or maladaptation (Hodgson & Schwanz, 2019; Huey et al., 2003; Richardson et al., 2014).

5 | EVOLUTION AND PLASTICITY

Whether examined at macro- or microgeographic scales, physiological variation among populations may reflect any combination of evolutionary divergence and phenotypic plasticity (Newman, 1992; Noble et al., 2018; Singh et al., 2020). Importantly, we distinguish here between active plasticity and a passive response to temperature driven by changes in biochemical rates (Havird et al., 2020). Without an appropriate experimental design, it is challenging to distinguish plasticity from evolution (Huey et al., 2003; Kawecki & Ebert, 2004; Sih et al., 2004; Via et al., 1995). Furthermore, the role

of plasticity in shaping phenotypes can manifest across different temporal scales. For example, trait differences due to plasticity between populations in the wild could be the results of developmental plasticity (Gomez-Mestre et al., 2010), plasticity in thermoregulatory behavior (e.g., basking preference; Adolph, 1990; Caldwell et al., 2017; Kearney et al., 2009; Refsnider et al, 2019), or reversible plasticity (thermal acclimation or heat hardening; Gilbert & Miles, 2019a; Ryan & Gunderson, 2020; Drummond et al., 2020; Phillips et al., 2016). Plasticity in traits at these different temporal scales will interact with selection in complicated ways, potentially either facilitating or hindering the evolutionary response to selection (reviewed in Catullo et al., 2019; Levis & Pfennig, 2016). The effect of plasticity can confound signatures of microevolution when environmentally induced trait changes mask differences in the genetic constitution of populations (D. O. Conover & Schultz, 1995). Thus, it remains difficult to make generalizations about the impact of plasticity on evolutionary processes; rather, the particulars of each population in its ecological context must be considered.

Though further tests are needed to understand the interaction of plasticity and evolution in the thermal traits of reptiles and amphibians, plasticity in response to the thermal environments of early development could lead to population-level adaptation over time (Noble et al., 2019). In reptiles, developmental plasticity for preferred or selected body temperatures has been observed in about half the studies that have tested for it, mostly by incubating eggs across a range of temperatures and measuring phenotypic traits at later (usually neonate) life-history stages (e.g., S. J. Arnold et al., 1995; Aubret & Shine, 2010; Blouin-Demers et al., 2000; Blumberget al., 2002; Esquerré et al., 2014; O'Steen, 1998; reviewed in Refsnider et al., 2019; Singh et al., 2020; Tamplin & Cyr, 2011). Unlike thermal preference, CT_{max} in reptiles appears to be little affected by developmental temperature (Abayarathna et al., 2019; Gunderson et al., 2020; Llewyn et al., 2018) though there may be more of an effect on CT_{min} (Dayananda et al., 2017; Du et al., 2010).

Beyond thermal limits, multiple other aspects of thermal performance curves are affected by developmental temperatures in amphibians. We have summarized these studies in Table 1, but note the important caveat that little work has been done to distinguish between reversible and nonreversible plasticity that takes place during development. Thus, it is currently unknown how much of the observed plasticity may be reversible given longer time scales. Nonetheless, there is much evidence for developmental plasticity on shorter time scales, especially in anurans. For example, high acclimation temperatures early in the larval period generally induce later metamorphic stages to prefer higher temperatures (i.e., higher T_{pref}; Floyd, 1984; Goldstein et al., 2017; Hutchison & Hill, 1978). Interestingly, thermal performance optima are negatively correlated with maximum development and growth rates (Gahm et al., 2020; Watkins, 2000; Watkins & Vraspir, 2006; Wilson & Franklin, 1999). However, it is unclear if this tradeoff between performance and plastic development persists through metamorphosis (Drakulić et al., 2016). Several studies suggest that the mechanisms of apparent differences along environment gradients are trait-dependent.

TABLE 1 Studies testing for developmental plasticity in thermal traits in amphibians. For a similar table covering reptiles, we direct readers to Refsnider et al. (2019)

Trait	Order	Species	Developmentally plastic?	If plastic, persistence length	Reference
CT_{max}	Caudata	Tiger salamander (*Ambystoma tigrinum*)	Yes	Persists from larval to neotenic stages but not in subadults	Delson and Whitford (1973)
T_{pref}	Anura	American bullfrog (*Rana catesbeiana*)	Yes	Generally increases through larval development	Hutchison and Hill (1978)
CT_{max}	Anura	American toad (*Anaxyrus americanus*) Woodhouse's toad (*Anaxyrus woodhousii*) Eastern narrow-mouthed toad (*Gastrophryne carolinensis*) Wood frog (*Rana sylvatica*) Western chorus frog (*Pseudacris triseriata*)	Yes	Persists through larval stages but is lost at metamorphic climax in most species	Cupp (1980)
CT_{max}	Anura	Southern toad (*Anaxyrus terrestris*) Northern leopard frog (*Rana pipiens*)	Yes	Persists through larval stages but may disappear at metamorphic climax depending on the species and acclimation temperature	Noland and Ultsch (1981)
CT_{max} (basal and heat-hardened)	Anura	American bullfrog (*Rana catesbeiana*)	Yes	Persists through larval stages, declines at metamorphic climax, and may be recovered in newly metamorphosed juveniles depending on acclimation temperature	Menke and Claussen (1982)
CT_{max}, CT_{min}	Anura	Cane toad (*Rhinella marina*)	Yes	Persists through larval stages but not at metamorphic climax	Floyd (1983)
T_{pref}	Anura	Cane toad (*Rhinella marina*)	Yes	Increased through larval development	Floyd (1984)
CT_{max}, CT_{min}	Anura	Wood frog (*Rana sylvatica*)	Yes	Unknown, different larval stages (before the metamorphic climax) were grouped in the analysis	Manis and Claussen (1986)
T_{opt}	Anura	Striped marsh frog (*Limnodynastes peronii*)	Yes	Not measured	Wilson and Franklin (1999)
T_{opt} and Thermal breadth	Anura	Pacific treefrog (*Hyla regilla*)	Yes	Unknown, only measured at one larval stage	Watkins (2000)
CT_{max}	Anura	Japanese Buerger's frog (*Buergeria japonica*)	Yes, depending on the population	Unknown, different larval stages were grouped in the analysis	Chen et al. (2001)
T_{opt}	Anura	Wood frog (*Rana sylvatica*)	Yes	Unknown, only measured at one larval stage	Watkins and Vraspir (2006)
T_{opt}	Anura	Striped marsh frog (*Limnodynastes peronii*)	Yes	Unknown, only measured at one larval stage	Seebacher and Grigaltchik (2015)
CT_{max}	Anura	Blacksmith treefrog (*Boana faber*)	Yes	Unknown, different early larval stages per species were grouped in the analysis	Simon et al. (2015)

(Continues)

TABLE 1 (Continued)

Trait	Order	Species	Developmentally plastic?	If plastic, persistence length	Reference
		Peters' Four-eyed Frog (Pleurodema diplolister)			
		Dog frog (Physalaemus cuvieri)			
		Cururu toad (Rhinella icterica)			
		Ornate forest toad (Rhinella ornata)			
T_{opt}	Anura	Common frog (Rana temporaria)	Yes	Through metamorphosis	Drakulić et al. (2016)
T_{pref}	Anura	Relict leopard frog (Rana onca)	Yes	Unknown, different larval stages (before the metamorphic climax) were grouped in the analysis	Goldstein et al. (2017)
T_{pref}	Anura	Leopard frog (Rana spp.)	Yes	Unknown, different larval stages (before the metamorphic climax) were grouped in the analysis	Lucas and Reynolds (1967)
CT_{max}, CT_{min}	Anura	Túngara frog (Engystomops pustulosus)	Yes	Unknown, different larval stages (before the metamorphic climax) were grouped in the analysis	Oyamaguchi et al. (2018)
CT_{max}, CT_{min}	Anura	Common frog (Rana temporaria)	Yes	Through metamorphosis, but not juveniles	Enriquez-Urzelai et al. (2019)
CT_{max}, CT_{min}	Anura	Common Frog (Rana temporaria)	Yes	Unknown, only measured at the metamorphic climax	Ruthsatz et al. (2020)

For example, studies of frogs in the family Ranidae demonstrate that among-population variation in hatching rates, hatchling size, mass at metamorphosis, and melanism (hypothesized to be thermally adaptive) is due to plastic responses to the thermal developmental environment, whereas differences in growth rate, developmental rate, and CT_{max} are genetically based (Alho et al., 2010; Orizaola, Quintela, & Laurila, 2010; Skelly & Freidenburg, 2000). Similarly, in a reptile species, common-garden experiments with the garter snake *Thamnophis elegans* exhibiting divergent life-history ecotypes demonstrate that local adaptation (genetic differences) and early-life thermal environment interact to shape physiological and morphological phenotypes, including growth rate and organismal metabolic rates (Addis et al., 2017; Bronikowski, 2000; Gangloff et al., 2015).

Common-garden experiments distinguishing heritable and plastic effects in phenotypes have been well-utilized in the context of temperature-dependent sex determination (TSD). TSD is a mode of sex determination in which the sex of the developing embryo is irreversibly determined by the temperature experienced during development (Valenzuela & Lance, 2004). TSD may present demographic challenges to many reptile and amphibian species in a warming world as sex ratios in populations become biased and lead to local extinction events (Huey & Janzen, 2008; Santidrián Tomillo et al., 2015), making this trait a good candidate to understand microevolutionary potential. In the painted turtle, *Chysemys picta*, nest-site choice and reproductive timing are highly plastic but exhibit little adaptive divergence; meanwhile, pivotal temperature (i.e., temperature that produces a 1:1 sex ratio) exhibits heritable variation (McGaugh et al., 2010; Refsnider & Janzen, 2016). Another study in *C. picta* examined within- and among-population variation in the physiological components (e.g., pivotal temperature and transitional range of temperatures) of TSD in 12 populations, finding evidence of microevolutionary divergence among populations, but high variation within populations in the pivotal temperature (Carter et al., 2019). Overall, there is evidence of evolution at the population and phylogenetic scales and even plasticity between sex-determining mechanisms (e.g., Holleley et al., 2015), indicating that TSD may be a labile trait depending on the specific parameter of interest and scale of investigation. Thus, though the roles of plasticity and microevolutionary divergence are difficult to assess independently, there is clear evidence for intraspecific variation in multiple thermal traits. Nevertheless, for most traits, realized phenotypes are modulated to some extent by plastic effects in the long- and short-term.

With respect to thermal tolerance and temperature-dependent metabolism, reptiles and amphibians exhibit some of the lowest short-term, reversible acclimation responses among animals (Gunderson & Stillman, 2015; Havird et al., 2020; Seebacher et al., 2015). For example, on average, the CT_{max} of reptiles increases by only 0.1°C for every 1°C of increase in acclimation body temperature (10% compensation), whereas amphibians exhibit 16% compensation (Gunderson & Stillman, 2015). Though the magnitude of thermal plasticity may be low in reptiles and amphibians, plastic responses can still evolve and be locally adaptive if the benefit of plasticity outweighs the cost of maintaining the mechanisms that produce it
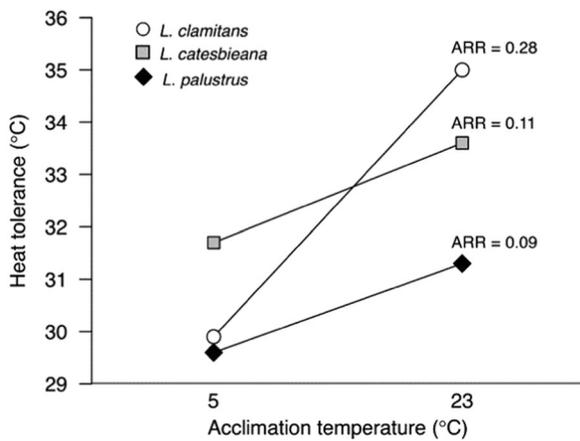
FIGURE 1 Mean adult heat tolerance of three frog species in the genus *Lithobates* when acclimated to two different thermal conditions. ARR is the acclimation response ratio, which represents the capacity for acclimation as the change in trait value per unit change in acclimation temperature. Data from Brattstrom (1968)

(Dewitt et ail., 1998; Gunderson et al., 2017; Kelly, 2019; Lande, 2014; West-Eberhard,2003; but see P. A. Arnold et al., 2019). We know relatively little about the evolutionary divergence in the plasticity of reptile and amphibian thermal traits. Nonetheless, divergent patterns of thermal plasticity can clearly evolve in some situations (Feder,1978 Gunderson & Stillman,2015; Tsuji, 1988). For example, frog species in the genus *Rana* [= *Lithobates*] have diverged in thermal tolerance plasticity (Brattstrom, 1968) and provide an instructive example of how plasticity can evolve and can confound evolutionary analyses. The green frog (*Rana clamitans*) has evolved greater heat tolerance plasticity (i.e., their phenotype changes more per unit of environmental change) than *Rana catesbeiana* and the pickerel frog (*Rana palustris*; Figure 1). The latter two species have a similar capacity for plasticity but have evolved different intercepts of their reaction norms. Furthermore, the relative heat tolerance of these species depends on acclimation conditions. At a 5°C acclimation temperature, one would conclude *R. clamitans* and *R. palustris* have similar heat tolerance to each other and that both have lower heat tolerance than *R. catesbeiana*. However, at a 23°C acclimation temperature, one would conclude that *R. clamitans* has greater heat tolerance than the other two species (Figure 1). Studies of the evolution of physiological plasticity should be directed toward the goal of describing patterns and broad conclusions about how and when plasticity evolves.

6 | ONTOGENY

Several efforts have been made to investigate how the thermal history of early life stages may affect thermal traits later in life in both amphibians (see above; Table 1) and reptiles (reviewed by Refsnider et al., 2019). Less attention, however, is given to how thermal traits themselves vary throughout ontogeny and how ontogenetic variation

evolves. To address this issue, we must observe and compare thermal physiology across ontogenetic stages (embryos, larval/juveniles, and adults) in multiple taxa (Figure 2). Although thermal dependence is inescapable at every life stage (embryo, larval/juvenile, adult, but see Tattersall et al., 2016), the thermal environment of both amphibians and reptiles may change dramatically during life history transitions (Johnston et al., 1996). Embryos of several reptile groups are able to display active thermotaxis within the egg (Du et al., 2011; Li et al., 2013; Zhao et al., 2013), but thermoregulatory opportunities in the wild are limited for most species (Cordero, Telemeco, & Gangloff, 2018; Telemeco et al., 2016; but see Ye et al., 2019). Temperature regimes in amphibian embryos are attributed mainly to the oviposition site chosen by reproductive adults (Méndez-Narváez et al., 2015). We do not know whether amphibian embryos per se are capable of either displaying thermotaxis or whether they actively thermoregulate in the manner of some reptile embryos.

The strength of environmentally induced selection varies across reptile and amphibian life stages. Embryos and aquatic larvae are generally more vulnerable than their terrestrial and adult counterparts to thermal extremes due to thermal-induced oxygen limitations and limited regulatory behaviors (Angilletta et al., 2013; Gangloff & Telemeco, 2018; Hoppe, 1978; Liang et al., 2015; Rollinson & Rowe, 2018; Turriago et al., 2015). Selection on embryonic and larval thermal tolerance should, therefore, be stronger than in adults, suggesting that physiological studies should explicitly consider stage-dependent variation. If adaptive maternal effects (such as incubation environment) are strongest during early developmental stages and fade later in life, selection on thermal tolerance should instead increase with ontogeny (Riska, 1991). Although desirable, few thermal traits are feasible to be measured in all life stages because of inherent methodological limitations, particularly regarding measurements in embryos. Some examples might include critical limits for cardiac performance (Angilletta et al., 2013) and lethal temperatures (Turriago et al., 2015). Still, it is possible to compare some aspects of a thermal performance curve (e.g., T_{opt}, B95) across life stages, even if the thermally dependent trait is different at each life stage (Box 1). To the extent that it is possible, we encourage researchers to consider including different life stages when measuring thermal traits (Sears et al., 2019).

Although still relatively unexplored, some patterns have emerged in how thermal physiology shifts across ontogeny (Table 2). For anurans, CT_{max} is greater at larval stages and decreases sharply at the metamorphic climax (Table 2), the period of rapid morphological restructuring in the transition from the aquatic to terrestrial anuran body plan (Burggren & Just, 1992). In some anurans, CT_{min} also decreases at the metamorphic climax (Enriquez-Urzelai et al., 2019; Floyd, 1983), but not in others (Menke & Claussen, 1982). In fact, individuals at the end of metamorphosis have reduced physiological and ecological performance overall (Arnold & Wassersug, 1978; Denver, 1997; Floyd, 1984; Wilbur, 1980). In some toads, an increase in CT_{max} occurs from juveniles to adults, suggesting the maturation of the underlying physiological systems (Sherman, 1980). Meanwhile, traits such as preferred temperature tend to increase as larval development progresses and peak at the metamorphic climax (Dupré & Petranka, 1985; Floyd, 1984;
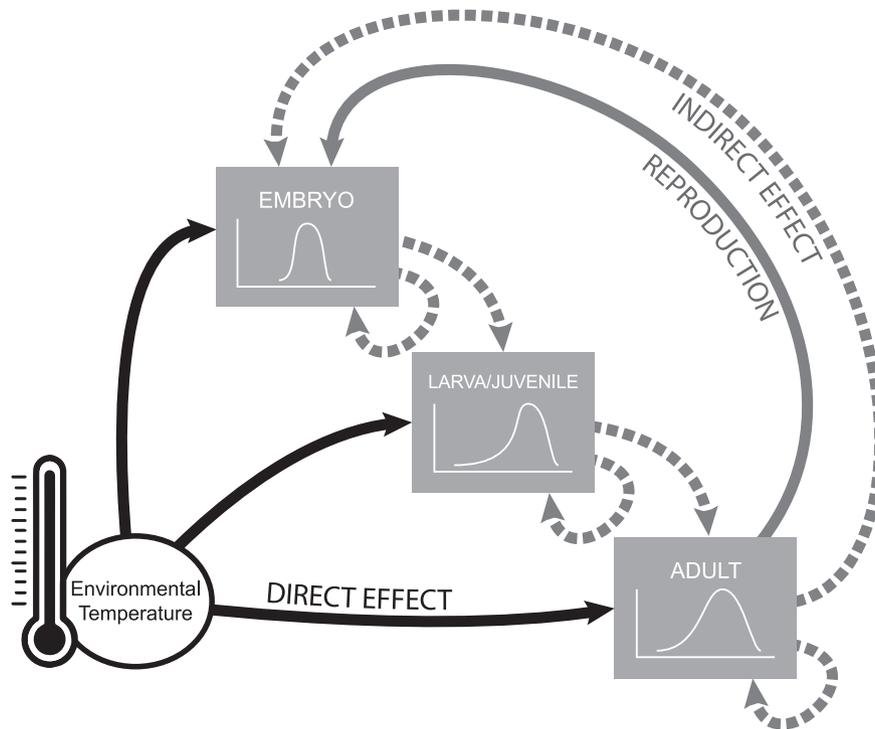
FIGURE 2 Flow chart depicting how the direct and indirect effects of temperature across ontogeny and between generations determine the evolution of thermal physiology in reptiles and amphibians. The grey boxes represent organismal life stages. Physiological responses (i.e., thermal performance curves) can differ for each life stage and mediate how environmental temperature (solid black arrows) experienced during a given life stage impacts phenotypic traits. The effects of temperature on previous life stages or generations can indirectly affect subsequent life stages through carry-over effects (dashed grey arrows). Similarly, within a life stage, the direct effects of temperature on one trait may confer indirect effects on a different trait. The strength, direction, and targets of selection will impact each stage differently and can be modulated by the plasticity of thermal responses. The net effect of selection across generations is determined at reproduction (solid grey arrow) and the evolutionary response to selection will be mediated by genetic variance and covariance of the traits in question. However, the effects of temperature can also carry-over to subsequent generations indirectly (dashed grey arrow)

Hutchison & Hill, 1978; but see Wollmuth et al., 1987). It has been hypothesized that tadpoles nearing metamorphic climax actively choose higher temperatures to accelerate development, perhaps to reduce predation risk (Dupré & Petranka, 1985).

Thermal physiology also changes during reptile ontogeny, but the pattern is different from that of amphibians. For most lizard species studied, adults can tolerate a wider range of body temperatures than juveniles (e.g., Telemeco, 2014; Virens & Cree, 2019; Table 2). However, neonates of different populations of the diamondback water snake (*Nerodia rhombifer*) tolerate higher temperatures than adults (Winne & Keck, 2005). Ontogenetic shifts in thermal tolerance generally parallel changes in microhabitat use and activity time across age classes, suggesting a tight match between environmental use and physiological phenotypes (Andrango et al., 2016; Maia-Carneiro & Rocha, 2013; Winne & Keck, 2005; Xu & Ji, 2006). For example, juveniles of the Italian wall lizard (*Podarcis siculus*) do not bask in sites used by adults and spend more time in vegetated areas; correspondingly, juveniles are less heat tolerant than adults (Liwanag et al., 2018). Thermal preferences in two species of racerunner lizards (genus *Eremias*) were higher in adults than in juveniles (Tang et al., 2013; Xu & Ji, 2006). In contrast, no difference in T_{pref} was observed between adults and juveniles of the six-lined racerunner

(*Aspidoscelis sexlineatus*; Paulissen, 1988) and no differences in thermoregulatory behaviors or thermal performance curves for sprint speed were found between juvenile and adult crested geckos (*Correlophus ciliates*; Aparicio Ramirez et al., 2020).

Many studies only examine thermal biological traits at one life stage, highlighting that evolutionary differences among taxa might be obscured. Reptiles and amphibians clearly comprise a mosaic of physiological patterns across their lifespans. At any given time, a physiological phenotype reflects a single snapshot in time, one that may have been different earlier and may yet change again. Comparing thermal traits across ontogeny allows us to understand how underlying mechanisms setting thermal limits might change as development progresses (e.g., Gangloff & Telemeco, 2018). Shifts in thermal physiology across ontogeny may also differ between sexes. For instance, growth and development rates among female wood frog larvae are more sensitive to temperature than in their male counterparts (Lambert et al., 2018). Recognizing sources of within-individual variation in thermal traits across ontogeny is paramount to predicting population responses to environmental changes (Agudelo-Cantero & Navas, 2019; Johnston et al., 2019; Klockmann et al., 2017; Pincebourde & Casas, 2015). For example, vulnerability assessments may integrate measures of thermal traits across ontogeny to detect which stages or life-history

TABLE 2 Amphibian and reptile species for which ontogenetic shifts in critical thermal limits (CT_{min}, CT_{max}, or both) have been tested

Class	Order (suborder)	Species	Thermal limit		Main pattern	References
			CT_{min}	CT_{max}		
Amphibia	Caudata	Eastern newt (*Notophthalmus viridescens*)		X	Larvae had a lower (~1°C) and more variable CT_{max} than efts and adults	Hutchison (1961)
		Tiger salamander (*Ambystoma tigrinum*)		X	Larval and neotenic desert salamanders had a CT_{max} 1°C higher than transforming or subadult salamanders	Delson and Whitford (1973)
		San Marcos Salamander (*Eurycea nana*)		X	Adult salamanders (summer) had in average a CT_{max} 1.4°C higher than juveniles (fall)	Berkhouse and Fries (1995)
	Anura	Western chorus frog (*Pseudacris triseriata*)		X	CT_{max} declined 0.5–2°C at the metamorphic climax, depending on acclimation temperature and population. Recently metamorphosed juveniles increased CT_{max}	Hoppe (1978); Cupp (1980)
		American toad (*Anaxyrus americanus*)		X	Tadpoles at the metamorphic climax displayed a lower CT_{max} (up to 2°C) and no heat hardening capacity compared to individuals at early developmental stages or recently metamorphosed juveniles	Cupp (1980); Sherman and Levitis (2003)
		Woodhouse's toad (*Anaxyrus woodhousii*)		X	CT_{max} decreased 1–2°C at the metamorphic climax, depending on acclimation temperature	Cupp (1980)
		Eastern narrow-mouthed toad (*Gastrophryne carolinensis*)		X	CT_{max} decreased 3–5°C at the metamorphic climax, depending on acclimation temperature and population	Cupp (1980)
		Wood frog (*Rana sylvatica*)		X	CT_{max} decreased 1–3°C at the metamorphic climax, depending on acclimation temperature	Cupp (1980)
		Fowler's toad (*Anaxyrus fowleri*)		X	CT_{max} of tadpoles decreased almost 5°C at the climax of metamorphosis, then progressively increased almost 4°C from metamorphosis to adulthood	Sherman (1980)
		Southern toad (*Anaxyrus terrestris*)		X	CT_{max} decreased less than 1°C at the metamorphic climax depending on the acclimation temperature	Noland and Ultsch (1981)
		Northern leopard frog (*Rana pipiens*)		X	CT_{max} decreased less than 1°C at the metamorphic climax depending on the acclimation temperature	Noland and Ultsch (1981)
		American bullfrog (*Rana catesbeiana*)	X	X	At the metamorphic climax, heat tolerance (CT_{max}) was lower while cold tolerance was higher (lower CT_{min}) than at early developmental stages. Both heat and cold tolerance were also reduced at the metamorphic climax.	Menke and Claussen (1982)
		Cane toad (*Rhinella marina*)	X	X	CT_{max} decreased almost 5°C at the metamorphic climax depending on acclimation temperature. CT_{min} increased more than 5°C at the metamorphic climax depending on acclimation temperature	Floyd (1983)
		African clawed frog (*Xenopus laevis*)		X	Tadpoles at the end of metamorphosis decreased their CT_{max} by 2°C. Still, individuals at those stages exhibited heat hardening	Sherman and Levitis (2003)

(Continues)

TABLE 2 (Continued)

Class	Order (suborder)	Species	Thermal limit		Main pattern	References
			CT$_{min}$	CT$_{max}$		
		Cuyaba dwarf frog (*Physalaemus nattereri*)		X	CT$_{max}$ decreased at the metamorphic climax, but this effect was less pronounced at a slow experimental heating rate	Agudelo-Cantero and Navas (2019)
		Western rough toad-frog (*Leptodactylus lithonaetes*)		X	Tadpoles' CT$_{max}$ is about 2.6°C higher than adults[1]	Beltrán et al.(2019)
		Common frog (*Rana temporaria*)	X	X	CT$_{max}$ decreased more than 2°C in individuals at the end of metamorphosis and recently metamorphosed juveniles. CT$_{min}$ increased at the metamorphic climax and then decreased in recently transformed juveniles	Enriquez-Urzelai et al. (2019)
Reptilia	Squamata (Lacertilia)	Six-lined racerunner (*Aspidoscelis sexlineatus*)		X	Juveniles and adults did not differ in average CT$_{max}$, but juveniles did have a wider CT$_{max}$ range than adults. Sample size was low for both age classes	Paulissen (1988)
		Ordos racerunner (*Eremias brenchleyi*)	X	X	Adults were more heat tolerant (2.8°C higher CT$_{max}$) and cold tolerant (1.7°C lower CT$_{min}$) than juveniles	Xu and Ji (2006)
		Multi-ocellated racerunner (*Eremias multiocellata*)	X	X	Thermal tolerance range was 4.7°C broader in adults compared to juveniles	Tang et al. (2013)
		Günther's whorltail iguana (*Stenocercus guentheri*)	X	X	Thermal tolerance range was 2.5°C broader in adults compared to juveniles	Andrango et al. (2016)
		Yarrow's spiny lizard (*Sceloporus jarrovii*)	X	X	Juveniles had CT$_{max}$ ~1°C higher than adults, but adults had lower CT$_{min}$ by ~3°C	Gilbert and Lattanzio (2016)[2]
		Italian wall lizard (*Podarcis siculus*)	X	X	Adults of both sexes had a higher CT$_{max}$ than juveniles by ~3°C and adult females had a lower CT$_{min}$ than juveniles by ~2°C	Liwanag et al. (2018)
		Rainforest sunskink, (*Lampropholis coggeri*)	X	X	Laboratory-reared juveniles tolerated a narrower range of body temperatures (effect sizes less than 1°C) than adults	Llewelyn et al. (2018)
		Lesueur's velvet gecko (*Amalosia lesueurii*)	X	X	Lab-incubated hatchlings at age 2 and 4 weeks and recaptured juveniles at age 6 months did not differ in their CT$_{max}$. Recaptured juveniles had CT$_{min}$ 1–2°C lower than hatchlings	Abayarathna et al. (2019)
		McCann's skink (*Oligosoma maccanni*)		X	CT$_{max}$ of juveniles was reduced by ~1°C compared to postpartum females but was not different from pregnant females or adult males	Virens and Cree (2019)
	Squamata (Serpentes)	Diamondback water snake (*Nerodia rhombifer*)		X	Neonates had a CT$_{max}$ 1.5°C higher than adults	Winne and Keck (2005)

Note: For each species, the main pattern found is reported.
[1]From 42 Gosner stage onwards.
[2]Juvenile data compared to adult data published by Beal et al. (2014).

transitions are at greater risk of suffering climate change impacts. This information may inform conservation efforts to take actions targeting the most susceptible life stages.

7 | SEX DIFFERENCES AND EVOLUTION

We have a limited understanding of how and where sexes differ in thermal traits, the mechanisms that may underlie these differences where they do appear, and the potential evolutionary significance of such differences (Lailvaux, 2007). For example, some studies indicate clear differences in selected temperatures, field body temperatures, or thermoregulatory efficiency between male and female lizards, though the direction of such differences is taxon-specific (Maia-Carneiro & Rocha, 2013; Ortega et al., 2016b; Woolrich-Piña et al., 2015; reviewed in Lailvaux, 2007). A meta-analysis of lizard species demonstrates that differences between the sexes are rare and, when they do occur, are small in magnitude (Huey & Pianka, 2007). Differences in selective pressures between the sexes can result in differences in both the shape of thermal performance curves and thermal limits (e.g., Lailvaux & Irschick, 2007), but the broader evolutionary implications for such differences are not well understood. Given the male bias in studies of thermal traits generally due to the exclusion of females, we suggest a fruitful avenue for researchers is the study of the drivers of sexual dimorphism in thermal physiology and the potential evolutionary consequences of such differences. Such work is notably prescient given the potential impacts, both positive and negative, of warming temperatures on reproductive output and success (Clarke & Zani, 2012; Diele-Viegas & Rocha 2018; Le Galliard et al., 2012; Lu et al., 2018) and the potential for temperature to override genetic sex-determining mechanisms (e.g., Holleley et al., 2015; Lambert et al., 2018).

8 | EVOLUTION AND CLIMATE CHANGE

A large question looms over our synthesis of thermal evolution in reptiles and amphibians in these unprecedented times: can thermal traits evolve quickly enough to keep pace with rapid climate change? Many studies have demonstrated that CT_{max} usually evolves more slowly than CT_{min}, meaning warming might be particularly problematic for herpetofauna (Muñoz et al., 2014; von May et al., 2017). However, it is important to consider why the ends of thermal performance curves evolve at different rates. Several factors may limit the evolution of CT_{max}, including genetic constraints (e.g., genetic correlations, low heritable variation) or biochemical constraints (e.g., limitations in the structural stability of proteins at high temperatures; Somero et al., 2017). Alternatively, CT_{min} may simply be exposed to selection more often. Minimum temperatures change at higher rates than maximum temperatures along environmental gradients such as latitude and elevation (Sunday et al., 2011, 2014). Behavior may be better able to buffer animals from heat versus cold extremes (Leal & Gunderson, 2012; Logan et al., 2019; Muñoz & Bodensteiner, 2019) and mechanisms underlying these limits may differ (Gangloff & Telemeco, 2018).

Biological responses to temperature include not just critical limits, but also optimum temperatures for performance, performance breadth, and other parameters describing the shape of a thermal performance curve (Angilletta et al., 2003, 2010; Gangloff & Telemeco, 2018; see Box 1). The pressing question for future work is: Which mechanism(s) responsible for the relative conservatism in high-temperature physiology, including different aspects of thermal performance curves across levels of organization (Iverson et al., 2020), matter for evolvability in the face of global change? If inherent constraints prevail, then hope for evolution to save organisms is slim. However, if the constraints emerge mainly from differential exposure to selection, then high-temperature evolution may be possible when selection does occur (e.g., Buckley et al., 2015; Gilbert & Miles, 2019b; Logan et al., 2014). Despite the inherent challenges in conducting long-term genetic experiments on generally long-lived organisms such as reptiles and amphibians, such work is critical to elucidating mechanisms of evolutionary constraint. Though studies suggest that some aspects of thermal physiology exhibit broad-sense heritability (Arnold et al., 1995; Sinervo, 1990), the few studies quantifying additive genetic variance in reptiles found little evidence of narrow-sense heritability (Logan et al., 2018; Martins et al., 2019). Further, divergence in warm-temperature physiological traits are sometimes observed at intra- and interspecific scales (Barria & Bacigalupe, 2017; Gunderson et al., 2018; Herrando-Pérez et al., 2019, 2020; Pontes-da-Silva et al., 2018; Salazar et al., 2019; Skelly & Friedenberg, 2000; van Berkum, 1986). The extent to which these findings can be generalized across taxa and contexts remains to be determined, toward the goal of building a synthetic understanding of how reptiles and amphibians might evolve in response to ongoing climate change.

9 | CONCLUSION

Is the thermal physiology of reptiles and amphibians evolutionarily rigid? When viewed comprehensively across the entire thermal performance curve and across all of ontogeny, we conclude that it is not. There are many examples of divergence in several aspects of thermal physiology at multiple taxonomic scales. Does that mean that all thermal traits evolve readily? The answer appears to be no. Different traits have different heritabilities and rates of macro- and micro-evolutionary change. Can evolution rescue reptiles and amphibians from global warming? We don't know. Future studies uncovering the genetic mechanisms that drive thermal evolution (e.g., Campbell-Staton et al., 2017; Garcia-Porta et al., 2019) and testing for heritability in thermal traits will provide crucial data to address this question. Though we conclude that conservatism writ broadly is not consistent with the evidence at hand, we do not mean to discount the importance of this hypothesis as a launching point for continuing work. The conservatism hypothesis better explains observed evolutionary dynamics at the warm end of the thermal performance curve. The mechanistic foundation upon which the conservatism hypothesis was built still holds in most cases—behavioral thermoregulation is

clearly a potent regulator of evolutionary change and a critical component of the thermal ecology of most ectothermic species. However, myriad interactions and limitations shape the relationship between thermoregulation and thermal physiology, often specific to ecological context and ontogenetic stage (Angilletta et al., 2002, 2003). Just as previous formative works in evolutionary biology were not accurate in every detail yet still provide a clear path of testable hypotheses (e.g., Darwin, 1859), tests of the conservatism hypothesis across taxa, ecological contexts, thermal parameters, and life-history stages continue to provide a nuanced understanding of the evolution of reptile and amphibian thermal traits.

DATA AVAILABILITY STATEMENT
There are no new data presented in this review.

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