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REVIEW

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The thermal ecology and physiology of reptiles and amphibians: A user's guide

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Abstract

Research on the thermal ecology and physiology of free-living organisms is accelerating as scientists and managers recognize the urgency of the global biodiversity crisis brought on by climate change. As ectotherms, temperature fundamentally affects most aspects of the lives of amphibians and reptiles, making them excellent models for studying how animals are impacted by changing temperatures. As research on this group of organisms accelerates, it is essential to maintain consistent and optimal methodology so that results can be compared across groups and over time. This review addresses the utility of reptiles and amphibians as model organisms for thermal studies by reviewing the best practices for research on their thermal ecology and physiology, and by highlighting key studies that have advanced the field with new and improved methods. We end by presenting several areas where reptiles and amphibians show great promise for further advancing our understanding of how temperature relations between organisms and their environments are impacted by global climate change.

KEYWORDS
climate change, critical temperatures, lizard, methodology, temperature, thermoregulation

1 | THE UTILITY OF REPTILES AND AMPHIBIANS IN THERMAL BIOLOGY RESEARCH

The climate crisis has become a central theme in ecology and other biological fields as scientists scramble to document biodiversity and create plans to save species from extinction. As evidence of accelerating climate change accumulated in the latter part of the 20th century, scientists began studying its impacts with heightened urgency. Google Scholar metrics show that publications on climate change rose from 15,000 per decade in the 1960s to 39,000 in the 1980s, but in the 1990s this number jumped to 700,000 publications and then skyrocketed to 1.4 million in the first decade of the 21st century. Recent reports of huge declines in specific animal taxa (marine animals: Lotze et al., 2019; insects: Sánchez-Bayoa & Wyckhuys, 2019; amphibians: Hof, Araújo, Jetz, & Rahbek, 2011; Rohr & Raffel, 2010; lizards: Sinervo et al., 2010; birds: Rosenberg et al., 2019) due to climate change and other human-induced factors have also stoked urgency. Future projections suggest even further acceleration of habitat loss and increasing climatic stress in most biodiversity hotspots (Habel et al., 2019). The extinction and redistribution of species due to climate change will have dramatic impacts not just on wildlife but also on humans and their well-being (Pecl et al., 2017; Ripple et al., 2017; Ripple, Wolf, Newsome, Barnard, & Moomaw, 2020). It is therefore essential that we continue to understand how climate change is impacting animals and other organisms, especially those that form important components of food webs and whose decline or extinction may have cascading effects on other organisms.

Nonavian reptiles (hereafter "reptiles") and amphibians are extraordinarily diverse groups, encompassing nearly 19,000 species from seven major orders. They display nearly the full gamut of life-history variation in vertebrate animals and occupy a bewildering array of habitats, from marine environments to mountaintops. The diverse physiological challenges they face are far from trivial, and as such, these animals also exhibit a broad array of adaptations that are synonymous with their diversification into these habitats. As ectotherms, reptiles and amphibians are sensitive to the effects of environmental temperature, especially given that their environments (and thus, body temperatures) typically experience dramatic thermal fluctuations daily, seasonally, and stochastically (Huey, 1982; Huey & Berrigan, 2001). Thus, behavioral plasticity and the ability to move in search of thermally suitable habitats are important strategies used to buffer climatic fluctuations (Diele-Viegas & Rocha, 2018; Huey et al., 2012; Sunday et al., 2014).

In addition to being foundational to their ecological communities, amphibians and reptiles are bioindicators of environmental quality because of their environmental dependence, habitat versatility, and distinct biological characteristics. Human activities and environmental change are the main causes of their decline, which has been extensively recorded around the world in the last few decades (e.g., Diele-Viegas, Figueroa, Vilela, & Rocha, 2020; Doherty et al., 2020; Gibbons et al., 2000; Greenberg & Palen, 2019; Sinervo et al., 2010; Stuart et al., 2004). Further, these anthropogenic impacts have exacerbated the spread of disease, putting many populations at further risk of decline or extirpation (Kolby & Daszak, 2016; Lorch et al., 2016). These declines are leading to a cascading effect of biodiversity loss throughout communities (Zipkin, DiRenzo, Ray, Rossman, & Lips, 2020).

For these reasons, amphibians and reptiles are important models for understanding fundamental questions in physiological ecology and for evaluating how environmental change impacts biodiversity. Aside from their biological characteristics, many species are also notable in being highly amenable to study and experimentation due to their local abundance, resilience to handling and monitoring, and ease of husbandry and captive rearing (Cagle, 1939; Heard, Scroggie, & Malone, 2009; Lovern, Holmes, & Wade, 2004; Sanger, Hime, Johnson, Diani, & Losos, 2008; Taylor & Booth, 2017; Viets, Tousignant, Ewert, Nelson, & Crews, 1993; Warner, 2014; Zimmerman, Vogel, & Bowden, 2010). Because of their ease of study, these groups are also amenable to long-term research in the wild. For instance, some established studies on turtles, lizards, and salamanders span decades, and these studies are documenting the temperature sensitivity of, and long-term changes in, a variety of traits including reproductive investment (Hedrick, Klondaris, Corichi, Dreslik, & Iverson, 2018; Miller, Clark, Arnold, & Bronikowski, 2011; Rollinson & Brooks, 2008; Rollinson, Farmer, & Brooks, 2012), phenological timing (Beebee, 1995; Edge et al., 2017; Janzen et al., 2018; Kirk, Galatowitsch, & Wissinger, 2019), growth rate (Angilletta, Steury, & Sears, 2004; Bronikowski, 2000; Gangloff, Vleck, & Bronikowski, 2015; Koper & Brooks, 2000), and survival (Keevil, Brooks, & Litzgus, 2018; Sinervo et al., 2010). For these reasons, ecologists and evolutionary biologists have long leveraged reptilian and amphibian systems to understand fundamental questions in physiological ecology.

As research on the thermal ecology and physiology of reptiles and amphibians continues to grow in scope and quantity, it is essential to maintain or even improve high quality methodologies as researchers also embrace new technologies. In this paper, we delve into the utility of amphibian and reptile models in thermal ecology and physiology studies by outlining the current best practices in measuring relevant variables with the goal of standardizing methods for students and scientists new to the field. Along the way, we highlight a selection of articles that elegantly demonstrate the utility of using these animals as model organisms in thermal studies; these studies are featured in two inset "boxes." Our goal is not to provide an exhaustive list of studies on the thermal ecology and physiology of reptiles and amphibians, of which there are thousands. There are many notable reviews of the thermal biology of amphibians (Brattstrom, 1963, 1979; Hutchison & Dupre, 1992) and reptiles (Andrews & Schwarzkopf, 2012; Avery, 1982; Brattstrom, 1965; Du, Shine, Ma, & Sun, 2019; Huey, 1982; Noble, Stenhouse, & Schwanz, 2018; Refsnider, Clifton, & Vazquez, 2019; While et al., 2018). Rather, we summarize the optimal methodologies and highlight important advances in theory and technology that will form the basis of decades of further research on the thermal physiology of reptiles and amphibians, especially as they relate to projecting the impacts of climate change on these diverse classes of organisms.

2 | BEST PRACTICES FOR MEASURING THERMAL VARIABLES IN STUDIES OF AMPHIBIANS AND REPTILES

What are the best practices in thermal studies of reptiles and amphibians, and what is the best equipment to use? Given the thousands of studies on the thermal ecology and physiology of reptiles and amphibians, it is natural that numerous methodologies are used by researchers. Below, we cover the major methods in thermal ecology and physiology by discussing the range of variables measured (Table 1; for additional thermal variables, see Pough & Gans, 1982) and equipment and techniques used (Table 2), as well as several major applications for the techniques. We begin with a focus on early life stages by summarizing techniques in evaluating development rate in reptiles and amphibians. Then we move on to methods for measuring major thermal variables in adults, circling back to address issues relevant to egg and larval stages when appropriate. We highlight the advantages and disadvantages of certain equipment and techniques and provide recommendations for the best possible methodology for a given research question. Importantly, we stress that all thermometers and sensors should be calibrated by the factory or researcher before every study and preferably at least annually thereafter.

2.1 | Measuring development rate in reptiles and amphibians

The timing of life cycle events in early life is a key focus in many empirical and theoretical studies that estimate current or future climate change impacts on population viability of amphibians and reptiles. Estimates of embryonic development rate can therefore be of central importance in determining the sensitivity of populations to climate change. In this section, we outline how development rate can be estimated and briefly point to a few applications. Estimates of development rate can be used in a variety of ways, such as constructing thermal performance curves (TPCs) for development (see Section 2.6 for more on TPCs), but to achieve these loftier goals typically requires estimation of development rate at one or more constant temperatures. To this end, there are generally three different types of approaches that can be leveraged. For a number of reasons, the best approach will depend on the circumstances, and may differ between amphibians and reptiles. For instance, assessing morphological features of embryos in transparent amphibian eggs can sometimes be done visually without impeding development, whereas in reptiles, assessment usually involves sacrificing embryos (but see Sparkman et al., 2018 on reptilian ultrasound), such that different methodologies may be favored in each group.

First, for reptiles, development rate can be estimated retrospectively by assessing the length of the incubation period, from egg laying to hatching, and taking the inverse (i.e., development rate = 1/incubation length; Andrews & Schwarzkopf, 2012). This quotient can also be multiplied by 100 to give percent development per day (Stubbs, Kearney, Whiting, & Mitchell, 2014; Woolgar, Trocini, & Mitchell, 2013). We call this retrospective development rate (Table 1), and this approach has a few benefits. Notably, retrospective development rate is noninvasive and does not require sacrifice of embryos, which is especially useful for species that are at-risk or in studies that link development to posthatching phenotypes. This method is commonly used in the reptile literature, producing broadly comparable estimates among- and within-species (Andrews & Schwarzkopf, 2012). Further, if retrospective development rate is estimated at several constant temperatures, then these data can be used in the program DEVARA (Dallwitz & Higgins, 1992), which allows the user to construct a TPC for development with relative ease (e.g., Mitchell, Kearney, Nelson, & Porter, 2008; Neuwald & Valenzuela, 2011; see also Georges, Beggs, Young, & Doody, 2005). However, retrospective development can be subject to a lack of precision. In particular, if the starting point or the end point of development cannot be estimated with accuracy, then retrospective development rate will over- or under-estimate development per unit time. For example, different groups of reptiles lay eggs at different stages of embryonic development, such that the developmental starting point can be uncertain: crocodilian eggs are laid with 9–20 pairs of somites (Laurin & Girondot, 1999); up to one-fourth of development can be completed by the time squamates lay eggs (Sanger, Losos, & Gibson-Brown, 2008); turtle eggs are invariably laid at the gastrula stage (Rafferty, Evans, Scheelings, & Reina, 2013). In addition to variability in the developmental timing of oviposition, there can be variability in hatch timing which may be unrelated to temperature (Rouleau, Massey, & Rollinson, 2019). For example, hatch timing is related to social cues in some turtle and snake nests (Aubret, Blanvillain, Bignon, & Kok, 2016; McKenna, Paladino, Tomillo, & Robinson, 2019), resulting in a discordance between the end of development and egg hatching. Different researchers may also define "hatching" in different ways, and there is a lack of consistency across studies (discussed in Morales-Mérida, Contreras-Mérida, & Girondot, 2019). The use of accelerometers to monitor hatchling movement in wild reptile nests (Morales-Mérida et al., 2019; Rollinson, Massey, Meron, & Leivesley, 2019) may help researchers pinpoint important phenological events, although distinguishing between egg hatching and nest emergence may be difficult with movement profiles alone.

There are several difficulties in applying retrospective development to amphibians. For instance, egg hatching in amphibians does not necessarily correspond to a common developmental stage (e.g., Warkentin, 2011). Further, metamorphosis is perhaps a more defensible earmark for the end of development than is egg hatching, but the timing of metamorphosis depends on a myriad of factors, including larval traits, which can obfuscate a useful interpretation of development rate. One solution to this problem is to recognize that neurulation is a developmental stage common to all amphibians (Stage 16 of Gosner (1960) in frogs and Stage 21 of Harrison (1969)

TABLE 1 Major variables used in thermal ecology and physiology studies of reptiles and amphibians

Variable name	Definition/calculation	Interpretation/examples
Major variables for developmental thermal biology		
Retrospective development rate	(1/incubation length) × 100	Noninvasive method of estimating percent development per day
Equivalent developmental age or morphological age	Time taken by an embryo to incubate to an equivalent morphological stage at a reference temperature	Maps directly onto developmental series, facilitating studies requiring precise estimates of developmental stage
OTR	Range of constant incubation temperatures that result in relatively high hatching success	Developmental rates within the OTR can be used to estimate an optimal temperature for development (T_{opt}) and a developmental zero (T0)
Optimum temperature for development (T_{opt})	The highest incubation temperature within the OTR	T_{opt} enhances fitness by maximizing the developmental rate without reducing egg survival. Exhibits phylogenetic signal and correlates with important climatic factors related to species distributions
Developmental zero (T0)	Estimated temperature at which the rate of embryo development is zero	Represents the lower critical temperature for embryos. Exhibits phylogenetic signal and correlates with important climatic factors related to species distributions
Major variables for thermal physiology of free-living stages		
Body temperature (T_b)	The temperature of an animal's body	Preferably measured internally, but sometimes measured on surface
Preferred body temperature (T_{set})	The T_b or range of T_b chosen by an animal	Usually measured in a laboratory gradient
Thermoregulatory accuracy (d_b)	$\lvert T_{\text{set}} - T_b\rvert$	High values represent low accuracy because T_b is much higher or lower than preferred; values approaching 0 represent high accuracy
Operative temperature (T_e)	Temperature that a nonthermoregulating animal could attain based on radiation, conduction, and convection	Measured with physical OTMs placed in microhabitats typically used by a species or via a mathematical model
OTM	Physical model used to measure T_e. Mimics size, shape, and absorptivity of animal	Often made of copper pipe with temperature data logger
Thermal quality (d_e)	$\lvert T_{\text{set}} - T_e\rvert$	High values represent low quality because T_e is much higher or lower than preferred; values approaching 0 represent high quality
Thermoregulatory effectiveness (E) following Hertz et al. (1993)	1 − (mean d_b/mean d_e)	E will approach 0 when animals do not thermoregulate, will approach 1 when animals thermoregulate carefully, and values are negative when animals actively avoid thermoregulation
Thermoregulatory effectiveness (I) following Blouin-Demers and Weatherhead (2002)	$d_e - d_b$	I is 0 when animals thermoconform, is negative when animals avoid thermally favorable habitats, and is positive when animals are thermoregulating
Thermoregulatory exploitation index (Ex)	The percentage of time an animal spends within its T_{set} range when it is possible to do so (when $d_e = 0$). Variation: the proportion of T_b that are above and below T_{set} when $d_e = 0$ in at least one of microhabitat	Higher values mean animals are better thermoregulators
Critical thermal maximum (CT_{max})	The upper T_b at which animals lose the ability to function	Often measured as the onset of spasms or loss of righting response
Critical thermal minimum (CT_{min})	The lower T_b at which animals lose the ability to function	Often measured as the loss of righting response
Gaping threshold (T_{gape})	The upper T_b at which animals begin to gape to increase evaporative cooling	Indicator of thermal stress. Not all reptiles and amphibians exhibit this response
Panting threshold (T_{pant})	The high T_b at which animals begin to rapidly breathe with their mouths gaping to increase evaporative cooling	Indicator of thermal stress. Not all reptiles and amphibians exhibit this response

TABLE 1 (Continued)

Variable name	Definition/calculation	Interpretation/examples
Voluntary maximum temperature (VT_{max})	The upper T_b at which animals retreat to shelter to avoid further heating	Nondamaging and ecologically relevant measurement of maximum thermal tolerance
Voluntary minimum temperature (VT_{min})	The lower T_b at which animals retreat to shelter to avoid further cooling	Nondamaging and ecologically relevant measurement of minimum thermal tolerance
Hours of activity (h_a)	The number of hours available for critical activities per day	Lower values of h_a might constrain the energy allocated to growth, maintenance and reproduction
Hours of restriction (h_r)	The number of h_r/day that T_e exceeds T_{set} or CT_{max}	High values of h_r associated with increased risk of local extinction
WT	The difference between CT_{max} and field-active T_b	High values mean animals are less likely to be extirpated due to climate change
Thermal safety margin	The difference between a species' upper thermal tolerance (often CT_{max} but sometimes VT_{max} or T_{pant}) and the high air temperatures it experiences in its environment	High values mean animals are less likely to be extirpated due to climate change
TPC	A continuous thermal reaction norm for a performance trait (e.g., running speed, growth rate)	See text for detailed discussion on TPC construction
Absolute thermal performance breadth (T_{br})	The range of T_b over which an ectotherm can perform ($CT_{max} - CT_{min}$)	Can specify a %T_{br}, for example the 80% T_{br} is the range of temperatures where 80% of maximal performance is met
Optimal/maximum trait performance (T_{opt})	The temperature associated with the maximum value of a given performance trait on a TPC	Not to be confused with optimum temperature for development of embryos (see above)

Abbreviations: OTM, operative temperature Model; OTR, optimal thermal range; TPC, thermal performance curve; WT, warming tolerance.

in salamanders), such that development rate can be estimated as time between egg laying and neurulation, rather than egg laying and hatching or metamorphosis (Bradford, 1990). To our knowledge, a parallel approach has not been adopted for retrospective development rate in reptiles.

Other approaches to estimating development rate usually require the ability to assess morphological features of the embryo, including the timing of appearance of morphological characters, and/or linear measures of character size. For example, Georges et al. (1994) and Webb et al. (1987) estimated the development rate of turtle and crocodile embryos, respectively, by measuring change in head width over time in several constant temperature treatments. Each temperature was therefore associated with a change in head size, expressed in μm/day. Other quantitative size features, such as straight line carapace length in turtles (Girondot & Kaska, 2014), can also provide good estimates of development rate, although hatchling mass is generally a poorer estimate of size because mass is relatively sensitive to hydric conditions (Monsinjon, Guillon, Hulin, & Girondot, 2017; see also Bodensteiner, Mitchell, Strickland, Janzen, & Herrel, 2014). There are two important caveats to this approach. First, the sizes of embryonic features are often subject to maternal effects, potentially affecting size changes over time and ultimately resulting in imprecise estimates of development rate. For instance, Webb et al. (1987) noted that egg size influences head width of embryos at late developmental stages, which introduces error into estimation of development rate at later developmental stages, but not earlier stages. Second, a meaningful estimate of development rate can only be achieved when the nature of the change in the focal morphological character (linear, exponential, etc.) is understood across the age of the embryo (e.g., Girondot & Kaska, 2014; Webb et al., 1987). To this end, we suggest that before choosing a quantitative trait, researchers should first explore how the relevant feature changes over the relevant portion of development in their study organism.

Lastly, development rate can be estimated from morphology in terms of “equivalent developmental age,” or “morphological age” (Rollinson et al., 2018; Webb et al., 1987; Webb, Manolis, Buckworth, & Sack, 1983). In this approach, a reference series of developmental stages is created by incubating eggs at given constant temperature (see table S9 in Rollinson et al., 2018 for many reptile examples), and the number of days it takes to reach each developmental stage is noted. Embryos may then be incubated at any constant temperature and the observed developmental stage can then be expressed in terms of the time it took the embryo in the reference series to reach the same developmental stage, or its “morphological age.” Development rate coefficients can then be derived, allowing the researcher to predict how many days of development at a particular temperature is required to achieve a specific developmental stage (Webb et al., 1987).

Notably, there may be a strong correlation between “morphological age” and size measurements (head width, carapace length, etc.), such that results obtained from these different approaches may be similar (Webb et al., 1987). However, for reasons outlined below, size measurements have at least one advantage over “morphological age.” In both approaches, the basic idea is to create a table with incubation duration at constant temperature that corresponds to a

TABLE 2 Major tools used in thermal ecology and physiology studies of reptiles and amphibians

Name	Description	Pricing
Buddy egg monitor (Avitronics)	Uses infrared transmitters and sensors to noninvasively measure the heart rate of reptile embryos; used to measure acute thermal tolerance of reptile embryos	$300
Infrared thermometer or camera	Measures surface temperature by focusing infrared radiation emitted from animal surface onto a thermopile. Digital temperature guns tell you temperature of an object; infrared cameras can also show temperature differences among objects (e.g., animal and substrate)	Thermometer: $50–100 camera: pricing varies widely, typically $350+
Mercury thermometer	Mercury expands or contracts along a scale as temperature changes. Currently not widely used to measure animal T_b due to risk of contamination if thermometer breaks	n/a
Alcohol thermometer	An alcohol (often ethanol) expands or contracts along a scale as temperature changes. A safer alternative to mercury thermometers	<$10
Thermocouple	Two wires of different metals are welded together at one end into a junction that creates a voltage when temperature changes. Currently the most commonly used thermometer to measure T_b, but accuracy ranges from ±0.5°C to 5°C	$5–100
Thermistor	Highly accurate thermometer (±0.05°C–1.5°C) measures temperature-dependent resistance changes in a polymer or ceramic resistor	$20+
Resistance temperature detector	Highly accurate thermometer (±0.1°C–1°C) measures temperature-dependent resistance changes in a metal resistor	$20+
Temperature-sensitive radio-telemetry (e.g., Holohil, Lotek)	Interpulse interval of radio-transmitter is temperature dependent	Pricing varies widely; radio-transmitters typically $200+
Miniature temperature data loggers (e.g., Thermochron iButton)	Miniature devices used to log operative temperature (in operative temperature models) or environmental temperature or body temperature (surface or internal). Accuracy for basic models is ±1.0°C	$30+
Temperature data loggers (e.g., Onset HOBO Pendant)	Devices used to log temperature, usually of the environment	$50+

Note: Many of these tools are produced by multiple companies; we provide examples of commonly used models and their approximate pricing in USD as of June 2020.

size measurement (e.g., head width) or a morphological stage. If a size measurement is used, then it is possible to derive the general shape of the relationship between size and development time. But if "morphological age" is used, the general pattern may be less meaningful, as only time to reach a specific morphological stage can be used, making it difficult to generalize the growth rate at other temperatures or fluctuating temperatures. For instance, under laboratory conditions, Rollinson et al. (2018) constructed a TPC for turtle embryos by estimating development rate between specific morphological ages. Next, they generated a model to predict morphological age in wild nests that experience thermal fluctuation. Although the model was able to explain most of the variation in morphological age in wild nests, accurate predictions of morphological age arose only when an additional covariate was added to the original model. The lack of accuracy in the original model might have occurred because different developmental stages appear to have different temperature sensitivities (Webb et al., 1987), and therefore development rate estimated across a specific series of developmental stages (as in Rollinson et al., 2018) does not necessarily reflect development rate across other developmental stages. Temperature sensitivity of size traits during different portions of development are more easily understood as they can be readily visualized by mapping size against embryo age at a constant temperature.

As a final note, there may be alternatives to estimating development rate under constant conditions in the laboratory. For instance, Girondot and Kaska (2014) develop a broadly applicable model of developmental timing using a time series of temperatures recorded in natural turtle nests, with parameters estimated in part using previously published data on retrospective incubation duration. Their model accurately predicts developmental stage and hatch timing of turtles in wild nests; their R code is also publicly available and relatively easy to implement (Girondot, 2020). Thus, if the goal of the study is to predict development rate in the wild, then such a study may require limited laboratory work (see also Georges et al., 2005; Girondot, Hassine, Sellos, Godfrey, & Guillon, 2010). Indeed, mean nest temperatures alone may poorly indicate developmental rates in the wild since fluctuating temperatures, which characterize natural nests, result in developmental rates that differ from constant temperatures, even if the mean temperature is identical.

Measuring temperature effects on development rate in the lab or in the wild is an essential component of understanding how current and future environmental temperatures may impact amphibian and reptile reproduction. Fundamentally, measuring temperature accurately and with minimal impact on animals, whether they be egg, larval, or adult stages, is important in this context. The next section dives deeply into methods for measuring body temperatures in multiple contexts.

2.2 | Measuring body temperatures of reptiles and amphibians

Perhaps the most central variable in the fields of thermal ecology and physiology is the body temperature (T_b; Table 1) of an animal. Figure 1 shows the T_b of a free-ranging amphibian or reptile as it thermoregulates over a 24-hr period, along with a number of additional variables commonly measured by thermal ecologists. We will discuss the other variables in Figure 1 as we introduce and define them throughout this paper.

Whether animals are free-ranging or maintained in captivity, measuring T_b accurately and at appropriate time intervals relies heavily on durable, easy to calibrate equipment and technology that minimizes interference and stress on study animals. Below we discuss the use of thermometers, cameras, and data-logging technology in measuring the T_b of reptiles and amphibians.

2.2.1 | Considerations of habitat and life stage

Measuring field T_b of embryos can be done by placing temperature loggers (e.g., Thermochron iButtons) or thermocouples in nests or egg masses and systematically recording temperatures throughout the incubation period. Nest temperatures vary greatly across space and time. For example, temperature varies across nesting microhabitats (e.g., sun vs. shade), across depths in the soil or water, and even within nests due to vertical thermal gradients (Booth, 2018). Additionally, temperatures change over time due to daily, seasonal, or yearly variation in temperature or, in large nests, due to metabolic heating of late-stage embryos (e.g., sea turtles). Ideally, nests should be located through some form of random searching to prevent biased estimates of mean nest conditions (e.g., Pruett, Addis, & Warner, 2019; Tiatragul, Hall, & Warner, 2020). Data loggers should be deployed across a diversity of

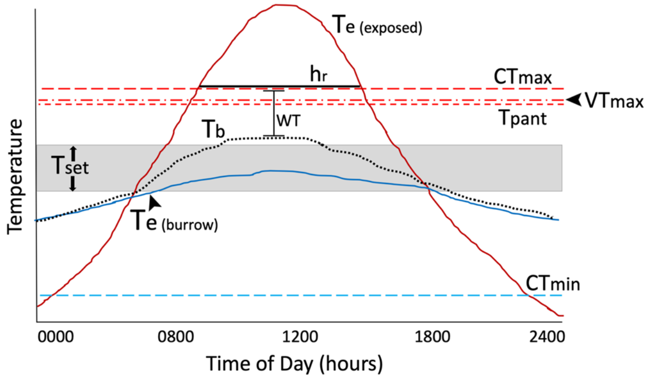

FIGURE 1 Schematic showing a free-ranging amphibian or reptile (body temperature, T_b) thermoregulating throughout the course of a day. Variables (Table 1) include the preferred T_b range (T_{set}); operative temperatures (T_e) in an exposed microhabitat and a refugium like a burrow; upper thermal tolerance limits including critical thermal maximum (CT_{max}), voluntary thermal maximum (VT_{max}), and panting threshold (T_{pant}); WT expressed as the difference between CT_{max} and T_b; and hours of restriction (h_r) or the time that this animal cannot remain in a given microhabitat (e.g., exposed) without overheating. Additional variables discussed in the text (e.g., VT_{min}) could also be mapped onto the figure but we have left these off for simplicity. WT, warming tolerance [Color figure can be viewed at wileyonlinelibrary.com]

habitats for wide-ranging species and throughout the duration of the nesting season for species that oviposit multiple times during the year (Pearson & Warner, 2018; Tiatragul et al., 2020). In large nests, data loggers may need to be deployed at the top and bottom of the nest to account for within-nest variation in temperature (e.g., Telemeco et al., 2016). Depending on specifications, data loggers may need to be waterproofed (e.g., wrapped in parafilm and tied in a balloon, coated with Plasti Dip® (Plasti Dip International, Blaine, MN), or waterproof models such as HoBo Pendants can be used) and effort should be made to ensure that water-proofing does not heavily influence temperature measurements. Many factors influence temperature and additional data may be necessary to understand thermal variation of nests (e.g., shade cover, soil moisture content, rainfall, air temperature). Importantly, both the mean and variance of nest temperature should be measured and considered when determining embryo T_b. Indeed, both mean and variance can influence important developmental phenotypes (Georges et al., 2005) and a fundamental challenge for embryo thermal ecology is to incorporate both mean and variance of nest temperatures in predictive models (Carter, Sadd, Tuberville, Paitz, & Bowden, 2018). For viviparous species, maternal T_b during pregnancy should be assessed via one of the methods outlined below. Finally, during laboratory assays of reptile eggs, egg temperature can be monitored by carefully poking a hole through the egg shell, inserting a thermocouple probe (discussed below), and sealing the probe in place with paraffin wax (see Gao et al., 2014).

Consideration of an animal's habitat and body size are important when determining how to measure its T_b. First, small aquatic ectotherms tend to be thermoconformers due to the high specific heat of water (e.g., Sos, 2007). Amphibian egg masses laid in water, along with most amphibian larvae and small-bodied aquatic amphibians and reptiles, are likely to match the temperature of the water, making water temperature a useful surrogate for T_b. However, larvae are able to behaviorally thermoregulate by moving within the water column (e.g., Freidenburg & Skelly, 2004). Notably, large-bodied ectotherms and those that bask in solar radiation on the water's surface or on the shore are unlikely to be thermoconformers. Despite low metabolic rates, large ectotherms can display inertial endothermy (Table 1) due to their low surface area to volume ratios, even considering the high heat capacity of water. For example, Leatherback Sea Turtles (*Dermochelys coriacea*) can have T_b much higher than surrounding ocean water (James & Mrosovsky, 2004). Terrestrial amphibians and reptiles can experience T_b dramatically different from surrounding air temperature due to the complex heat exchange processes of conduction, convection, radiation, and evaporative cooling (Angilletta, 2009). Clearly, measurement of the actual T_b of animals is essential for all study organisms, especially terrestrial and large or basking aquatic reptiles and amphibians.

2.2.2 | Measuring surface body temperatures

The first question a researcher must ask is whether to measure internal or external (surface) temperature. Due to thermal inertia, the internal T_b and surface temperatures of large ectotherms may be very different. In most applications in thermal ecology and physiology (see below), measuring internal T_b is preferable because that temperature is what is being experienced by the animal's tissues, including the thermoregulatory centers in the animal's central nervous system. However, there are multiple examples of situations in which collecting internal T_b data is not possible due to risks involved in capturing and handling sensitive animals, safety issues for researchers studying dangerous animals, and other concerns. We treat these scenarios as examples in the following section on how to measure T_b.

Measuring the surface temperature of a reptile or amphibian is typically accomplished using an infrared (IR) thermometer (aka “IR guns”) or thermal imaging camera (Table 2). The main benefit of these techniques is that animals need not be captured to collect data, thus reducing stress on the animal, preserving natural behaviors, and eliminating the risk of altering the subject's T_b. For example, surface temperature data may be collected instead of internal temperature when researchers are collecting data on endangered nocturnal frogs or salamanders; their internal T_b are likely to be similar to their surface temperature, and researchers can collect data very rapidly without disturbing the animals. Another example is a researcher wishing to collect T_b data on denning rattlesnakes, which are often seen inside crevices. Trying to extract the snakes from the crevices would be dangerous both to the snakes and the researcher, and so collecting surface temperature data would be preferable in this case.

A thermal imaging camera is an instrument that creates an image using IR radiation and translates it into visible light for visualization. A standard camera operating in the visual range only captures light waves between 400 and 700 nm, whereas a thermal imaging camera spans the range of 1,000–14,000 nm. Many models of thermal cameras automatically self-calibrate to their new environment every few minutes to optimize the accuracy of readings. They also provide a full thermal image of the environment surrounding the subject, which allows assessment of microhabitat selection (e.g., in lizards, Goller, Goller, & French, 2014). By collecting data on the surrounding environment, the thermal camera also grants the user the ability to monitor thermal aspects of the environment in real time, allowing for moving animals to be easily tracked. Thermal cameras can also measure temperature across different body parts, with important implications for studying regional heterothermy and for relating surface T_b to core T_b (Sannolo, Mangiacotti, Sacchi, & Scali, 2014). For example, eye temperature and temperature at the base of the tail best match temperatures recorded by a cloacal probe in lizards across a range of sizes (Barroso, Carretero, Silva, & Sannolo, 2016).

There are important technical considerations when using a thermal imaging camera, for which we direct readers to Tattersall (2016) and Barroso et al. (2016) for excellent and thorough discussion of the topic. Arguably the most important parameter to consider is the emissivity, which is a measure of how an object interacts with and emits radiation. An appropriate emissivity setting is critical for accurate temperature readings and plays a large role in heat transfer calculations. For biological tissues, emissivity generally ranges from

0.95 to 0.98 (Tattersall, 2016). Fortunately, this can often be adjusted after images are captured and changed as needed in downstream analyses. Another important consideration is the distance between the camera and the subject. The greater the distance between them, the more atmospheric interference, and the less accurate the calculations will be (Tattersall, 2016). One drawback of thermal imaging cameras and IR thermometers is that they cannot measure temperature through glass or other reflective surfaces; in this case they will only read the thermal energy reflected back to the camera. Importantly, with IR thermometers, distance from the measured object determines the measured area, therefore the closer we can get, the smaller the radius of measurement and more precisely the specimen is measured. Often misleading is the laser-pointer feature of many IR thermometers, which can lead the operator to believe that the instrument is measuring a narrowly focused area. IR thermometers can also be inaccurate on smaller subjects, even at close distances. In small lizards the difference between core and surface temperatures should be minimal (±1°C; Jones & Avery, 1989; Luna & Font, 2013). However, T_b measurements of lacertid lizards collected with IR thermometers overestimated T_b compared to internal T_b (Carretero, 2012). Thermal imaging cameras detect both epidermal and dermal heat, while IR thermometers are limited to the epidermal layer (Tattersall & Cadena, 2013). As with thermal imaging cameras, care must be taken to follow the technical specifications of the instrument, to understand the biology of the organism, and to establish a repeatable protocol when conducting measures.

2.2.3 | Measuring internal body temperatures

Although surface temperatures can be informative in some situations, in most cases it is desirable to collect data on the internal T_b of an animal. The technology best suited for doing this depends on the study methodology. In general, studies in which animals are point-sampled utilize the "grab and jab" (Avery, 1982) technique, where a thermometer is used to measure the cloacal T_b of the animal. In contrast, longer-term studies of marked individuals typically use temperature-sensitive radiotelemetry or temperature data loggers. Below, we discuss each method and provide examples of applications in which these techniques are commonly used and recommendations on best practices.

The grab and jab technique involves capturing an animal and taking its internal T_b as rapidly as possible by inserting a thermometer into its cloaca. Speed is of the essence when grabbing and jabbing because heat is rapidly transferred from a researcher's warm hand into an animal's cooler body, or vice versa. Types of thermometers used in the grab and jab include mercury thermometers, alcohol thermometers, thermocouples, thermistors, and resistance temperature detectors (RTDs; Table 2), but thermocouples are the most commonly used. The first major treatise on thermal biology of reptiles used thermocouples (Cowles & Bogert, 1944), but these were fairly clunky. The most commonly used thermometer at the time and for decades thereafter was the mercury thermometer, especially the Schultheis "quick-reading" thermometer that was designed specifically for taking cloacal temperatures of reptiles. However, digital thermocouple probes have largely replaced the Schultheis because they are easier to read and eliminate danger of mercury contamination if a thermometer breaks. In general, thermocouples are inexpensive and easy to use, making them the thermometer of choice for the grab and jab. However, their accuracy varies widely, so caution must be taken to test and calibrate all thermocouples. Alternatives to thermocouples include thermistors and RTDs, which measure temperature-dependent resistance changes in a resistor (polymer or ceramic resistors for thermistors, metal resistors for RTDs) and are typically more accurate than thermocouples.

While the grab and jab technique might be appropriate for capturing snapshots of data on animals that are captured opportunistically, long-term field studies on individuals are usually better served by collecting T_b data with either temperature-sensitive radio-telemetry or with the use of temperature data loggers. Using these techniques precludes the need to recapture and handle the animals multiple times, which reduces stress on the animal, facilitates ease of data collection by researchers, and can often provide continuous data on T_b when researchers are not present. Radio-telemetry was first used to study snakes in the early 1970s (reviewed in Újváry & Korsós, 2000) and companies soon began producing radio-transmitters with interpulse intervals proportional to temperature. In this temperature-sensitive radio-telemetry, the researcher records interpulse intervals and can later use factory-provided calibration curves to calculate the temperature of the animal. Radio-transmitters on collars, backpacks, or other external devices, or epoxied to the surface of an animal's skin or shell, provide surface temperature data. Radio-transmitters either force-fed or surgically implanted into the animal's body provide short-term or longer-term internal T_b data, respectively. The continued miniaturization of radio-transmitters over time has facilitated studies of even very small amphibians and reptiles. Most manufacturers offer temperature-sensitive transmitters at prices just slightly higher than regular transmitters, often making the investment worthwhile even when the goal of the study is not directly related to thermal ecology or physiology. However, measuring the interpulse interval by hand (e.g., with a stopwatch) can be inaccurate and researchers only obtain data when they radio-track an animal (point sampling). Taylor et al. (2004) showed that T_b patterns calculated from point-sampling yield a dramatically different overall picture of the daily T_b of a snake compared to techniques that continuously log T_b data because researchers tend to visit their sites at nonrandom times of day and only typically log a single T_b sample per individual tracked. Numerous data-logging solutions were developed to mitigate this problem (Beaupre & Beaupre, 1994; Peterson & Dorcas, 1992). Several companies now produce receivers with data acquisition capability (e.g., Telonics, Lotek) that when solar-powered and paired with a tall stationary antenna can log thousands of T_b data points, as long as animals are within range. Local acquisition and storage of T_b data will likely be replaced by satellite-based radio-telemetry technology and data-loggers as their technology continues to improve, miniaturize, and become more affordable.

For larger animals like heavy-bodied snakes, turtles, crocodilians, tuatara, and large-bodied amphibians, attaching/implanting temperature data-loggers to the animal is an excellent choice. Thermochron iButton data-loggers can be programmed to store temperature data at chosen intervals and are commonly used to collect temperature data by gluing them to an animal's body or surgically implanting them inside the body cavity. For example, many snake researchers implant iButtons alongside radio-transmitters and download the data when they remove the iButton and radio-transmitter. A major benefit of data-loggers like iButtons is that data are continuously recorded (Taylor et al., 2004) and data acquisition is not limited to the range of a receiver as with temperature-sensitive radio-transmitters. However, a downside of data-loggers is that they must be retrieved to collect the data; if radio-transmitters fail or if an animal is carried away by a predator, the data are lost. iButtons are typically used to study animals that are large enough such that the data-logger mass (3.5 g after dipping in sealant) along with the radio-transmitter mass if present are together <5% of the animal. However, several groups have recently developed methods to miniaturize iButtons (Lovegrove, 2009; Robert & Thompson, 2003; Virens & Cree, 2018) to as low as 0.3 g such that they can reasonably be attached to animals as small as 6.6 g. When properly coated, these miniaturized iButtons can also be surgically implanted to collect internal T_b from small animals, such as lizards (Rusch & Angilletta, 2017; Sears et al., 2016). For very large animals, like crocodilians and some turtles, lizards, and snakes, it is possible to attach or implant larger data loggers like Onset HOBO Tidbit data loggers (e.g., Fitzgerald & Nelson, 2011; Harlow, Purwandana, Jessop, & Phillips, 2010; Merchant, Williams, Trosclair, Elsey, & Millsa, 2007; Wolf, Walters, Rochford, Snow, & Mazzotti, 2016). Some manufacturers produce specialized devices to measure temperature, depth, pressure, and other variables, which are primarily applicable for large, diving, marine vertebrates like sea turtles. Nonetheless, miniaturization is all the rage right now as manufacturers such as Star-Oddi and Lotek produce smaller and smaller devices for tracking animals and measuring their temperatures.

We have gone over in detail the current best practices for measuring T_b. But what is the point of it? What insights can T_b give us into the lives of reptiles and amphibians? Researchers have used T_b data for countless applications. In the following sections, we introduce additional temperature variables and discuss how they are used along with T_b to provide important insights into the ecology and physiology of reptiles and amphibians.

2.3 | Preferred body temperature and thermoregulatory accuracy

Several decades ago, researchers recognized the importance of measuring the preferred T_b of ectotherms in studies of thermal ecology and physiology (Dawson, 1975). The preferred T_b of animals has numerous names and abbreviations in the literature, but here we refer to it as the set-point T_b, or T_{set}. T_{set} can be calculated as a single value (often the median T_b of animals free to choose where to thermoregulate in a laboratory gradient) or as a range of values (often the interquartile range of T_b chosen; Figure 1 and Table 1).

Embryos are little able to thermoregulate (Cordero, Telemeco, & Gangloff, 2018; Telemeco et al., 2016; but see Shine & Du, 2018); however, T_{set} of embryos can be indirectly assessed by considering nesting behavior of females in both the lab and field. In field studies, data loggers such as iButtons should be deployed at randomly selected locations at a typical nest depth in the ground or height in the water column. Data loggers should also be deployed in maternally selected nests as temperature differences between randomly and maternally selected nest sites indicate thermal preference of nesting females, which may relate to the thermal ecology of embryos (Mitchell, Maciel, & Janzen, 2013; Pruett et al., 2019). For studies of preference in the lab, gravid females can be placed in a thermal gradient and allowed to oviposit in the preferred location (e.g., Warner & Andrews, 2002). A powerful research plan involves quantifying both random and maternally selected nest temperatures in the field and then incubating eggs under each of these conditions in the lab to assess the consequences of nest-site selection on embryo development (see Tiatragul et al., 2020). Additionally, eggs can be split between randomly and maternally selected nests using a split-clutch design to assess embryo development and survival in the field (Mitchell et al., 2013). Although females typically nest in microhabitats that enhance embryo development (vs. what is generally available); nest temperatures are not always optimal. For example, females may construct nests in microhabitats that reduce the potential for depredation (of the nest or the female), but consequently result in suboptimal incubation temperatures. Moreover, prevailing weather patterns can heavily influence nest temperature. Thus, plasticity in nesting behavior may be insufficient to compensate for warming due to global change (Telemeco, Fletcher, et al., 2017). Finally, eggs can be incubated at a diversity of constant temperatures in the lab to determine the optimal temperatures for development; however, three things must be considered. First, embryo survival is often high across a range of temperatures (optimal thermal range [OTR]; Andrews & Schwarzkopf, 2012; Mueller, Bucsky, Korito, & Manzanares, 2019a), but many phenotypes (e.g., body size, post-hatching performance) may be optimal at a single temperature. Second, a single temperature may not optimize all phenotypes. Third, nest temperatures are rarely constant, so optimal conditions based on constant temperatures may not correlate with optimal conditions in the wild.

For adult amphibians and reptiles, measuring a meaningful T_{set} for a species represents several trade-offs for the researcher. On the one hand, T_{set} should be measured in a laboratory setting where researchers can ensure that animals have access to a wide range of ambient temperatures without being impacted by other variables like predators, prey, and a host of other factors that could constrain field-active T_b. On the other hand, animals may be stressed in the laboratory, and T_{set} measurements in lab gradients may be short in time due to study design constraints. While measuring T_{set} from field-active animals as a range of T_b selected might mitigate the problem of stressed animals in the lab, it is generally accepted that behavioral constraints in the field are more problematic than the impacts of stress in the lab. Researchers therefore tend to utilize gradients constructed in the lab (methods vary, but animals must have access to a wide enough range of temperatures that they can thermoregulate at their desired T_b). Some variety of thermal probe (Table 2) is inserted in their cloacae or a thermal imaging camera mounted above the gradient and animals are allowed to thermoregulate for a period of time (Camacho & Rusch, 2017). The length of time varies widely, but researchers should attempt to allow animals to thermoregulate for as long as possible to ensure they are behaving somewhat normally and that the data encompass potential circadian rhythms in thermoregulation. Typically, using the interquartile range of selected T_b for one 24-hr period is ideal for establishing T_{set}, although sometimes significantly shorter or more specific time periods are appropriate, for example when attempting to reduce diel variation and characterize T_{set} only during active hours (Camacho & Rusch, 2017) or when studying endangered animals that scientists are only permitted to handle for limited periods of time (e.g., Ivey et al., 2020).

T_{set} data collected in a laboratory are typically treated as a set value in thermal ecology applications (see below). However, an animal's T_{set} can change if its physiological conditions change (reviewed in Camacho & Rusch, 2017; Hertz, Huey, & Stevenson, 1993). For example, some viviparous female reptiles choose higher T_b when they are gestating, presumably to facilitate rapid development of young (Daut & Andrews, 1993); however, other species may actually choose *lower* T_{set} when pregnant to improve offspring fitness (Mathies & Andrews, 1997). Animals with recent meals may choose higher T_b to help facilitate digestion (Gatten, 1974), and ectotherms with infections may show behavioral fever where they temporarily increase their T_{set} (Richards-Zawacki, 2010). Dehydrated reptiles (Crowley, 1987; Sannolo & Carretero, 2019) and those exposed to hypoxic gas (Gangloff & Telemeco, 2018; Hicks & Wood, 1985) exhibit lower T_{set}, likely to lower metabolic demand or reduce water loss. If a general T_{set} value or range of values is desired for thermal ecology applications (see below), then researchers should ensure that a large enough sample size of animals in various relevant physiological states are included.

In thermal ecology, a major application of T_{set} is calculation of the thermoregulatory accuracy (d_b) of free-living ectotherms (Hertz et al., 1993). The variable d_b is calculated as the absolute value of the difference between the T_{set} and the field-active T_b of animals (Table 1). Low values of d_b represent high thermoregulatory accuracy because animals are able to achieve their T_{set} or close to it in the field. In contrast, high values of d_b represent low thermoregulatory accuracy because T_b is either much higher or lower than T_{set}. Some authors (e.g., Ivey et al., 2020) have begun calculating d_b as the raw difference between T_{set} and T_b rather than the absolute value of the difference to provide more information: negative d_b values occur when T_b is lower than T_{set}, while positive d_b values occur when T_b is higher than T_{set}. In other words, a negative d_b indicates that an animal cannot thermoregulate at temperatures as high as it would prefer, whereas a positive d_b value reflect an animal that cannot cool itself to the preferred body temperature. Very low or very high values of d_b may reflect ecological constraints (e.g., foraging, hiding from predators, finding mates, or conducting other activities when ambient temperatures are not conducive for thermoregulating at T_{set}). While d_b is an interesting variable in its own right, it is mainly used in conjunction with thermal quality of the environment to explore the thermoregulatory effectiveness of an animal in a given habitat (see Section 2.4). Before delving into this, we must first explore measurement of the thermal quality of a habitat.

2.4 | Operative temperatures and habitat thermal quality

Studies of the thermal ecology of reptiles and amphibians seek to elucidate the thermal relationships between these animals and their environments. To do so, it is often necessary to characterize the thermal properties of an environment, which can be accomplished with either mathematical or physical operative temperature models (OTMs). Mathematical OTMs use microclimate data (e.g., air temperature, ground temperature, solar radiation, wind speed, etc.) as inputs and solve heat-balance equations to estimate animal body temperature (for reviews and examples see Angilletta, Sears, & Pringle, 2009; Campbell & Norman, 1998; Fei et al., 2012; McNab, 2002). Mathematical OTMs are heavily used in mechanistic niche modeling (see Section 2.8), but frequently do not provide the resolution desired for field studies of thermal ecology and behavior. By contrast, physical OTMs allow fine-scale resolution and are heavily used in field studies. These models are physical objects that mimic the size, shape, and absorptivity of focal animals allowing measurement of instantaneous operative temperature (T_e) in a given environment (Figure 1 and Table 1). Regardless of the model used, estimated T_e illustrates the range of possible temperatures of a nonthermoregulating animal in a given microhabitat. We focus here on physical OTMs (just "OTMs" hereafter). OTMs have been described, validated, and discussed in great detail elsewhere (Bakken, 1992; Bakken & Angilletta, 2013; Dzialowski, 2005), so our goal here is not to go into exhaustive detail about constructing and interpreting OTMs. Instead, we provide basic recommendations for using OTMs in thermal ecology studies and then review a major application of OTMs (mathematical or physical) in thermal ecology: calculating the thermal quality of various habitats.

OTMs have been used for decades to characterize the thermal environment available to animals (the first were water-filled beer cans!; Heath, 1964). Probably the most commonly constructed OTM is a hollow copper pipe painted to match the absorptivity of the animal, with a temperature data logger inside, and capped on both ends with copper or PVC caps. In some cases, especially with very small animals for which the shape of the animal could be very important for heat exchange, researchers electroplate a data logger inside a wax mold of an animal to create a hollow copper cast of the animal (Bakken & Gates, 1975). In extremely small lizards, Vickers and Schwarzkopf (2016) showed that small data-loggers on their own provided very accurate measurements of lizard T_b in the wild, suggesting that these could be used as an OTM without additional model material. Similarly, placing data loggers within artificial or real nests as described above in Section 2.2.1 constitutes using a logger as an OTM for eggs. For most OTMs, copper is the material of choice due to its high heat conductance. Given that the purpose of an OTM is to measure the instantaneous T_e based on radiation, conduction, and convection, OTMs by definition should have zero heat capacity, and so should be empty (Bakken & Gates, 1975). However, hollow OTMs may overestimate the range of T_e available to large-bodied animals who experience much more inertia when heating and cooling (Seebacher & Shine, 2004). In certain applications, water-filled biophysical models may be appropriate if the goal is to mimic the thermal inertia of the animal's body (Lutterschmidt & Reinert, 2012). Water-filled models are not strictly OTMs and as such we recommend referring to them as physical models. OTMs can also be modified easily to permit novel approaches to important questions regarding thermoregulation, such as how posture affects T_b (Brewster & Beaupre, 2019). Recent technological advances in 3D printing can facilitate the cheap, quick production of identical operative models, although the choice of size, type of material, and material density should be considered and calibrated carefully (Watson & Francis, 2015). The importance of calibration of OTMs or physical models against actual animals cannot be overstated, as error from improper construction and use of OTMs can be high (Bakken & Angilletta, 2013; Dzialowski, 2005). Dzialowski (2005) provides a helpful review and guide for how to properly calibrate models.

While OTMs can be used for numerous applications, one of the most common uses is to calculate the thermal quality (d_e) of the environment (Hertz et al., 1993). The variable d_e is the absolute value of the difference between operative temperature (T_e) and preferred T_b (T_{set}). High values of d_e therefore represent poor thermal quality because environmental temperatures are either too low or too high, while values of d_e close to zero represent good thermal quality because the animal is presumably better able to thermoregulate near its T_{set}. The uses of d_e are numerous in physiological ecology studies on reptiles and amphibians. Several notable examples include assessing suitability of a fire-disturbed habitat for amphibians (Hossack, Eby, Guscio, & Corn, 2009), comparing lizard habitat use in gradients of altered landscapes (Thompson, Halstead, & Donnelly, 2018), examining how females choose appropriate nesting sites (Angilletta et al., 2009), evaluating habitat suitability for certain species and predicting how it will change as global climate change progresses (Vicenzi, Corbalán, Miles, Sinervo, & Ibargüengoytía, 2017), and many more. In addition, d_b and d_e together are often used to calculate an index of thermoregulatory efficiency that combines several variables discussed above. Hertz et al. (1993) defined the index of thermoregulatory effectiveness (E; Table 1) as 1 − (mean d_b/mean d_e), where E will approach 0 when animals do not thermoregulate and will approach 1 when animals thermoregulate carefully. Values are negative when animals actively avoid thermoregulation, indicating thermoregulatory trade-offs due to other factors like the need to feed, hide from predators, find mates, and so forth. A slightly more straightforward option is calculating thermoregulatory effectiveness (I; Table 1) as $d_e - d_b$ (Blouin-Demers & Weatherhead, 2002), where values of 0 represent thermoconformity, negative values mean animals avoid thermally favorable habitats, and positive values mean that animals are thermoregulating. Another similar metric is the thermoregulatory exploitation index (Ex; Table 1), calculated as the percentage of time an animal spends within its T_{set} range when it is possible to do so (e.g., when $d_e = 0$; Christian & Weavers, 1996).

As a metric of habitat suitability, thermal quality, and the associated variables of E, I, and Ex are important components of thermal ecology studies because they measure how close animals' T_b is to the temperature they *want* to be (T_{set}). Indeed, researchers often calculate the hours of activity (h_a; Table 1) as the time available for critical activities per day and the hours of restriction (h_r; Table 1) as the number of hours per day that T_e exceeds T_{set}, or when animals would necessarily exceed their T_{set} by being active and instead might enter refugia to reduce T_b (Caetano et al., 2020; Sinervo et al., 2010). However, ectotherms may exceed their T_{set} in the wild to conduct important activities like foraging and mating (Camacho et al., 2018; Cowles & Bogert, 1944). So, h_r can also be expressed as the hours in a given day that T_e exceeds upper thermal tolerance (Figure 1; Ivey et al., 2020). In that light, exploring variables that encompass thermal tolerance, as opposed to thermal preference, are important because they encompass limits below and above which animal T_b *cannot* perform activities essential for life. In addition, thermal tolerance limits are essential components of TPCs (Section 2.6).

2.5 | Estimating thermal tolerance of reptiles and amphibians

The critical thermal maximum (CT_{max}) and minimum (CT_{min}) define the limits of a range of T_b in which an individual of a species can perform a given function, such as locomote (Figure 2 and Table 1). Although animals may rarely experience these temperatures in nature, CT_{min} and CT_{max} are some of the most widely measured thermal parameters in reptiles and amphibians and thus provide our best ability to compare thermal biology across species (e.g., Sunday, Bates, & Nicholas, 2011). Conceptually, CT_{min} and CT_{max} provide information about the absolute tolerance of species because ectotherms rapidly die if they fail to cool or heat further. The difference between the CT_{min} and CT_{max} is the absolute thermal performance breadth (T_{br}), which represents the range of T_b over which an ectotherm can perform (e.g., locomote). However, more conservative estimates of T_{br} may be more informative; for example, the 80% T_{br} defines the range of temperatures where 80% of maximal performance is met. Animals with the same CT limits could have very different 80% T_{br} based on whether they are thermally specialized (narrow 80% T_{br}) or

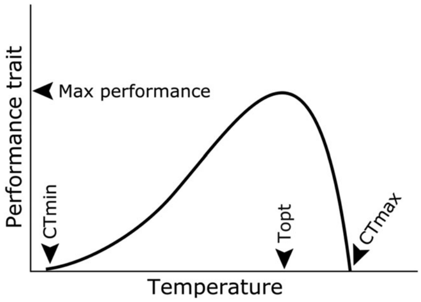

FIGURE 2 A thermal performance curve. Depicted are the critical thermal minimum (CT_{min}), critical thermal maximum (CT_{max}), and temperature that yields highest value for performance (T_{opt})

general (wide 80% T_{br}). Other related variables are also occasionally used; these include the gaping threshold (T_{gape}), panting threshold (T_{pant}), and voluntary limits (VT_{min} and VT_{max}), which may frequently provide more ecologically relevant measures of thermal limitation than critical limits. While Kubisch et al. (2016) define the VT_{min} and VT_{max} as the first and third interquartile range of T_b selected in a gradient, we define them as the lowest and highest T_b tolerated by animals (Table 1) per Camacho et al. (2018). Other relevant variables include the warming tolerance, or the difference between CT_{max} and T_b (Brusch, Taylor, & Whitfield, 2016), and the thermal safety margin, or the difference between a species' upper thermal tolerance (often CT_{max} but sometimes VT_{max} or T_{pant}) and the high air temperatures it experiences in its environment (Table 1; Sunday et al., 2014). These variables are important in understanding vulnerability of a species to warming climates. The following two sections discuss the best practices for measuring thermal tolerance in embryos and adults.

2.5.1 | Thermal tolerance of embryos

When considering critical temperatures of early life stages, it is important to remember that egg and/or larval stages have critical temperatures that may not match those of adults. This, in part, results from fundamental differences between embryos and posthatching stages. For example, CT_{max}/CT_{min} of posthatching stages are often determined by loss of righting ability; however, such a state does not apply to embryos. Thus, terms like CT_{max}/CT_{min} may not be appropriate to describe embryo critical temperatures (see Hall & Sun, 2020). Lethal temperatures (e.g., LT50) are often considered rather than critical temperatures of performance. Regardless, no population is viable in the absence of proper embryo development; therefore, responses of early life stages to thermal stress are critical to evaluate against the backdrop of climate change (Levy et al., 2015; Telemeco, Fletcher, et al., 2017). A powerful method to assess thermal tolerance is to incubate eggs in at least five constant temperatures and measure egg survival as well as a diversity of embryo and hatchling phenotypes. Indeed, assessing egg survival alone may be insufficient to describe thermal tolerance since some temperatures can result in high hatching success but poor hatchling performance or viability (Mueller, Ruiz-García, García-Gasca, & Abreu-Grobois, 2019b). Additionally, there are four vital considerations when measuring thermal tolerances of early life stages.

First, the method for measuring embryo thermal tolerance will influence conclusions about the potential for thermal stress due to climate warming (see Hall & Sun, 2020). Embryo thermal tolerance has historically been assessed by incubating eggs at various constant temperatures and monitoring egg survival and/or embryo development (e.g., Sanger, Kyrkos, Lachance, Czesny, & Stroud, 2018). Such data allow for the estimation of important phenotypes such as the OTR, optimal developmental temperature (T_{opt}), and developmental zero (T0, at which development rate is zero) (see Andrews & Schwarzkopf, 2012; Table 1; note that T_{opt} is also a term used to denote the T_b at which an animal shows optimal performance of a physiological trait, see Section 2.6). Responses to constant temperatures provide important baseline information regarding the thermal physiology of embryos; however, temperature varies considerably throughout the incubation period and constant temperatures may not be ecologically relevant for many species. Only recently have embryo responses to acute thermal stress been considered, when a seminal study paved the way for future work in this area (Box 1; Angilletta, Zelic, Adrian, Hurliman, & Smith, 2013). Acute thermal tolerance has been measured using heat shocks, thermal ramps, or extreme thermal fluctuations that mimic the daily rise and fall of nest temperatures (Gao et al., 2014; Hall & Warner, 2019; Smith, Telemeco, Angilletta, & VandenBrooks, 2015). When measuring acute thermal tolerance, cooling/heating rates should reflect temperature changes in natural nests (Angilletta et al., 2013; Levy et al., 2015). Moreover, egg temperature should be monitored throughout the assay. When using heat/cold shocks or thermal fluctuations, consider that egg containers (e.g., Petri dishes, glass jars, plastic boxes) may not reach the same temperatures as incubators; therefore, temperatures inside these containers should be monitored with temperature loggers and/or thermocouples (see Hall & Warner, 2019). Importantly, the difference in critical temperatures obtained via chronic versus acute exposure to thermal stress can be dramatic. For example, Hall and Warner (2020) found that the lethal temperature differed by 12°C for squamate embryos depending on whether acute or chronic methods were used. Understanding both chronic and acute thermal tolerance is likely more important for embryos than for adults due to the inability of embryos to behaviorally thermoregulate in most circumstances. Thus, both mean and maximum/minimum nest temperatures may need to be considered to effectively predict egg survival in the wild. However, according to the thermal variation in the natural nests for embryonic development in reptiles (Booth, 2018), cold tolerance of embryos might be of weak ecological relevance. Most embryos are extremely unlikely to encounter serious cold stress during development in the reproductive season (usually summer). Consequently, most studies focus on heat tolerance of embryos (see details in Hall & Sun, 2020), with very few on cold tolerance.

Box 1: Measuring reptile embryonic thermal tolerance

The critical thermal maximum (CT_{max}) is considered an essential trait in traditional thermal biology (Angilletta, Niewiarowski, & Navas, 2002; Huey & Kingsolver, 1989), most notably for predicting the effect of climate warming on ectotherms. Although ecophysiologists have been interested in the effects of temperature on reptile embryos since the early 20th century (see details in While et al., 2018), it was not until 2013 that Angilletta et al. (Angilletta et al., 2013) measured the acute heat tolerance of reptile embryos for the first time via quantifying the CTmax of cardiac performance. By monitoring embryonic heart rate during warming of fence lizards (*Sceloporus undulatus*) from four geographic populations, they hoped to discover geographic patterns of embryonic CT_{max}.

They included four populations that spanned the species' geographic range: Atlantic County, NJ; Edgefield County, SC; Costilla County, CO; and Gila County, AZ. They monitored embryonic heart rates during continuous heating by water bath. The heating rate was similar to rates of increase recorded from natural nests: 3°C/hr starting at 34°C. During heating, the heart rates and temperatures of embryos were monitored synchronously by IR sensors (Buddy; Avitronics, UK) and a thermocouple. The temperature at which the heart rate could no longer be detected was recorded as the CT_{max} of cardiac performance for each individual. Overall, heart rates increased with temperature from 34°C to 41°C, remained stable from 41°C to 44°C, then dropped sharply between 44°C and 47°C. The median upper lethal temperature was ~46.5°C, and no latitudinal variation in CT_{max} was observed (see details in fig. 3 of Angilletta et al., 2013).

In this groundbreaking experiment, Angilletta et al. (2013) determined acute embryonic heat tolerance (i.e., CT_{max} of heart rate) for the first time, and this has resulted in a new era of reptile embryonic research. Other studies have only considered upper thermal limits using chronic temperature treatments (e.g., constant temperature incubation or repeated daily temperature cycles; Carlo, Riddell, Levy, & Sears, 2018; Levy et al., 2015). Given that nest temperatures can fluctuate widely for some species, but not others (Booth, 2018), using chronic temperature treatments to determine lethal limits may not be relevant for many species. For species like *S. undulatus*, which demonstrate wide fluctuations in nest temperature (Angilletta et al., 2013), methodologies similar to that used by Angilletta et al. are necessary to determine a realistic estimate of embryo heat tolerance. Since the publication of these data, multiple studies have used this or similar protocols to measure heat tolerance of other species (e.g., Gao et al., 2014; Hall & Warner, 2019, 2020; Smith et al., 2015). Importantly, unlike posthatching stages, embryo CT_{max} as measured by Angilletta et al. (2013) equates with the lethal temperature; therefore, use of the term CT_{max} may be somewhat misleading (see Hall & Sun, 2020).

The significance of the study is far-reaching. For species with distinct life-history stages, especially for oviparous reptiles, embryos might be the most vulnerable to heat events caused by climate warming. So, embryonic heat tolerance should be considered if we wish to predict species responses to climate warming, especially to stochastic heat events. Once we can calculate the embryonic CT_{max}, some straightforward predictions, methods, and models can be developed. For example, calculating thermal safety margins is possible with the calculation of CT_{max}, and this is necessary to predict vulnerabilities to climate warming (e.g., Sunday et al., 2014). Thus, the embryonic CT_{max} is helpful for understanding the thermal adaptation and responses to climate warming during early ontogenetic stages.

Importantly, the Buddy Egg Monitor (https://www.avitronics.co.uk/) has served as a critical tool to assess embryo thermal tolerance in two ways. First, researchers have monitored heart rate while steadily increasing temperature until the point of cardiac arrest (e.g., Angilletta et al., 2013; Gao et al., 2014). A similar method can be used to assess cold tolerance by cooling eggs (see Levy et al., 2015). Second, the monitor has been used to assess embryo survival after exposure to brief thermal extremes (e.g., thermal fluctuations, Smith et al., 2015; heat shocks, Hall & Warner, 2020). There are some important considerations when using the Buddy. First, the monitor can heat eggs over long periods of time, and long-term measurements at a single temperature should be avoided (Sartori, Taylor, Abe, & Crossley, 2015). However, heating from the monitor is minimal compared to temperature changes due to experimental design (i.e., thermal ramps); thus, long term measures while continually increasing environmental temperature (as in Angilletta et al., 2013) are permissible, so long as egg temperature is carefully monitored. A thermocouple should be attached to the outside of small eggs (<1 g) or inserted into large eggs to monitor egg temperature throughout the assay (see Gao et al., 2014). Over short intervals, however (i.e., 1–2 min), the monitor may not heat eggs appreciably (Hulbert et al., 2017). Thus, heating from the monitor is likely of little concern when simply assessing embryo survival after a treatment or quickly measuring heart rate at a given temperature. Importantly, there are several models of the Buddy in circulation and each may vary in their tendency to heat eggs. It is critical that researchers report the model number for their Buddy because some models are no longer available for purchase. This will enhance our ability to compare results across studies. For example, several studies assessed how the Buddy might heat eggs (Hulbert et al., 2017; Sartori et al., 2015), but these used different models and no single study has assessed heating with multiple models simultaneously. Ideally, a pilot study should be conducted to determine how use of the Buddy may influence embryo development and/or egg temperature during assays (e.g., Hulbert et al., 2017). Additionally, studies using the Buddy monitor should include a control group where heart rate is not monitored if other developmental or hatchling phenotypes are to be measured to control for potential effects of the Buddy assay.

A second issue to consider when measuring embryo critical temperatures is that thermal tolerance may shift with ontogeny. For example, Turriago et al. (2015) observed that the median upper lethal temperature (LT50) increased across three anuran developmental stages (embryos, hatchlings, tadpoles) in four species. Hall and Warner (2019) found that survival during acute thermal stress was greatest mid-development for squamate embryos. Thus, a basic protocol for any research program should be to determine embryo responses to extreme temperatures at a minimum of three developmental time points (e.g., early, mid, and late developmental stages). This is challenging because of among-species diversity in the timing of oviposition with respect to development (see Section 2.1 above). For example, squamate embryos are often oviposited at the limb bud stage, and responses of earlier stage embryos to temperature (e.g., gastrula stage) may be difficult to assess.

Third, the ecology of the study organism will dictate the relative importance of responses to chronic versus acute thermal stressors. There is vast diversity in nesting behavior across reptiles and amphibians and, not surprisingly, concomitant diversity in the variability of incubation temperatures in the wild (Booth, 2018). For example, some amphibians lay egg masses directly in the sun and many reptiles construct relatively shallow nests. Conversely, other amphibians may oviposit in concealed or shaded areas and many reptiles construct nests relatively deep underground. Embryo responses to acute thermal stress may be highly ecologically relevant for the former, while responses to chronic thermal conditions may be more relevant for the latter. Additionally, the rate at which nest temperatures rise and fall can vary; therefore, assays that measure critical temperatures should use rates similar to field conditions (e.g., Angilletta et al., 2013) and report the rates used. Heating/cooling rates may influence the critical temperatures measured (as for posthatching stages; see below).

Finally, many reptiles have temperature-dependent sex determination. Under temperature-dependent sex determination, the outcome of sex depends on temperatures experienced during a critical window of development, roughly during the middle-third of embryonic development (Bull, 1980). Thus, pivotal temperatures (i.e., those predicted to result in a 50/50 sex ratio, under constant temperature incubation) and the timing of these thermal effects may be just as important to consider as critical temperatures for these species. Suitable temperatures allowing balanced sex ratios may be major drivers of nest-site selection (Mitchell et al., 2013) or geographic ranges of species (Bodensteiner et al., 2019; Carter et al., 2019; Rödder, Kwet, & Lötters, 2009).

2.5.2 | Thermal tolerance of posthatching stages

Hundreds of studies have measured the CT_{min} and CT_{max} of adult reptiles and amphibians in various contexts, including examining acclimation and plasticity, geographic variation, analysis of h_r, and many others (Cowles & Bogert, 1944; Gunderson & Stillman, 2015; Hutchison, 1961; Lutterschmidt & Hutchison, 1997a, 1997b). Methods for measuring critical temperatures are united in that animals are cooled or heated until they lose coordinated physiological function (as opposed to death due to cardiac failure as measured in embryos); apart from that, methods are widely variable. Studies vary dramatically in how animals are heated or cooled (conductive, convective, radiative), in the type of thermometer used (Table 2), in cooling/heating rate, and in the metric used to establish when the CT_{min} or CT_{max} has occurred. Probably the most common metric is the loss of righting response, where an animal becomes too cold or too hot to coordinate a righting response when it is flipped onto its back. Lutterschmidt and Hutchison (1997a) recommended using the onset of muscular spasms as an endpoint for CT_{max} instead; in many amphibians, the onset of spasms occurs at a slightly higher T_b than CT_{max}. However, in many lizard species, lethal temperatures can be reached with no onset of spasms (Camacho & Rusch, 2017), making loss of righting response the metric of choice for most reptile studies.

Given the abundance of studies using critical temperatures in thermal applications, it is essential that confounding variables be controlled to the greatest extent possible (Camacho & Rusch, 2017). This is especially true when the most basic systems for measuring critical temperatures are employed (cooling/heating in water baths, or using heating lamps to heat animals). We provide several recommendations for minimizing confounding variables. First, calibration of thermometers is an absolute must. When possible, we recommend RTDs or thermistors (Table 2) be used to achieve the greatest accuracy, although thermocouples or other thermometers are permissible as long as they are carefully calibrated. Second, the cooling/heating rate should be controlled and kept constant to the greatest possible extent. Cooling/heating rates can greatly impact the critical temperatures measured (e.g., Kolbe, Van Middlesworth, Losin, Dappen, & Losos, 2012; Rezende, Castañeda, & Santos, 2014), and yet many studies fail to measure and report rates. Cooling/heating rates can be measured as either the change in T_b over time (e.g., in animals cooled or heated in a water bath) or the change in ambient air temperature over time (e.g., in animals cooled or heated by radiation or convective flow). Third, CT_{max} and especially CT_{min} may be plastic to varying degrees in reptiles and amphibians (see Section 2.6) and this must be accounted for as appropriate for the question under study. For example, if a researcher is interested in measuring the natural tolerances of populations, reflecting both genetic adaptation and potential plasticity in response to local climatic conditions, data should be collected from animals freshly captured in the field. Field-portable devices that cool or heat animals with convective flow of customized gas mixtures into flippable chambers where LORR can be observed allow researchers to measure critical temperatures very far from their laboratories (DuBois, Shea, Claunch, & Taylor, 2017; Ivey et al., 2020; Shea et al., 2016). Alternatively, if animals from multiple locations are being studied to characterize the CT_{max} of a species or to study acclimation responses, animals should be maintained in uniform, controlled conditions after capture such that all animals are able to acclimate to a consistent baseline. Unfortunately, the exact length of this acclimation period is rarely certain, and we suggest at least a week. Finally, body size can impact CT_{max} data (Claunch et al., 2020), so statistical models should include body size especially if the focal species vary greatly in body size. Importantly, studies attempting to measure multiple thermal traits should measure critical temperatures last because exposure to these temperatures, especially CT_{max}, could be damaging and affect future measurements.

2.6 | Creating TPCs

TPCs are a class of continuous reaction norms that describe how a performance trait changes as a function of temperature (Huey & Stevenson, 1979). These performance traits, which are often expressed as rates, encompass a wide array of measures at different levels of biological organization, from cellular (e.g., enzyme activity), to physiological (e.g., oxygen consumption, heart rate), to whole-organism (e.g., locomotor function, growth). TPCs for nonintegrative performance traits are often Gaussian and negatively skewed, with a temperature value producing maximum trait performance (T_{opt}), and are bounded by CT_{max} and CT_{min}, the upper and lower temperature values where performance drops to zero (Figure 2).

A TPC provides a continuous estimate of performance across a biologically relevant range of temperatures, and is thus useful in a number of applications. First, a TPC describes important thermal parameters, especially T_{opt} and CT_{max}, which allows the calculation of thermal safety margins (Deutsch et al., 2008), as well as CT_{min}, the totality of which facilitates an estimate of thermal tolerance ranges. TPCs have also been used to explain a high degree of variation in development rate under thermal variability (e.g., natural nest temperatures: Girondot & Kaska, 2014; Rollinson et al., 2018), integrated with temperature-dependent sex determination models to noninvasively estimate sex ratios (Massey, Holt, Brooks, & Rollinson, 2019), and to predict the impacts of increased climate warming (Deutsch et al., 2008; Levy et al., 2015) and variability (Vasseur et al., 2014) on ectotherms. Furthermore, a large body of empirical data comparing thermal performance across geographic distributions has provided insights into how thermal sensitivity evolves (Angilletta, 2009; Buckey & Huey, 2016; reviewed in Bodensteiner et al., 2020).

There are several important caveats to consider before constructing a TPC (reviewed in Sinclair et al., 2016). Notably, the thermal performance of an organism at a particular temperature may change as the organism moves through ontogenetic stages (Berger, Friberg, & Gotthard, 2011). Indeed, TPCs of embryo survival are remarkably different from curves for phenotypes of posthatching stages (Telemeco, 2014; van der Have, 2002). TPCs may also be locally adapted and thus different between populations lacking gene flow (Angilletta, 2009). To account for variation in TPCs throughout ontogeny and among populations, authors should aim to construct specific TPCs for discrete periods of their study organism's life-cycle (e.g., separating out the embryonic, juvenile, and adult phases), and measure performance within specific populations. Next, an important factor to consider is that the duration of exposure during acclimation to temperature treatments can affect performance, and can induce pathologies at high and low temperatures especially (Kingsolver & Woods, 2016; Schulte, Healy, & Fangue, 2011). Although it may be possible to model these “time-dependent effects” (Kingsolver & Woods, 2016), authors should carefully consider the duration of exposure to treatment temperatures they are using, in light of ecologically relevant durations for thermal exposure (also see Section 2.1). Additionally, repeated-measures experiments should randomize the order that individuals are exposed to each temperature treatment. Last, several environmental factors other than temperature, such as nutritional status of individuals (Brett, Shelbourn, & Shoop, 1969; Gilbert & Miles, 2016) or hydration (Preest & Pough, 1989), can influence thermal performance, so it is important to be cognizant of the health of individuals in the experiment, and any other major differences between experimental and natural conditions.

Different procedures are used to measure performance, depending on the species' habitat requirements, the life stage of the study organism, and the trait in question. However, the basic principle underlying construction of a TPC is to measure organismal performance at a series of T_b. At least five temperature treatments are recommended (Angilletta, 2009), as too few treatments can result in erroneous modeling of the TPC (Knies & Kingsolver, 2010). Furthermore, a broad spread of temperatures spanning the range of temperatures the organism would experience in nature is ideal; temperature treatment selection may be informed by published values of critical temperatures, T_{set}, or T_{opt} for the species, or by pilot studies. Once planned, temperature treatments generally occur in temperature-controlled chambers set to constant temperatures. These chambers can include programmable incubators or environmental chambers (for eggs and tadpoles), controlled environment rooms that house animal enclosures (for adult animals), and water baths/aquaria (for larger aquatic organisms).

For experiments studying development or growth, long-term or chronic exposures resulting in measurable ontogenetic changes may be necessary (e.g., Oyamaguchi et al., 2018). In such cases, authors typically measure the change in a morphological metric (such as body length or mass) over time, including entire ontogenetic stages. It is also common to estimate embryonic development rates by taking the inverse of time-to-hatch at a certain temperature (units of $time^{-1}$; see Section 2.1 above for further details on estimating development rate in embryos). An important additional consideration when exposing animals to chronic temperatures, even those approximating T_{set} or T_{opt}, is that reptiles and amphibians typically experience cool-down periods at night, rendering constant temperature exposure unnatural. Thus, we recommend that experiments testing chronic effects of temperature on performance in diurnal species manipulate daytime active temperatures, but allow all animals to cool during night time inactivity.

For traits such as metabolic rates and locomotor performance, authors typically acclimate the organism in test chambers over the course of minutes or hours (e.g., Richter-Boix et al., 2015; Ruiz-Aravena et al., 2014). Different species require different acclimation periods to test chambers (Chabot, Steffensen, & Farrell, 2016), and this acclimation period serves several purposes, including reducing handling stress or stress due to a new or confining environment. Authors can test different acclimation periods to reduce these stress effects, while also reducing time-dependent effects resulting from long exposures. In some cases, animals may need to be trained to perform in the testing chamber beforehand (e.g., training animals to swim continuously in a flume: Elsworth, Seebacher, & Franklin, 2003), and the final trait value may need to be size-adjusted before being plotted, according to convention for the trait.

Once trait values are determined at different temperatures, a continuous function is used to model the TPC. There are many functions that can be used to model a TPC, and the function that provides an optimal fit is likely to differ based on the trait itself (Schulte, 2015), among other biological factors. To select the best function from a group of candidate models, while minimizing overfitting, an information-theoretic approach (Akaike Information Criterion [AIC]) is recommended over simply selecting functions with high r2 (detailed explanation can be found in Angilletta (2006)). Several commonly used candidate functions are described in Table 3, but this list is not exhaustive; Angilletta (2006) and Shi and Ge (2010) provide additional lists and equations of important candidate functions. To finish creating a TPC, trait value data can be modeled with appropriate candidate functions using statistical software (such as the *nls* or *drc* packages in R [R Core Team], or TableCurve [Systat Software, Inc.]). The resulting models can then be compared using AIC to select the best function for the TPC.

2.7 | Studying acclimation and stress effects

Variation in techniques is inevitable when so many hundreds of studies are conducted on thermal ecology and physiology by different research groups with varying research questions, goals, and resources (Camacho & Rusch, 2017). One major component of interest when studying variables like T_{set}, critical temperatures, and others is whether those values are representative of animals in their natural state in the field. Two major factors, acclimation and stress, could potentially impact thermal variables to the extent that data obtained may be skewed from what might be representative of free-living animals.

Thermal acclimation has been studied extensively in embryos. Heart and metabolic rates often acclimate to incubation temperature, but the direction and magnitude differs among species. For example, Du et al. (2010) found that for some species, heart rates were higher for embryos incubated at cooler temperatures (i.e., countergradient acclimation). This indicates that embryos may

TABLE 3 Common candidate functions used to model thermal performance curves with descriptions of usage

Function	Description
β-Distribution	Originally used to describe the physiological performance of plants (Yan & Hunt, 1999), this function was the most parsimonious of several candidates for describing metabolic rates in eight species of reptiles (Tomlinson, 2019)
Gaussian	This function was favored among several candidates by information theory to characterize locomotor performance in lizards (Angilletta, 2006)
Performance	This was suggested to be ideal for modeling ectotherm development rates based on a weighted average of several indicators (Shi & Ge, 2010)
Sharpe-Schoolfield	Based on laws governing biochemical reaction dynamics, this function is derived mechanistically with the assumption that a single enzyme controls developmental dynamics (Sharpe & DeMichele, 1977; modified by Schoolfield, Sharpe, & Magnuson, 1981)
Polynomial	This is an easily modeled class of functions that enable biologically meaningful comparisons between families or populations (Izem & Kingsolver, 2005); fourth-order polynomials (for five temperature treatments at minimum) are preferable (Angilletta, 2006)
GAM	GAMs may be ideal to model embryo heart rates across temperature because they allow researchers to model a nonlinear response without specifying a function (Angilletta et al., 2013); they also have applications in quantifying among-individual variation in performance curves (Vickers, Aubret, & Coulon, 2017)
Dose response curves (e.g., log-logistic; Weibull)	Dose response curves are useful for modeling sex ratios across temperature for species with temperature-dependent sex determination; (several key functions for modeling the temperature-sex reaction norm are available in Godfrey, Delmas, & Girondot, 2003)

Abbreviation: GAM, general additive modeling.

compensate for relatively cool incubation temperatures by upregulating metabolism; however, other species showed no effect. Conversely, Sun et al. (2015) found that respiration rates were greater for Chinese Softshell Turtle (*Pelodiscus sinensis*) eggs that were incubated at warmer temperatures than those incubated at cooler temperatures (i.e., cogradient acclimation). Few studies have considered how baseline incubation temperatures might influence embryo critical temperatures, but there appears to be species-specific variation in this relationship as well (Hall & Warner, 2018; Sun et al., unpublished). Moreover, even brief exposure to thermal extremes can influence embryo physiology (e.g., heart and developmental rates: Hall & Warner, 2019); thus, researchers should assume that incubation temperature results in thermal acclimation for their model species and carefully control baseline temperatures when measuring thermal phenotypes. Additionally, temperature during early ontogenetic stages may program thermal phenotypes of later life stages (Mueller, Bucsky, et al., 2019a; Singh, Das, & Rhen, 2020). This must be considered when measuring larval or adult phenotypes and making comparisons across studies where individuals or populations experience different thermal developmental conditions. Few studies have explicitly assessed the relationship between incubation temperatures and thermal phenotypes of hatchlings and adults (e.g., Gunderson, Fargevieille, & Warner, 2020; Mueller, Bucsky, et al., 2019a). These studies often report mixed results with respect to the types of critical temperatures affected (e.g., upper vs. lower critical temperatures; Abayarathna, Murray, & Webb, 2019). Moreover, some species exhibit no effect of incubation temperature on adult critical temperatures (Gunderson et al., 2020). Thus, relationships between incubation temperatures and thermal physiology of hatchlings and adults are likely also species-specific. For these reasons, great effort should be made to control the potential for acclimation effects due to both field and lab conditions. For example, when collecting eggs from field nests or recently captured females, the time between oviposition and collection should be minimized, reported, and accounted for in analyses. If this time is not known, a subset of eggs from each clutch should be dissected and embryos should be staged to estimate the time since oviposition. Moreover, during incubation studies, a temperature logger should be kept in each incubator to quantify among-incubator differences in temperature (which often exist, even when incubators are set to the same temperature). Additionally, because T_b of gravid females can influence offspring phenotypes, temperature loggers should be deployed in various locations throughout a random subset of cages when collecting eggs from breeding colonies. All these temperatures should be reported to enhance comparisons across studies. If acclimation effects are of interest, eggs can be incubated at various constant (or fluctuating) temperatures and the phenotype(s) of interest can be assessed in late-stage embryos at several common temperatures (Du et al., 2010). Additionally, it may be important to assess posthatching phenotypes since some acclimation effects may only be evident after hatching (Mueller, Bucsky, et al., 2019a).

Regarding thermal data collection on adult amphibians and reptiles, many studies use animals that have been held in captivity for various amounts of time. This means that the animals are subject to the conditions of the captive setting and are therefore likely to acclimate to them. This is a potential problem because variables like T_{set} and critical temperature can in some species change rapidly and mask natural variation in these values (Ballinger & Schrank, 1970; Pintor, Schwarzkopf, & Krockenberger, 2016). T_{set} can be influenced by numerous variables, including hormones, sex, reproductive state, feeding, and others (reviewed in Camacho & Rusch, 2017). In their review of plasticity of thermal tolerance, Gunderson and Stillman (2015) found that aquatic ectotherms exhibit about twice the plasticity as terrestrial species. Among terrestrial species, the CT_{min} appears to be more plastic than the CT_{max}, especially in highly seasonal habitats. In general, however, plasticity in thermal tolerance is extremely low in most amphibians and reptiles, an observation that may be attributed to the “Bogert Effect,” or the idea that effective behavioral thermoregulation buffers animals from selection on physiological traits (Huey, Hertz, & Sinervo, 2003). In other words, amphibians and reptiles are typically such excellent behavioral thermoregulators that they have little exposure to natural selection and thus ability to adapt (reviewed in Bodensteiner et al., 2020). These results have important implications for the responses of amphibians and reptiles to climate change, in that low plasticity may mean that these animals generally have a low ability to cope with warming temperatures beyond their capacity for thermoregulation. In some situations, variables may be plastic enough that extensive laboratory acclimation could mask potentially important biological variation. Aside from acclimation, other factors associated with captivity, like food and water availability, access to gradients in which to thermoregulate, and lighting can impact thermal variables (reviewed in Camacho & Rusch, 2017). If animals must be kept in captivity then care should be taken to create terrarium habitats mimicking natural conditions to the greatest possible extent.

One obvious way to prevent laboratory acclimation from affecting thermal variables is to measure them as soon as possible after capture. The advent of cheap and/or field-portable devices for measuring thermal variables allows researchers to measure these variables at remote field stations or in the field itself in some cases (DuBois et al., 2017; Ivey et al., 2020; Sauer, Sperry, & Rohra, 2016; Shea et al., 2016). Still, this is not always possible due to logistics and experimental design. Also, it is possible that the stress from capture could impact thermal variables. It is clear that high temperatures can impact the rate of corticosterone release (Claunch et al., 2017; Dupoué, Brischoux, Lourdais, & Angeliera, 2013; Gangloff, Holden, Telemeco, Baumgard, & Bronikowski, 2016; Narayan, Cockrem, & Hero, 2012; Telemeco, Gangloff, et al., 2017), and elevated circulating corticosterone can affect thermoregulatory behavior (Belliure & Clobert, 2004; Belliure, Meylan, & Clobert, 2004; Preest & Cree, 2008). However, the extent to which these changes in thermal behavior feedback to affect corticosterone release, or the effects of corticosterone on other thermal variables are uncertain. Until more data are collected on how stress may affect measurement of thermal variables, we recommend that whenever possible, data be collected as soon as possible after capture to avoid acclimation to laboratory conditions. When this is not possible, animals must be maintained in laboratory conditions that match those of their natural habitat to the greatest possible extent and periods in captivity should be reported and included in analyses (Camacho & Rusch, 2017).

So far, we have largely considered observational and experimental approaches to understanding the thermal ecology and physiology of amphibians and reptiles. However, a major new tool has emerged in the field of thermal ecology over the past decade: mechanistic models to predict species distributions currently, as well as in the past and future, based on thermal relationships between animals and their environments. In the next section, we delve into the recent advent of these modeling tools and explain how scientists are using them to identify populations at risk due to climate change.

2.8 | Incorporating thermal biology data into models predicting species' responses to climate change

A frequent motivation for thermal biology research is improvement of forecasts for species' responses to climate change. However, modelers and experimentalists often fail to communicate about how best to produce models and the model outputs that are most desirable. Common forecasting models go by numerous names including “species distribution models,” “ecological niche models,” and “bioclimatic envelope models,” among others. These models generate probabilities of occurrence for focal species under various climate scenarios (e.g., past, current, future, etc.). Two broad methodological classes exist: correlative and mechanistic, having a stronger focus either on a species' realized or fundamental niche. While the realized niche is the proportion of the niche space which is actually occupied in geographic space, the fundamental niche represents all environmental conditions permitting infinite population existence even if these conditions are not realized in geographic space (Peterson, Papes, & Soberón, 2015). Correlative approaches generate predictions by correlating current climate data with historical presence/absence data (often presence-only). The correlation is then extrapolated to predict probabilities of occurrence under varied climate scenarios (Araújo & Peterson, 2012; Elith & Leathwick, 2009; Porfirio et al., 2014). These models implicitly capture the biotic and abiotic processes limiting species' ranges by relying on correlates with measurable environmental variables and are an important tool for predicting current distributions (Enriquez-Urzelai, Kearney, Nicieza, & Tigley, 2019). However, the fundamental niche may be poorly represented by the realized niche, leading to correlative models overestimating range shifts in nonequilibrium contexts.

While correlative approaches consider current distributions (presence/absence, presence-only, or abundance) and environmental variables to model species distributions, mechanistic models incorporate biological and physiological processes in an attempt to directly model the fundamental niche of a species (Peterson et al., 2015; Soberón & Nakamura, 2009). Probabilities of occurrence are then generated by determining whether predicted climate conditions allow individuals to remain within the experimentally estimated fundamental niche of the organism (Buckley et al., 2010; Kearney & Porter, 2009; Peterson et al., 2015). Unlike correlative models, mechanistic models typically require input of T_b rather than coarse climate measures. Thus, mechanistic niche models are ommonly paired with a biophysical model that uses heat and mass-balance principles to translate climate into T_b (e.g., Kearney & Porter, 2017; Kearney, Isaac, & Porter, 2014). Although mechanistic models have many conceptual advantages over correlative models (for in depth reviews see Enriquez-Urzelai et al., 2019; Kearney & Porter, 2009; Peterson et al., 2015), they require large amounts of experimental data to estimate parameter values and predict range shifts, and thus are far less common than correlative models. Many foundational mechanistic models were developed using reptiles and amphibians, especially lizards. Here, we briefly describe some of the most notable of these models, and the data most needed to advance mechanistic modeling in additional species.

All mechanistic models attempt to estimate the fundamental niche and relate those to climate, but models vary greatly in their complexity and reliance on first principles. The simplest models compare experimentally derived estimates of thermal tolerance (e.g., CT_{max}, VT_{max}, T_{pant}) with maximum temperatures potentially experienced. However, translating critical temperature exposure into a probability of occurrence can be challenging. A heavily used approach involves estimating hours when individuals could be active in their environment (h_a; can also be expressed as hours of restriction, $h_r = 24 - h_a$) and then estimating energetics or reproductive output given this activity time (Adolph & Porter, 1993, 1996), or comparing predicted h_a to h_a observed in nature (Pontes-da-Silva et al., 2018; Sinervo et al., 2010, 2018). A high-profile paper by Sinervo et al. (2010) notably applied the latter approach to evaluate the extinction risk of lizards worldwide and concluded that 39% of populations will go extinct by 2080. To do this, the global model of Sinervo et al. (2010) indirectly estimated h_a for 34 lizard families, by assuming that T_b tracks air temperature, daily temperature follows a 24 hr sine wave around the mean, and lizards are not active when air temperatures are outside T_{set}. They then compared these h_a estimates to family specific estimates of minimum h_a needed for population persistence. The simplicity of this approach allowed Sinervo et al. (2010) to apply the model broadly, but the model has been criticized for lacking direct physiological and energetic mechanisms and relying on air temperatures rather than operative body temperatures, thereby ignoring microhabitat variation and the capacity for lizards to behaviorally thermoregulate (Clusella-Trullas & Chown, 2011; Kearney, 2013). In an extension of the model, Sinervo et al. (2018) addressed the criticism regarding microclimatic variation by leveraging a high-resolution microclimate data set (microclim, Kearney et al., 2014) to estimate maximum operative body temperatures when calculating h_r in *Phrynocephalus* lizards. However, it did not address behavioral thermoregulation nor physiological and energetic mechanisms. Most notably, Kearney (2013) used a combination of biophysical and dynamic energy budget (DEB) models to demonstrate that activity restriction is actually a measure of environmental thermal stress that is correlated with extinction risk, instead of an explanation for the extinctions. Thus, classification of the activity restriction models of Sinervo et al. (2010, 2018) as truly *mechanistic* rather than *correlative* is questionable.

Multiple models incorporate more mechanistic details about the biology and physiology of animals (e.g., Buckley, 2008; Enriquez-Urzelai et al., 2019; Kearney, 2012; Levy et al., 2015), than simple activity-restriction models (Sinervo et al., 2010, 2018). As a result, they are more difficult to produce, but potentially more useful. Such complex mechanistic models follow a similar conceptual framework: the first input is climate data, either directly recorded from weather stations or produced as output from global circulation models. Climate data are then converted to microclimate data which is used as input to a biophysical model to estimate T_b of the animal. A suite of potential T_b is typically calculated for animals in diverse microenvironments such as full sun, shade, or within a retreat. Decisions are then made about how the animal will thermoregulate either by incorporating a formal model of behavioral thermoregulation or, more commonly, assuming the animal will maintain its T_{set} whenever possible and seek shelter when not possible. These calculations are repeated hourly throughout the activity period for every grid cell on the map where the species might occur. For each grid cell, hourly T_b are then input to foraging and bioenergetic models to estimate hourly energy acquisition and expenditure, growth, and allocation to reproduction. This process allows prediction of population growth rates for every point on the map under any climate.

The first of these data-heavy mechanistic models was developed by Buckley (2008) for the lizard *Sceloporus undulatus*, considering only posthatching lizards, and was later extended by Levy et al. (2015) to include the full ontogeny (eggs, hatchlings, and adults). These “mechanistic models” are really composites of many models run in series to simulate the effects of a climate scenario on population dynamics. They require validated functions relating climate to T_b (the biophysical model), available T_b to selected T_b (a model of thermoregulation), and selected T_b to foraging rate, energy assimilation rate, growth rate, egg development rate, survival probability, and reproductive rate (bioenergetic models). These models are extremely data intensive because every parameter is estimated from controlled experiments. Buckley (2008) and Levy et al. (2015) used both data from the literature and their own experiments to create statistical models relating T_b to each biological rate, thus parameters were largely slopes and intercepts from linear statistical models, or similar parameters from nonlinear statistical models. By contrast, Kearney (2012) repeated the analysis of Buckley (2008) using DEB theory to mechanistically relate T_b to energy acquisition, growth rate, maturation, and reproductive rates in *S. undulatus*. Kearney (2012) argues that the DEB approach requires estimation of fewer parameters (24 vs. 28 in Buckley, 2008) and is more directly linked to first principles, although predicted population responses to climate change were broadly similar. A major advantage of the DEB approach is that it provides a unified framework based on first principles that can be used to model diverse species (Kooijman, 2000). However, many of the DEB parameters are virtually impossible to estimate directly and instead require iterative, multivariate regression analyses to convert standard measurements into the needed parameter values (Kearney, 2012). Even so, the DEB model is now readily implemented in R via the NicheMapR package (Kearney & Porter, 2020).

Although data intensive, a major advantage of the foraging-energetic and DEB approaches is that they allow sensitivity analyses where individual parameter values are adjusted to determine their impact on predicted population growth rates. For example, the model of Levy et al. (2015) demonstrated that extinction risk in *S. undulatus* is driven by reproductive failure when embryos experience critically high nest temperatures. However, when the parameters controlling nesting behavior were adjusted such that modeled females dug slightly deeper nests or placed their nests in slightly shadier microenvironments, reproductive failure was averted. As a result, the predicted consequences of climate change transitioned from population extinction to growth. Based on this sensitivity analysis, Telemeco, Fletcher, et al. (2017) directly tested the capacity of female *Sceloporus tristichus* (within the *S. undulatus* species group) from a threatened population to alter their nesting behavior as needed to buffer the population from climate change. Unfortunately, females did not place their eggs in deeper or more-shaded nests after exposure to elevated temperatures while gravid, nor were their embryos heat hardened (Telemeco, Fletcher, et al., 2017). Such directed hypothesis formation and testing was only possible as a result of the detailed mechanistic modeling of Levy et al. (2015). Additionally, similar sensitivity analyses could allow focused recommendations to managers about the interventions that will have the greatest positive impacts on population growth rates. Even more than their ability to produce predictions about extinction risk, detailed mechanistic models provide a system for directing study and management that is not possible with more correlative or data-light approaches.

Descriptions of the data needed to produce mechanistic models akin to those of Buckley (2008), Levy et al. (2015), and Kearney (2012) are given in Box 2. For the time being, development of such models is not possible for the vast majority of species. Until then, researchers have begun implementing hybrid modeling frameworks that utilize both correlative and mechanistic approaches. These models do not provide the capacity for sensitivity analyses of detailed mechanistic models, but should produce more reliable predictions for how species will be affected by climate change than purely correlative approaches (e.g., Mathewson et al., 2017; Vicenzi et al., 2017). This hybrid framework allows the implicit derivation of biotic interactions such as required shade levels and activity windows from readily available data such as climate data, occurrence data, and commonly measured estimates of thermal biology such as CT_{max} and T_{set}. Including these biological traits in an otherwise correlative model reduces the risk of extrapolation thereby allowing better forecasts (Enriquez-Urzelai et al., 2019). However, only a few studies have incorporated bioenergetics, plasticity, and evolutionary adaptation into distribution models (Enriquez-Urzelai et al., 2019; Riddell, Odom, Damm, & Sears, 2018; Wisz et al., 2013).

Box 2: Facilitating production of detailed mechanistic niche models

Recent advances in microclimate and biophysical modeling (e.g., Kearney, 2019; Kearney & Porter, 2017; Lembrechts & Lenoir, 2020) mean that availability of appropriate thermal biology data is now the rate-limiting step for production of detailed mechanistic species distribution models. Inclusion of appropriate life-history and ecophysiological traits greatly improves model performance, leading to more accurate forecasts and facilitating sensitivity analyses to identify the traits that most limit species distributions in diverse environments (Camacho & Rusch, 2017; Diele-Viegas & Rocha, 2018, Diele-Viegas et al., 2020). Information on thermoregulatory behavior, time of activity, breeding period including reproductive triggers and constraints, and thermal physiology, for example, are some of the traits that should be included to provide the most useful models (e.g., Rödder, Schmidtlein, Veith, & Lötter, 2009; Wilms, Wagner, Shobrak, Rödder, & Böhme, 2011). However, the huge variety of methods used by empiricists to estimate physiological parameters and variation in parameters measured, as described in Section 2.8, results in data with varied utility for model production and accuracy (Caetano et al., 2020; Carter, Kearney, Hartley, Porter, & Nelson, 2017). Unfortunately, experimentalists frequently fail to measure the traits that are most needed by modelers. For example, critical thermal limits (CT_{min} and CT_{max}) are of minimal use for mechanistic modeling because animals rarely if ever experience these T_b. Rather, modelers require data on field active temperatures (T_b), the preferred T_b range (T_{set}), and voluntary thermal limits (VT_{max} and VT_{min}) to construct naturalistic rules for thermoregulation. Next, modelers need information on how naturally experienced temperatures affect performance, specifically energy assimilation, growth rate, and reproduction. Unfortunately, the most commonly used performance measure by experimentalists, running performance, is of little use for mechanistic niche models because running is primarily powered by anaerobic metabolism in reptiles and amphibians (Bennett & Licht, 1972; Gleeson, 1991), whereas long-term functions such as digestion, growth, and reproduction are powered through aerobic metabolism. Finally, to create the best models, we need information on how these aerobic performance measures change across ontogeny, and the capacity for thermal performance to change via phenotypic plasticity, acclimation, and evolution. With the appropriate thermal biology data, tools are in place to rapidly increase production of detailed mechanistic models that can guide both future research and management.

Combining micro and macroclimate data to predict thermal conditions actually experienced by individuals also improves model forecasts. The set of climatic variables most commonly used in both correlative and mechanistic models is the WorldClim database, which is based on a macroclimatic approach that interpolates climate layers and elevation data from different sources (Fick & Hijmans, 2017; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). It presents monthly climate data for minimum, mean, and maximum temperature and precipitation, along with 19 bioclimatic variables derived from the main climatic data that represent annual trends, seasonality, and extreme environmental factors. Future conditions are available for 19 general circulation models, four representative concentration pathways (greenhouse gas concentration trajectory), and two time periods (2,050, average for 2,041–2,060; and 2,070, average for 2,061–2,080). All layers are available from 30-s to 10-min resolutions, being interpolated from weather station data using thin plate smoothing splines. WorldClim 2.0 also offers monthly surfaces of solar radiation, vapor pressure and wind speed (Fick & Hijmans, 2017). Alternatively, 19 bioclimatic variables for three decades (1980s, 1990s, and 2000s) based on remote sensing are available from the MERRAclim data set at spatial resolutions of 2.5–10 min (Vega, Pertierra, & Olalla-Tárraga, 2017). For the continental United States, the GRIDMET data set provides constantly updated meteorological data from 1979 to yesterday at very high spatial resolution (~4 km; Abatzoglou, 2013). Despite being a very useful tool, macroclimate environmental layers are focused on global-scale predictions. Considering that the climate is changing faster on a larger scale compared to smaller scales (Allen et al., 2018; Potter, Woods, & Pincebourde, 2013), any extrapolation from macro to microscale relying on the WorldClim data set, such as the approach of Sinervo et al. (2010), is likely to lead to pessimistic forecasts of thermal suitability in models interested in local evaluations.

Microclimates are the link between climate and environmental conditions experienced by the animals in the wild, and drive heat and mass exchange with the organism (Kearney & Porter, 2009, 2017). Different attempts to measure microclimate conditions are currently used, including empirical measurements and biophysical projections. Empirical measurements are made in the field by small data loggers and usually focus on air/soil temperature, relative humidity, and solar radiation. These measurements are useful, but limited in space, time and in the range of variables measured (Kearney & Porter, 2017) and may lead to lower predictive accuracy than other methods (Caetano et al., 2020). Biophysical projections, on the other hand, rely on available databases (e.g., climate, weather, terrain, soil, vegetation) to model microclimatic conditions, so the range of variables resulting from these models depends on data availability. Kearney et al. (2014) published the "microclim" data set containing all global microclimatic conditions needed to compute heat and water balances of organisms in terrestrial environments at ~15 km resolution, considering three generic substrates (soil, rock, and sand) and six shade levels. The “microclim” data set was developed using the NicheMapper FORTRAN program first described by Beckman et al. (1973) and Porter et al. (1973), but the program is now available for public use via the NicheMapR package in the R programming environment (Kearney & Porter, 2017, 2020), allowing users to estimate microclimate parameters for different substrates, soil depths, resolutions, and so forth.

The choice of method used must be made carefully and consider the appropriate scale and question. For example, the model of Sinervo et al. (2010) used relatively simple inputs with climate modeled assuming sinusoid temperature change around values from the WorldClim data set, and biology modeled using activity temperatures and occurrence data. As a result, it required relatively low computation time and memory use and could be applied to diverse species, but provided coarse estimates that may have low accuracy and precision. By contrast, more data intensive models such as those of Kearney (2012) and Levy et al. (2015) modeled climate with high-resolution microclimate data filtered through biophysical and thermoregulation models to estimate hourly T_b and then used DEB theory or statistical models from controlled experiments to model bioenergetic rates and thus population growth rates. This approach requires orders of magnitude more data and computational capacity, but is more refined, being ideal for small scale assessments and sensitivity analyses. Hybrid approaches combining correlative models with readily available biological data similar to that included in the Sinervo et al. (2010) model can be a good strategy to increase the accuracy and precision of climate-change response forecasts. These models leverage many of the strengths of both approaches, requiring moderate computational power and data more readily available to researchers.

3 | FUTURE DIRECTIONS

We have described recent advances and best practices in measuring the thermal biology of reptiles and amphibians and how that information can be used to understand the evolutionary history, ecology, and risk of climate-change induced decline of these animals. What is now most needed to advance our understanding? We think that additional development is most needed in two broad areas: (a) increased measurement of natural variation in thermal performance and tolerance and (b) improved description of the mechanisms that drive this variation.

Historically, much research sought to define thermal tolerances and behavior, resulting in production of single values to describe entire species. Single measures are attractive, especially for managers, but ignore growing research demonstrating that both thermal behavior and tolerance change across ontogeny and from prior experience, resulting in important intraspecific variation (Angilletta, Sears, Levy, Youngblood, & VandenBrooks, 2019). Currently, formation of generalities about how thermal biology varies among individuals and populations within a species is not possible because few species have been examined (reviewed in Bodensteiner et al., 2020). Thus, further work describing such variation is needed. In particular, research characterizing full TPCs for multiple traits across multiple life-history stages and contexts would be useful. We recommend focusing on TPCs rather than simply measuring critical temperatures because the effects of sub-critical temperatures on performance will have the greatest impacts on a species' competitive ability and capacity to live in a given environment (e.g., Telemeco, Gangloff, et al., 2017). For the greatest impact, such thermal-performance curve measures should also be paired with information about how thermal behavior changes by examining field T_b and laboratory T_{set} in each stage/context. Numerous contexts in addition to ontogenetic stage and prior exposure should also be considered. For example, the thermal biology of organisms will be dependent on interactions with other extrinsic and intrinsic factors to affect performance, including oxygen availability and capacity (Gangloff & Telemeco, 2018), hydric conditions (Garcia-Porta et al., 2019; Riddell, Roback, Wells, Zamudio, & Sears, 2019; Rozen-Rechels et al., 2019; Sannolo & Carretero, 2019), and metabolic state (Virens & Cree, 2019). Another frequently ignored context that could greatly affect thermal performance and behavior is the presence (or absence) of competitors on the landscape (Rusch & Angilletta, 2017). Ecological theory tells us that partitioning the fundamental niche into realized niches will largely determine whether or not a species can persist in a given habitat (Case & Gilpin, 1974; Jacob et al., 2018; Tracy & Christian, 1986). For example, competition for thermal and hydric resources can shape interactions between syntopic lizard species (Langkilde, Lance, & Shine, 2005; Osojnik, Žagar, Carretero, García-Muñoz, & Vrezec, 2013; Žagar, Carretero, Osojnik, Sillero, & Vrezec, 2015). However, we have yet to describe a framework for characterizing how these interactions might shape thermal biology and the outcome of competitive interactions.

When designing future experiments, care should be taken to expose animals to naturalistic thermal variation. Constant temperatures may be appropriate for testing acute effects of temperature during the activity period, but more chronic experiments need to utilize variable temperature regimes to provide biological rather than pharmacological measurements (Carter et al., 2018; Fabrício-Neto, Gavira, & Andrade, 2019; Georges et al., 2005; Hall & Warner, 2020). Historically, most experiments used constant temperatures due to technological constraints (While et al., 2018). However, technology no longer has to be constraining; numerous environmental chambers and incubators allow production of naturalistic diel and seasonal temperature variation (e.g., Greenspan et al., 2016). The exact regimes chosen will depend on the ontogenetic stage examined. During egg incubation, temperature regimes should replicate naturalistic soil temperatures based on nest depth, shade cover, and geographic location (e.g., Telemeco et al., 2016). Recent development of microclimate datasets such as “microclim” (Kearney et al., 2014) allow extraction of hourly temperature data at any location on the globe, under any soil type, nest depth, and solar radiation regime, greatly facilitating design of naturalistic incubation studies. Microclimate datasets can also be used to produce thermal regimes for free-living stages, although to be meaningful, experiments with adults should also account for behavioral thermoregulation (Blouin-Demers, Kissner, & Weatherhead, 2000; Sun, Wang, Wang, Lu, & Du, 2018; Telemeco, Fletcher, et al., 2017).

Proper description of behavioral thermoregulation is key in planning monitoring of amphibians and reptiles, which generally tend to hide, and only in given thermal circumstances (e.g., basking) are exposed. Many secretive species are difficult to find in the wild, making presence/absence data tenuous, and so monitoring efforts must take into consideration the timing of a given species' activity. Furthermore, when analyzing data, only data collected during thermally optimal periods should be considered in the calculation of population size estimates (Germano & Williams, 2005; Tinkle & Ballinger, 1972).

Given the large amount of potential variation that could affect thermal behavior and performance, it would be preferable to mechanistically predict how thermal traits vary across contexts. However, the mechanisms underlying thermal performance are not currently well understood. Genomic methods offer much promise for describing these mechanisms, but nontrivial challenges linking the genome to phenome exist. For example, many genes in reptiles and amphibians are as yet undescribed, and the physiological mechanisms underlying thermal performance, tolerance, and behavior are still largely unknown (Campbell-Staton et al., 2017, 2020; Garcia-Porta et al., 2019). For example, the mechanism(s) setting absolute thermal tolerances in reptiles and amphibians is hotly debated, with some data supporting failure of subcellular mechanisms (e.g., classical and marginal stability hypotheses, Hochachka & Somero, 2002), some supporting failure of organ systems such as the cardiovascular and respiratory system (oxygen and capacity limited thermal tolerance hypothesis; Hall & Warner, 2020; Pörtner, 2001; Smith et al., 2015), and some data suggesting a combination of these mechanisms (e.g., hierarchical mechanisms of thermal limitation, for a full review see Gangloff & Telemeco, 2018). Thus, much work is needed to provide a more mechanistic understanding of why reptiles and amphibians display the thermal preferences, performances, and tolerances observed. This study is all the more critical as the study of these organisms provides valuable insights that can guide our understanding of the complex consequences of the current global climate crisis. Estimated climate-change susceptibility complements IUCN Red List assessments of extinction risk and serves as a warning flag highlighting the need for intensive monitoring and potentially conservation action for affected species. As amphibians and reptiles are at risk of heat-induced extirpations due to climate change, success in their conservation requires coordinated efforts at advancement of our understanding of their thermal physiology, using the most appropriate and up-to-date methodologies.

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