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CONCEPTUAL MODEL FOR THERMAL LIMITS ON THE DISTRIBUTION OF REPTILES

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Abstract.—Recent climate change has re-invigorated scientific interest in the dynamics of geographic distributions of organisms. Climate responses and their biogeographical ramifications can be predicted indirectly by studying variation in fitness-related traits across environmental gradients in wide-ranging species. We review evidence for such variation in reptiles. Clinal variation in seasonal timing (onset) of nesting is common but may offer only minor compensation. In contrast, clinal variation in nesting behavior in two wide-ranging species suggests that reptiles can use nest site choice to counter climate differences. We suggest that when range boundaries located at climate extremes are determined by thermal conditions of embryos (vs. the adult stage) they cannot be predicted by the combination of environmental temperatures and thermal tolerances of embryos alone. We propose that nest site choice can reduce or eliminate the environmental variation that would be experienced by embryos in nests selected randomly with respect to temperature or factors influencing temperature. We also hypothesize that this compensation is limited at climate extremes; when temperatures are too cold for behavioral compensation (e.g., due to lack of suitably warm nest sites), reptiles can only invade colder climates by evolving viviparity. Animals with temperature-dependent sex determination (TSD) are more vulnerable to climate change than those with genetic sex determination (GSD) because the complete production of one sex in TSD species would occur before complete embryonic failure in GSD species. Collectively, research on reptiles suggests that range boundaries at climate extremes are determined by: (1) thermal limits and compensatory thermoregulation of free-living adults; (2) thermal limits of embryos; (3) the extent of compensatory nest site choice behavior; (4) mode of sex determination; and in cold climates (5) reproductive mode (oviparity vs. viviparity).

Key Words.—Bogert effect; environmental gradients; geographic distribution; nest site choice; range margin; temperature-dependent sex determination; viviparity;

INTRODUCTION

Understanding what limits the geographic distributions of organisms is a major aim of ecologists (see Gaston 2003 and references therein). Although scientists have been interested in predicting the distributions of organisms for more than a century (Merriam 1894; Griggs 1914 in Gaston 2003), the advent of human-accelerated climate change and its implications for conservation have reinvigorated the focus on the dynamics of geographic distributions. For example, recent climate warming has already resulted in geographic range margin shifts in the direction of the poles (Parmesan and Yohe 2003; Root et al. 2003; Rosenzweig et al. 2008). Many species with limited distributions such as those restricted to islands are particularly prone to extinction because they cannot shift their ranges (e.g., Mitchell et al. 2008). Conversely, many wide-ranging species are ideal for understanding determinants of geographic distributions because they have successfully met the challenges of diverse climates (e.g., Doody et al. 2006).

Predicting how organisms shift their geographic distributions relies upon knowledge of the mechanisms involved (Kearney and Porter 2004; Mitchell et al. 2008). Stated another way, we need to know *how* organisms respond to different climates. For instance, what biological features and life stages of an organism set the boundaries of its geographic distribution? The distributional boundaries of species can be shaped by a great variety of factors, including temperature, resource availability, competition, predation, physical barriers, and genetic makeup (Macarthur 1972; Brown and Lomolino 1998). However, the actual mechanisms setting geographic boundaries in a given species are often poorly known (Gaston 2003).

Measuring changes in geographic distributions of longer-lived animals is often difficult due to constraints imposed by long generation times and short funding cycles. However, potential climate responses and their biogeographical ramifications can be predicted indirectly by studying variation in fitness-related traits across environmental gradients in wide-ranging species (Fielding et al. 1999; Doody et al. 2006). Specifically, we can reveal mechanisms (e.g., nest site choice) for adjusting to diverse climates by studying clinal variation in traits. Theoretically, these mechanisms can then be used to help explain current geographic range margins at

TABLE 1. Nest site characteristics reflecting behavioral traits that vary across environmental gradients in reptiles. Pivotal temperature variation is also included.

Trait	Species	References
openness	*Chelydra serpentina*, *Physignathus lesueurii*	Ewert et al. 2005 Doody et al. 2006
depth	*Physignathus lesueurii*	Doody 2009
aspect	*Physignathus lesueurii*	Doody et al., unpubl. data
pivotal temperature	*Chelydra serpentina*	Ewert et al. 2005
seasonal timing of nesting (onset)	*Apalone spinifera* *Chelydra serpentina* *Chrysemys picta* *Trachemys scripta* *Physignathus lesueurii*	Doody 1995 Iverson et al. 1997 Moll 1973 Moll & Legler 1971; Medem 1975; Moll & Moll 1990; Vogt 1990 Doody et al. 2006

climate extremes. Lastly, we can use clinal variation and its underlying mechanisms as a surrogate for predicting responses under future climates.

In general terms, thermal tolerance is likely to set geographic range margins of ectothermic animals at climate extremes because their physiological and developmental processes are underpinned by environmental temperatures (Pough 1980). The range of environmental conditions which are favorable for reproduction and development may be narrower than that tolerated by adult morphs (Gaston 2003 and references therein). Accordingly, the concept that the egg stage sets boundaries for geographic distributions of oviparous ectotherms such as reptiles has gained favor (Mell 1929; Muth 1980; Shine 1987; Kearney and Porter 2004; Parker and Andrews 2007). Incubation conditions of developing eggs are known to influence offspring fitness directly via embryonic survival and indirectly through the fitness consequences of developmentally plastic traits of offspring (see Deeming 2004). Moreover, the general lack of post-laying parental care in reptiles (reviewed in Shine 1988) underscores the importance of climatic conditions in establishing range margins in these species through effects on embryonic conditions.

Herein we review evidence for directional variation in fitness-related traits across environmental gradients in reptiles. A fitness-related trait is some characteristic of an organism that is likely to influence fitness (e.g., Zijlstra et al. 2003). Specifically, we examine variation in maternal traits that influence incubation conditions in oviparous species. Our synthesis does not include clinal variation in maternal reproductive components such as

clutch frequency, clutch size, or the composition of eggs, but rather focuses on behavioral traits such as nest site choice, and to a lesser extent seasonal timing of nesting. We propose that nest site choice buffers against environmental extremes, reducing or eliminating selection for shifts in physiological optima (thermal tolerance of developing embryos), a concept developed for thermoregulation in adults (Huey et al. 2003). We introduce a conceptual model that illustrates the biogeographical consequences (range margin dynamics) of reptiles based on this hypothesis. We discuss this synthesis in the context of the response repertoires that species possess for dealing with climate change.

VARIATION IN TRAITS ACROSS ENVIRONMENTAL GRADIENTS

Nest site choice.—Studies of clinal variation in nesting traits in reptiles are rare. However, such studies on Snapping Turtles (*Chelydra serpentina*) and Water Dragons (*Physignathus lesueurii*) indicate that at least wide-ranging reptiles can use nest site choice to counter climate differences (Table 1). Both Snapping Turtles and Water Dragons responded to extensive latitudinal gradients in temperature by nesting in more open areas in cooler climates (Ewert et al. 2005; Doody et al. 2006). At a finer scale, Water Dragons nested more superficially (shallower depths) at colder sites across an elevational gradient near the cold climate range margin (Doody 2009). The evidence for behavioral compensation is indirect in all of these studies. Compensation was assumed in the lizards because nest temperatures were similar across latitudes; nest temperatures were not recorded for the turtles. Moreover, embryonic survival and offspring sex ratios were not recorded in these studies, despite the presence of temperature-dependent sex determination (TSD) in both species. Future studies should attempt to address this knowledge gap to confirm the extent of compensation in both nest temperatures and the fitness consequences in terms of embryonic survival and offspring sex ratios. For example, is embryonic mortality particularly high, and are sex ratios heavily biased, in range margin populations at climatic extremes (but see below)?

Offspring sex ratios.—The single study quantifying offspring sex ratios across environmental gradients in a TSD species demonstrated limits to maternal compensation for cold temperatures through nest site choice, assuming that heavily-skewed sex ratios are less than optimal (Doody et al., unpubl. data). Water Dragons, in which females are produced by cool and warm temperatures and males by intermediate temperatures (Harlow 2001; Doody et al. 2006),

exhibited a clinal pattern of offspring sex ratios. At the coldest site offspring sex ratio was 0.95 in favor of females in a year with typical air temperatures; in an unusually hot year sex ratios were still biased toward females (0.71; Doody et al., unpubl. data). Associated nest temperatures indicated that only 'cooler' females were produced at the coldest site (i.e., those that developed at temperatures below the lower pivotal temperature; Doody et al., unpubl. data). Apparently, mothers could not produce more males because they were already nesting in the hottest sites available, in open areas, exclusively on the north-facing side of a mountain gorge (Doody et al., unpubl. data).

Seasonal timing of nesting.—It is common, indeed almost pervasive, for organisms in warmer climates to breed earlier than their cold climate counterparts, and this occurs both within and among species (e.g., Goldsworthy and Shaunessy 1994; Hoffman et al. 2003). This phenomenon is related to the length and intensity of the previous winter, especially in ectothermic animals. Animals must reach some threshold of energy balance in order to reproduce, and energy acquisition in reptiles generally begins in spring (Zug et al. 2001; Pough et al. 2003). Hence, mature eggs are shelled and laid later in colder climates. Nevertheless, data on clinal variation in seasonal timing of nesting are uncommon for reptile species, and herein we include some examples from the literature (Table 1). In general, the onset of nesting begins days to weeks earlier in warmer climate populations compared to cooler climate populations, and this would be expected to compensate to some extent for climate differences. Doody et al. (2006) noted that while clinal variation in seasonal timing of nesting in Water Dragons occurred, it was not sufficient to fully compensate for environmental temperature differences across their geographic distribution. Because the length of the breeding season is also protracted in cooler climates, earlier onset of nesting is generally associated with a longer nesting season due to more clutches deposited per season. Thus, any rigorous examination of the influence of altitude/elevation on phenotypes, offspring survival, and demographic consequences should also consider reproductive frequency, or the number of clutches produced within a year.

NEST SITE CHOICE AS A BUFFER
TO CLIMATE EXTREMES

Huey et al. (2003) coined and described the 'Bogert effect', whereby behavioral adjustments can reduce or eliminate the environmental variation that would be experienced by a non-regulating organism. The authors demonstrated that thermoregulatory behaviors likely inhibit selection for evolutionary shifts in thermal physiology across environmental gradients, a notion somewhat counter to the classic 'behavioral drive' theory proposing that behavior initiates new evolutionary events (Mayr, 1963). Lizards at higher elevations basked more, resulting in body temperatures that were more similar among different elevations than would be expected from null (operative) models (see Huey et al. 2003 and references therein).

We contend that an analogous phenomenon occurs in the reptilian egg, when reproduction limits distributional boundaries. First, we assume a reaction norm of optimal egg temperatures such that a limited range of egg temperatures provides the highest fitness returns. The variable of importance here could be embryonic survival or hatchling survival, and there is evidence for such a fitness curve in reptilian embryos, mainly from laboratory incubations (Deeming 2004). Assuming this incubation temperature range is the target for all populations, those populations at climatic extremes in wide-ranging species will be challenged to produce egg temperatures within this range. In other words, if reptiles nested randomly with respect to spatial characteristics influencing nest temperatures, eggs in cold climate nests would be considerably colder than the optimal temperature range, while eggs from hot climate nests would be hotter than optimal. However, reptiles often do not nest randomly with respect to environmental conditions (e.g., Rauch 1988; Wilson 1998). In a relevant example, Water Dragons nested exclusively on the north-facing (warm) side of a mountain gorge at a cold climate range margin; and more superficially with increasing elevation at the cold end of the range (Doody 2009; Doody et al., unpubl. data). Artificial nest temperatures from the south-facing (cooler) side of the gorge in the former study would have produced all one sex at best and complete embryonic failure at worst (Doody et al., unpubl. data). Thus, a more random spatial distribution of nests would have resulted in nest temperatures far below the optimal range. Thus, nest site choice reduced the environmental variation (extremes) that would have been experienced by Water Dragon embryos placed randomly with respect to aspect. More generally, this suggests that nest site choice can reduce or eliminate environmental variation that would be experienced by embryos placed randomly with respect to environmental temperatures (or factors influencing embryonic temperatures).

This buffering effect supports the notion that nest site choice behaviors inhibit selection for evolutionary shifts in embryonic, thermal tolerance across environmental gradients (Huey et al. 2003). Such a 'Bogert effect for embryos' thus assumes that optimal thermal tolerance ranges of embryos would be similar across different climates, an untested prediction. Another prediction would be that the pivotal temperatures would not differ across environmental gradients in a given species. Unfortunately, results from studies investigating clinal

variation in pivotal temperatures are rare and equivocal. Pivotal temperatures did not differ across a latitudinal gradient in Water Dragons (Doody et al. 2006; for similar more circumstantial evidence in turtles see also references therein). However, pivotal temperatures were shifted across latitude in the Snapping Turtle (Ewert et al. 2005). Could this difference in pivotal temperature variation between the lizard and the turtle be explained by the extent of behavioral compensation via nest site choice? Although highly speculative, nest site choice behavior could be more labile in the lizard and more conserved in the turtle. Both Water Dragons and Snapping Turtles nest in more open areas at cooler latitudes, but perhaps the turtles cannot adjust attributes such as nest depth or aspect, at or near range margins (but see Janzen 1994). A possibly relevant difference between nesting lizards and turtles is that lizards often nest at sites within their home ranges (i.e., in areas familiar to mothers; but see Angiletta et al. 2004), whereas many aquatic species such as Snapping Turtles would be less familiar with their nesting sites because they generally emerge from their aquatic habitats only to nest. In support, natal homing is known to occur in a few turtle species (Bowen and Karl 1996; Freedberg et al. 2005). Although the comparison is not quantified, turtle nest depth appears to be limited to hind limb length (except in species that body-pit), as opposed to lizards, which excavate nest cavities much deeper than the length of their (digging) front limbs.

BIOGEOGRAPHICAL RAMIFICATIONS: RANGE MARGIN DYNAMICS

When they reflect the thermal tolerance of an organism, we predict that the range margin boundaries of organisms at climate extremes are not strictly set by the critical thermal maxima and minima of embryos alone, but are also influenced by the availability of suitable nest sites and/or the extent of maternal, behavioral compensation. Maternal compensation via nest site choice would extend the geographic range margin boundary beyond the boundary set by critical thermal values of embryos alone (null model). Nest site choice would thus allow oviparous organisms to further invade climate extremes. However, there are two lines of evidence suggesting limits to behavioral compensation. First, Water Dragon mothers nested in the hottest available sites at a cold climate range margin, but still produced 95% females in a typical year (Doody et al., unpubl. data). Second, there is ample evidence that the evolution of viviparity facilitated further invasion of cold climates where oviparity via nest site choice apparently failed (Tinkle and Gibbons 1977; Blackburn 1982, 1985; Shine 1983). Finally, because the complete production of one sex in TSD species would occur prior to the

complete embryonic failure in either TSD or GSD species, the range margin boundary at climate extremes in TSD species would hypothetically occur between the boundaries set by nest site choice and by viviparity, given all else equal. Theoretically, the extent of range margin boundaries of reptiles at climate extremes are thus determined by: (1) critical thermal maxima and minima of adults; (2) critical thermal maxima and minima and the extent of compensatory nest site choice behavior; (3) reproductive mode (oviparity vs. viviparity); and (4) mode of sex determination. The latter two of these may apply to other oviparous ectotherms, provided that temperature is currently setting range margin boundaries via reproduction (e.g., at climate extremes). An important assumption of our idea is that thermal tolerances are setting range limits vs. hydric conditions through the risk of desiccation (Doody 2009). Studying hydric relations of flexible-shelled reptile eggs in nature is challenging due to the difficulty in measuring water potentials. Water potential varies temporally with stochastic rainfall events, and disturbing the nest chamber undermines accurate measurements.

IMPLICATIONS FOR CLIMATE CHANGE RESPONSES

Although there have been significant advances in methods for modeling the future distributions of organisms (Porter et al. 2002; Kearney and Porter 2004; Mitchell et al. 2008), formal empirical tests of these models will require the passing of many years or decades. However, we can understand species' repertoires for responding to climate change by determining which traits have been adjusted across climates, particularly in wide-ranging species (Fielding et al. 1999; Doody et al. 2006). For example, pivotal temperatures in Water Dragons do not vary across latitudes (Doody et al. 2006). From this we would predict that variation in pivotal temperatures might not be subject to selection for offspring sex ratios in Water Dragons, although theoretically both behavioral and pivotal temperature shifts could occur in parallel, especially at range margins. Snapping Turtles exhibited clinal variation in pivotal temperatures (Ewert et al. 2005), suggesting that pivotal temperatures are a likely target for selection on offspring sex ratios, and thus can be used to counter climate change in that species.

It is currently difficult to assess the ability of organisms to use nest site choice behavior to counteract climate change. It is clear from our review that nest site choice offers some behavioral compensation, but two issues remain unclear. First, the *extent* of this compensation is unknown. Numerous, independent origins of viviparity in squamate reptiles suggest limits to behavioral compensation. Variation in seasonal timing of nesting resulted in only minor compensation in

Water Dragons (Doody et al. 2006), a result not unexpected in a wide-ranging species spanning climates with a diversity of temperatures. Second and relatedly, we do not know if the observed compensation represents among-generation change in nest site choice behavior (strong genetic underpinning), or simply phenotypic plasticity (Doody et al. 2006). Formally solving the latter issue will require experimental manipulation (i.e., common garden or reciprocal transplants).

FUTURE DIRECTIONS

Our conceptual hypothesis is based on limited evidence, due to the paucity of studies of clinal variation in nesting in reptiles. Nevertheless, our conceptual synthesis provides a framework for future research and offers testable predictions. First and foremost, the idea that nest site choice offers behavioral compensation in the egg stage needs confirmation, ideally using the null model approach outlined by Huey et al. (2003) for thermoregulating adults. Second, the generality of that idea is unknown. Further studies of clinal variation in nest site choice are needed, and their value would be greatly strengthened if nest temperature were also measured. The inclusion of measured consequences in offspring sex ratios, other phenotypes, and embryonic survival in such a study would be particularly valuable, albeit challenging. Third, studies at climate extremes that manipulate eggs into sites with different thermal regimes would be useful for understanding the current limits to behavioral compensation, and in testing the idea that nest site choice extends range margin boundaries beyond those set by the thermal tolerance of embryos alone. Finally, measuring body temperatures of oviparous mothers during the period that eggs are incubating in nature would provide insights into how viviparity would improve embryonic survival and phenotypic quality at cold climate extremes (Andrews 2000; Shine et al. 2003).

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