Influence of Incubation Temperature on Hatchling Phenotype in Reptiles[*]

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ABSTRACT

Incubation temperature influences hatchling phenotypes such as sex, size, shape, color, behavior, and locomotor performance in many reptiles, and there is growing concern that global warming might adversely affect reptile populations by altering frequencies of hatchling phenotypes. Here I overview a recent theoretical model used to predict hatchling sex of reptiles with temperature-dependent sex determination. This model predicts that sex ratios will be fairly robust to moderate global warming as long as eggs experience substantial daily cyclic fluctuations in incubation temperatures so that embryos are exposed to temperatures that inhibit embryonic development for part of the day. I also review studies that examine the influence of incubation temperature on posthatch locomotion performance and growth because these are the traits that are likely to have the greatest effect on hatchling fitness. The majority of these studies used artificial constant-temperature incubation, but some have addressed fluctuating incubation temperature regimes. Although the number of studies is small, it appears that fluctuating temperatures may enhance hatchling locomotor performance. This finding should not be surprising, given that the majority of natural reptile nests are relatively shallow and therefore experience daily fluctuations in incubation temperature.

Introduction

Temperature during embryonic development in reptiles has a major influence on the phenotype of hatchlings. Development temperature can influence hatchling sex ratio (reviewed in Valenzuela 2004; Valenzuela and Lance 2004), morphology (reviewed in Deeming 2004), locomotor performance (Table 1), posthatch growth (Table 2), and behavior (reviewed in Deeming 2004). This is not a comprehensive review of all these influences, but it concentrates on two particular areas that were featured in the symposium session "Reproduction in Reptiles and Amphibians" at the 2004 Third International Conference for Comparative Physiology and Biochemistry. The first area of interest is the influence of global warming on reptile nest temperatures and its consequence for species that have temperature-dependent sex determination (Georges et al. 2004a; Nelson et al. 2004a), and the second is the potential influence of incubation temperature on hatchling fitness through its effects on locomotor performance and posthatch growth (Booth et al. 2004). Both these areas have come to prominence recently and will continue to be a focus for reptile life-history studies in the near future.

Possible Influence of Global Warming on Reptile Incubation

It has been argued that global warming will adversely affect reptile populations because of the influence that incubation temperature has on hatchling phenotype and because this influence would be particularly deleterious to species that have temperature-dependent sex determination (TSD) by causing the skewing of hatchling sex ratios (Davenport 1989; Janzen 1994; Formia 1996; Miller 1997; Nelson et al. 2004a; Valenzuela 2004). However, many reptile species with TSD have persisted through numerous ice ages over the past 100,000 years despite large changes in mean climatic temperatures. In these cases, the change in temperature presumably occurred slowly enough to allow species to shift their range, timing of nesting, choice of nest site microenvironments, or pivotal temperature range. In modern species such as the tuatara (*Sphenodon punctatus*) that have restricted ranges and incubation periods that extend through the entire year, range shifting and changing of nest timing are not possible, so changes in nest site microenvironment choice or pivotal temperature are the only options (Nelson et al. 2004a). Recent theoretical work by Georges et al. (2004a) suggests that global warming may not necessarily lead to a change in the hatchling sex ratio of reptiles with TSD if

Table 1: List of studies that have experimentally tested the influence of incubation temperature on locomotor performance of hatchling reptiles

Taxon, Species	Increase or Decrease in Locomotor Performance with an Increase in Incubation Temperature	Authors
Chelonian:		
Apalone mutica	Increase	Janzen 1993
Apalone spinifera	Intermediate temperature best	Doody 1999
Pelodiscus sinensis	Increase	Du and Ji 2003
Gopherus polyphemus	No influence	Demuth 2001
Emydura signata	Intermediate temperature best	Booth et al. 2004
Chelonia mydas	Increase	Booth et al. 2004
Lizard:		
Sceloporus virgatus	Decrease	Qualls and Andrews 1999
Bassiana duperreyi	Increase	Shine et al. 1995, 1997; Shine and Harlow 1996; Elphick and Shine 1998
Nannoscincus maccoyi	Decrease	Downes and Shine 1999
Lampropholis delicata	Increase	Downes and Shine 1999
Saproscincus mustelina	Increase	Downes and Shine 1999
Eumeces chinensis	Decrease	Ji and Zhang 2001
Podarcis muralis	Decrease	Van Damme et al. 1992; Brana and Ji 2000
Takydromus wolteri	Decrease	Pan and Ji 2001
Takydromus septentrionalis	Decrease	Lin and Ji 1998
Snake:		
Coluber constrictor	Increase	Burger 1990
Pituophis melanoleucus	Decrease	Burger 1991

they construct shallow nests that are exposed to high daily cyclic fluctuations in nest temperature.

In many shallow (<30 cm below ground surface) reptile nests, there is little difference (<0.5°C) in daily mean temperature at different levels below the soil surface, but the range in daily fluctuations of temperature at different depths is considerable (e.g., Packard et al. 1985; Palmer-Allen et al. 1991; Georges 1992; Bodie et al. 1996; Booth 1998; Demuth 2001; Nelson et al. 2004a; Fig. 1). Larger differences in mean daily temperature at different levels within the nest have been reported occasionally (e.g., nest 9 in Packard et al. 1985). Eggs in most reptile nests are located 5–30 cm below the soil surface, where significant diurnal cycles of temperature occur (Fig. 1). Only large reptiles such as sea turtles lay their eggs at depths >40 cm, where diurnal fluctuations in temperature are absent (Booth and Astill 2001). The magnitude of daily temperature cycle fluctuation influences the hatchling phenotype (Webb et al. 2001; Ashmore and Janzen 2003; Shine 2004) and the hatchling sex ratio in species with TSD (Vogt and Bull 1984; Bull 1985; Georges et al. 1994). This has important consequences for TSD species that have a large clutch size because eggs are usually deposited over a range of depths within the nest. Although the mean daily temperature is reasonably uniform throughout the

nest in these circumstances, the eggs at the top of the nest are exposed to a greater daily range of temperature than eggs at the bottom of the nest. Hence, hatchlings from different levels within the same nest will have different sex ratios. This phenomenon can be explained by the effect of temperature on embryonic development (Georges et al. 2004b). Because embryonic development rate is greater at higher temperature, more embryonic development will occur at temperatures above the daily mean than below it when embryos are exposed to cyclic fluctuations in temperature. Thus, it is the relative proportion of embryonic development taking place above the pivotal temperature (the constant temperature at which a 50 : 50 sex ratio is achieved) rather than the proportion of time spent above the pivotal temperature that determines the sex of a hatchling under a fluctuating temperature regime (Georges 1989; Georges et al. 1994, 2004b).

Georges (1989) developed a constant-temperature equivalent (CTE) model based on the degree-hour approach for predicting hatchling sex ratios under conditions of daily temperature fluctuations. This model was further developed and empirically tested in loggerhead sea turtles *Caretta caretta* (Georges et al. 1994). The model assumes a linear relationship between embryonic development rate and incubation temperature and ac-

Table 2: List of studies that have experimentally tested the influence of incubation temperature on posthatch growth rates in reptiles

Taxon, Species	Posthatch Growth Rate Affected by Incubation Temperature?	TSD?	Authors
Chelonioan:			
Chelydra serpentina	Yes, intermediate temperature fastest	Yes	Brooks et al. 1991; McKnight and Gutzke 1993; Bobyn and Brooks 1994; Rhen and Lang 1995
Gopherus polyhemus	Yes, higher temperatures fastest	Yes	Demuth 2001
Pelodiscus sinensis	No	No	Ji et al. 2003
Chrysemys picta	Yes, higher temperature faster	Yes	Janzen and Morjan 2002
Malaclemys terrapin	Yes, lower temperature faster	Yes	Roosenburg and Kelly 1996
Gopherus agassizii	Yes, intermediate temperature fastest	Yes	Spotila et al. 1994
Emydura signata	Yes, higher temperature faster	No	Booth et al. 2004
Elseya sp.	No	No	Y. Ingen-Housz and D. T. Booth, unpublished
Lizard:			
Cyclura nubila	Yes, higher temperature faster	Unknown	Alberts et al. 1997
Podarcis muralis	Yes, lower temperature faster	Unknown	Van Damme et al. 1992; Brana and Ji 2000
Eublepharis macularius	Yes, higher temperature faster	Yes	Tousignant and Crews 1995
Sceloporus virgatus	Yes, higher temperature faster	No	Qualls and Andrews 1999
Sceloporus undulatus	Yes, higher temperature faster	No	Andrews et al. 2000
Sphenodon:			
Sphenodon punctatus	Yes, higher temperature faster	Yes	Nelson et al. 2004*b*
Crocodilian:			
Alligator mississippiensis	Yes, intermediate temperature faster	Yes	Joanen et al. 1987
Crocodylus porosus	Yes, high temperature faster	Yes	Webb and Cooper-Preston 1989
Crocodylus niloticus	Yes, high temperature faster	Yes	Hutton 1987

curately predicts hatchling sex ratios in sea turtle eggs incubated under daily fluctuating temperature regimes (which in nature do not normally experience daily fluctuating temperatures because of the depth of the nest), but it is unable to accurately predict hatchling sex ratios in the pig-nosed turtle *Carettochelys insculpta* hatching from natural nests that experienced daily temperature fluctuations (Georges et al. 2005). Pig-nose turtle eggs have a narrow pivotal range, producing all males when incubated at temperatures below 31.5°C and all females when incubated at temperatures above 32.5°C (Young et al. 2004). Eggs in natural nests are also able to survive short periods of exposure to temperatures as low as 18°C and as high as 45°C (Georges et al. 2005).

Refinement of the CTE model to account for the curvilinear relationship between embryonic development rate and incubation temperature at the upper and lower extremes of viable temperatures (Georges et al. 2004*b*, 2005) resulted in the accurate prediction of hatchling sex in pig-nosed turtles (Georges et al. 2005). At the Ithala symposium, Georges and coworkers reported their use of the improved curvilinear CTE model to explore what would happen to hatchling sex ratios over a range of mean daily temperatures (26°–40°C) and a range of daily temperature fluctuations (0°–6°C) in pig-nosed turtles. When there is no temperature fluctuation (i.e., incubation temperature remains constant throughout the sex-determining period), CTE is equal to the incubation temperature, and an increase in incubation temperature causes an increase in the likelihood of producing 100% female hatchlings. However, as the daily fluctuating temperature range increases, CTE converges toward the pivotal temperature range, so there will be very little effect on hatchling sex ratio with changes in mean daily temperature if daily fluctuation of egg temperature exceeds ±4°C. In shallow exposed nests, large daily temperature fluctuations result in developmental inhibition at the high and low extremes (Georges et al. 2005), and sexual outcomes become progressively less responsive to changes in mean nest temperature (Georges et al. 2004*a*). This is a counterintuitive finding, but it indicates that some TSD reptile species may be buffered from
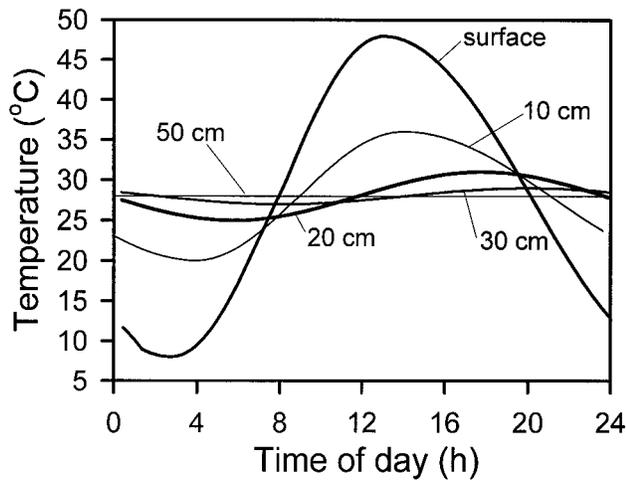
Figure 1. Stylized typical daily temperature profiles (D. T. Booth, unpublished data) in a soil exposed to full sun on a cloudless summer day, from the surface to a depth of 50 cm at a Brisbane River turtle *Emydura signata* nesting site (27°32′S, 153°00′E). This species lays its eggs 10–20 cm below the ground's surface. The daily mean temperature from all depths is 28°C, but the daily range varies remarkably with soil depth from 40°C at the soil's surface to 0°C at 50 cm. Note a temporal shift in the timing of maximum and minimum temperatures at different depths within the soil and that the soil heats faster than it cools.

change in mean climatic temperatures through the interaction of temperature on embryonic development rate and the physical attributes of shallow nests. This model can explain why some TSD species that have a wide latitudinal range do not have significantly different pivotal temperatures despite the fact that they experience differences in mean daily nest temperatures (e.g., *Pseudemys scripta*, Bull et al. 1982; *Physignathus lesuerii*, Doody et al. 2005). In these cases, daily temperature fluctuation would have to be great enough to reach the upper and lower extremes of embryonic developmental inhibition.

In other TSD species in which pivotal temperature does vary with population location (Bull et al. 1982; Mrosovsky 1988; Ewert et al. 1994; Morjan 2003), the daily temperature fluctuations may not reach the upper and lower extremes where embryonic development is inhibited, and thus, mean nest temperature would influence sexual outcomes. All sea turtle species construct deep nests, and consequently, their eggs do not experience daily fluctuations in incubation temperature. Many species have wide latitudinal range in rookery location, and pivotal temperature differs between populations (Limpus et al. 1985, 1993; Mrosovsky 1988), a finding consistent with the predictions of Georges et al. (2004b, 2005) when using their curvilinear CTE model. Thus, the sex ratio of sea turtle hatchlings is expected to change with seasonal changes in temperature as has been reported (Mrosovsky and Provancha 1992). However, it has been argued that population differences in sea

turtle pivotal temperatures are insignificant and that the differences reported in the literature may be artifacts caused by differences in the methodology used to estimate pivotal temperature (Mrosovsky 1988). Empirical testing of the curvilinear CTE model predictions is needed. This could be done by exposing eggs of pattern 1 (Ewert et al. 1994) TSD species to a range of mean temperatures and, at the same time, a range of daily temperature fluctuation amplitudes. The prediction is that at constant temperature and low-amplitude daily temperature fluctuations ($<\pm4°C$), sex ratio would change dramatically from 100% of one sex to 100% of the other sex with increasing mean temperature. In contrast, the sex ratio would remain relatively constant as mean incubation temperature increased if daily temperature fluctuations exceeded $\pm4°C$.

Influence of Incubation Temperature on Reptile Posthatch Fitness

In addition to sex ratio outcomes, incubation temperature can influence other hatchling attributes such as size and morphology (see Deeming 2004 for review). It is generally not known whether phenotypic changes induced by differences in incubation temperature significantly influence the fitness of hatchlings. Attributes such as locomotor performance and posthatch growth are thought to be the most likely traits to influence posthatch fitness (Booth et al. 2004; Nelson et al. 2004a). There is a general increase in locomotor performance with increasing incubation temperature in turtles and the reverse situation in lizards (Table 1).

In studies where the mean incubation temperature is kept constant but daily fluctuations in temperature are varied, an increase in locomotor performance occurs with an increase in daily temperature variance (Shine and Harlow 1996; Webb et al. 2001; Ashmore and Janzen 2003). Improved locomotor performance in hatchlings is generally assumed to be advantageous because it may lead to a greater ability to avoid predation (Janzen 1993). Hence, given that all the species tested to date construct shallow nests that are normally exposed to daily temperature fluctuations, it is not surprising to find that locomotor performance is maximized under a daily fluctuating temperature incubation regime.

Swimming performance of green turtle *Chelonia mydas* hatchlings within the first few hours after hatching has a large influence on hatchling fitness. This is because the highest rate of predation on hatchlings occurs in the water within the first 30–60 min of swimming as they pass through the gauntlet of fish predators in the waters surrounding natal beaches (Gyuris 1994, 2000; Pilcher et al. 2000). Male hatchlings incubated at 26°C are poorer swimmers than male and female hatchlings incubated at 28°C or 30°C (Booth et al. 2004; Fig. 2), so it is anticipated that predation of male hatchlings will be greater than that of females during this critical period. The anticipated higher mortality of low-temperature males due to their poorer
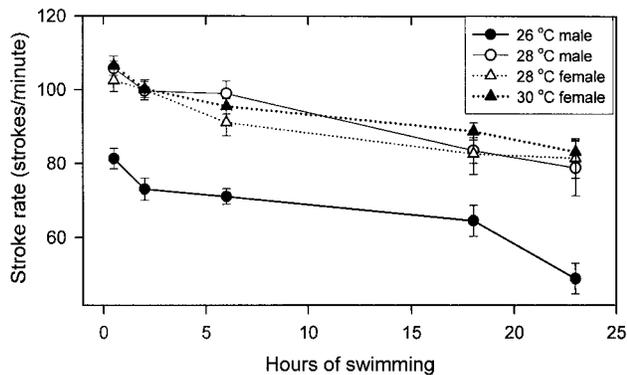
Figure 2. Power stroke rate of green turtle *Chelonia mydas* hatchlings incubated at different temperatures from the Heron Island rookery during the frenzy swimming phase immediately after hatchlings were placed in water (Booth et al. 2004). Data are means ± SE.

swimming ability, coupled with the fact that green turtle rookeries predominantly produce female hatchlings (Booth et al. 2004), would have the effect of producing a highly female-dominated cohort of hatchlings reaching the open ocean.

Incubation temperature influences the hatchling size in many reptiles (see Deeming 2004 for a review), with a tendency for larger (in terms of body dimensions) but not always heavier hatchlings to be produced at lower temperatures (reviewed in Booth 2000; Deeming 2004). The larger size of hatchlings from eggs incubated at cooler temperatures is due to more yolk material being converted to tissue during a longer incubation period (Booth 2000). It is not known whether this temperature-dependent difference in partitioning of yolk and tissue mass has fitness consequences for hatchlings. However, a larger body size with a smaller yolk reserve may be advantageous to a hatchling entering an environment where food is easily obtained. The larger size may allow hatchlings to escape gape-limited predators, swim faster, and successfully handle larger prey items. On the other hand, if the hatchling is entering an environment where food is scare or difficult to locate, then a smaller body size and a large residual yolk reserve may be advantageous because the larger yolk could supply the hatchling with energy for a longer period than a smaller yolk supply. To test these hypotheses, empirical experiments in which posthatch growth and mortality of hatchlings from different thermal regimes are needed, preferably in a field situation.

In addition to its effect on size at hatching, incubation temperature can influence posthatch growth (Table 2). There is a general trend for higher incubation temperatures to result in faster posthatch growth rates, but there are exceptions to this trend (Table 2). Gender probably confounds the temperature effect in species that have both sexual dimorphism in adult body size and TSD. Faster growth rate is considered to be advantageous because hatchlings spend relatively less time exposed to gape-limited predators, are able to handle larger prey

items (i.e., the "bigger is better" hypothesis), and reach sexual maturity faster because reptiles have indeterminate growth where size and not age determines when sexual maturity occurs.

The vast majority of reptile eggs are laid in shallow nests where daily cyclic fluctuation in temperature occurs, and therefore future studies examining the influence of incubation temperature on hatchling quality should include daily cyclic temperature fluctuation regimes. Four studies have examined the effect of fluctuating incubation temperature on hatchling locomotor performance; three found that fluctuating temperatures enhanced performance (Shine and Harlow 1996; Webb et al. 2001; Ashmore and Janzen 2003), and one showed no effect (Demuth 2001). The challenge for the future is to extend these pioneering studies and to conduct studies that examine the effect of varying magnitudes of fluctuating incubation temperatures on posthatch growth and survival in nature. In such studies, small lizards or snakes are probably the best model animals because they are relatively short-lived, compared with turtles and crocodilians.

Acknowledgments

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