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Female turtles from hot nests: is it duration of incubation or proportion of development at high temperatures that matters?

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Summary. Mean daily temperature in natural nests of freshwater turtles with temperature-dependent sex determination is known to be a poor predictor of hatchling sex ratios when nest temperatures fluctuate. To account for this, a model was developed on the assumption that females will emerge from eggs when more than half of embryonic development occurs above the threshold temperature for sex determination rather than from eggs that spend more than half their time above the threshold. The model is consistent with previously published data and in particular explains the phenomenon whereby the mean temperature that best distinguishes between male and female nests decreases with increasing variability in nest temperature. The model, if verified by controlled experiments, has important implications for our understanding of temperature-dependent sex determination in natural nests. Both mean nest temperature and "hours spent above the threshold" will be poor predictors of hatchling sex ratios. Studies designed to investigate latitudinal trends and inter-specific differences in the threshold temperature will need to consider latitudinal and inter-specific variation in the magnitude of diel fluctuations in nest temperature, and variation in factors influencing the magnitude of those fluctuations, such as nest depth. Furthermore, any factor that modifies the relationship between developmental rate and temperature can be expected to influence hatchling sex ratios in natural nests, especially when nest temperatures are close to the threshold.

Key words: Temperature-Dependent sex determination – Sex ratios – Thermal model – Reptiles

The influence temperatures has on the outcome of sexual differentiation in reptiles is now well established, having been demonstrated for turtles from eight families (though not Trionychidae or Chelidae), crocodilians and some lizards (reviewed by Bull, 1980, 1983 with subsequent original data by Webb et al. 1986; Alho et al. 1985; Georges 1988; Thompson 1988a). For most species, females are produced at high temperatures and males at low temperatures. A very narrow range of temperatures, referred to as the threshold temperature, produces both males and females and divides the male producing temperatures from the female producing temperatures (Bull 1983). A few species have upper and a lower thresholds with females produced at both extremes (Yntema 1976; Gutzke and Paukstis 1984). The critical period for sex determination, during which embryonic sex can be irreversibly influenced by temperature, is generally considered to lie in the middle third of development (Yntema 1979; Bull and Vogt 1981).

Most studies of sex determination of reptiles have been conducted in the laboratory at constant temperatures and the influence of temperature on sex in natural nests is less well understood. Seasonal variation in nest temperatures during the period critical for sexual differentiation, wide daily fluctuations in nest temperature, and thermal gradients within single nests may all be expected to complicate comparisons between field and laboratory data. In early field studies, nests with mean daily temperatures above the threshold, established in the laboratory, were expected to yield females whereas nests with mean temperatures below the threshold were expected to yield males (Pieau 1973, 1975). Results of field studies were broadly in agreement with laboratory studies – females typically emerge from hot exposed nests, males from cool shaded nests (Bull and Vogt 1979; Morreale et al. 1982) – but it was soon apparent that mean nest temperature was not the best predictor of hatchling sex. Predominantly female hatchlings of *Emys orbicularis* emerged from nests with longer daily exposure to temperatures below than above the threshold of 28.5° C (Pieau 1982). The mean temperature in these nests was considerably lower than the threshold. Hatchling sex ratios in natural nests of *Chrysemys picta* were most closely related to time spent between 20.0 and 27.5° C, the upper and lower threshold temperatures, and not mean nest temperature (Schwartzkopf and Brooks 1985). Both the mean and variance in temperature were required to account for sex ratio differences among nests of map turtles in the genus *Graptemys* (Bull 1985). A single mean nest temperature was inadequate as a threshold for natural nests, because the mean temperature that best discriminated male and female nests decreased as temperatures fluctuated more widely.

By way of explanation, several authors have noted that because embryonic developmental rates are greater at higher temperatures than at lower temperatures (within limits), more development will occur at temperatures above the mean than below it (Bull and Vogt 1981; Pieau 1982; Mrosovsky et al. 1984; Bull 1985). The onset of the critical period for sex determination appears to be time-dependent (Bull and Vogt 1981) but it has not yet been determined whether the outcome of sexual differentiation depends on the relative time spent at temperatures above and below the threshold or on the relative proportions of development taking place at temperatures above and below the threshold. In this paper, I present a model involving developmental rates, their relationship to temperature, fluctuating nest temperatures, and the assumption that if more than half of embryonic development occurs above the threshold temperature, then females will be produced, otherwise males will be produced. The model is used to explore the consequences of this assumption for sex determination in natural nests. While not specifically tested, support for the model is drawn from various published studies of incubation and sex determination in natural nests.

Model description

The model assumes that

1. Developmental rate ds/dt increases linearly with increasing temperature T during the period in which temperature exerts its influence on sex.

$$\frac{ds}{dt}=A(T-T_0) \qquad A>0 \tag{1}$$

where A is the rate of increase and T_0 is the minimum temperature for embryonic development. The model is constrained by the biologically realistic assumptions that growth cannot be reversed ($ds/dt \geq 0$) and that no growth can occur at temperatures below 0° C ($T_0 \geq 0$).

2. Temperature varies on a daily cycle about a stationary mean according to the formula

$$T=R\,\mathrm{Cos}(t)+M \qquad 0 \leq R < M \tag{2}$$

where T is temperature in degrees centigrade, and R is the maximum deviation of temperature from the mean temperature M. To simplify the algebra without loss of generality, time t is measured in units such that 2Π units = 24 h.

3. Female hatchlings will emerge from nests for which the effective nest temperature, T', exceeds the threshold temperature, males and females will emerge from nests with T' equal to the threshold, and males will emerge from nests with T' less than the threshold. The effective nest temperature T' is defined as the temperature above which half of embryonic development occurs.

The variables and parameters of the model are illustrated in Fig. 1. The model assumes that temperatures fluctuate daily about a stationary mean (Fig. 1). Cases where there is a strong seasonal trend in temperature during the period critical for sex determination and cases where temperatures are affected by stochastic events such as rainfall (Packard and Paukstis 1985), are not specifically dealt with by the model. Throughout this paper, threshold temperature refers to the laboratory threshold established under constant conditions.

Given the mean nest temperature M and amplitude $2R$ of the diel cycle, we require the temperature T' above and below which half the embryonic development occurs. Provided nest temperatures are always greater than the minimum temperature for development (i.e. $M-R \geq T_0$), the solution can be obtained by integrating the developmental rates as they vary along the diel temperature cycle such that

$$\int_0^{t'} \frac{ds}{dt}\,dt = \int_{t'}^{\pi} \frac{ds}{dt}\,dt \tag{3}$$

where t' is the time at which temperature T' is achieved.

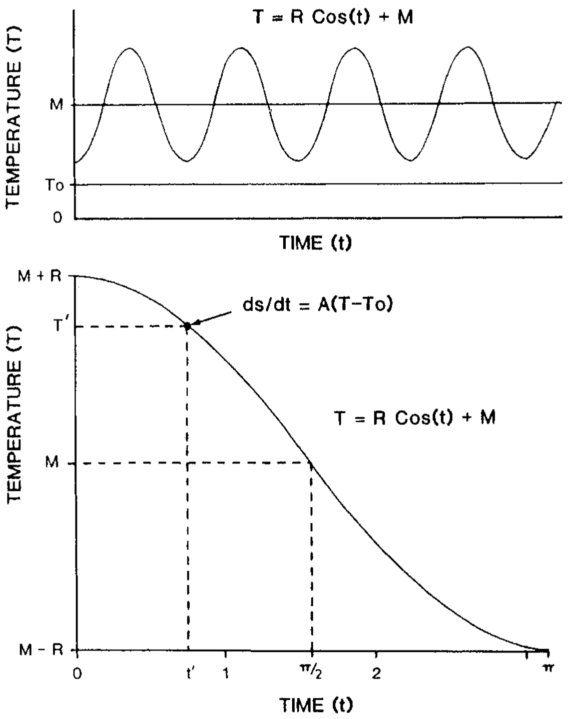

Fig. 1. Definition of functions, variables and parameters used to model nest temperatures and development rates. Abbreviations: T, temperature; t, time in units such that 2Π units = 24 h; T', temperature above which half of embryonic development occurs; t', time that temperature T' is achieved; T_0, minimum temperature for embryonic development; M, mean nest temperature; R, extent of temperature fluctuations above and below the mean; ds/dt, rate of development at an arbitrary point on the diel temperature curve

Substituting $A(T-T_0)$ for ds/dt, $R \cdot \mathrm{Cos}(t)+M$ for T and evaluating the integrals yields

$$t'=\frac{\Pi}{2}-\frac{R}{M-T_0}\,\mathrm{Sin}(t') \tag{4}$$

which has no exact solution and must be solved iteratively for t'. The value $t'=\Pi/2$ is an appropriate initial value for biologically realistic values of the constants R, M and T_0. The required value of T' can be obtained by substituting the iterative solution for t' in (2).

The slightly more complicated case where nest temperatures drop below T_0 and development ceases for part of each day yields the following equations

$$\int_0^{t'} \frac{ds}{dt}\,dt = \int_{t'}^{t_0} \frac{ds}{dt}\,dt \tag{5}$$

where t_0 is the time that nest temperature first drops to T_0 and is given by

$$t_0=\mathrm{Cos}^{-1}\left[\frac{T_0-M}{R}\right] \qquad 0<t_0 \leq \Pi \tag{6}$$

Evaluating the integrals as above yields

$$t'=\frac{t_0}{2}+\frac{R}{2(M-T_0)}\,\mathrm{Sin}(t_0)-\frac{R}{M-T_0}\,\mathrm{Sin}(t') \tag{7}$$

which again must be solved iteratively for t'. The value of the first two terms of the right hand side of the equation is an appropriate seed. Cases where nest temperatures drop below the minimum temperature for development will not be considered further, because this situation does not apply to data used to validate the model.

Effective nest temperature T' will exceed the mean nest temperature M by

$$\delta = R \cdot \mathrm{Cos}(t') \quad (8)$$

Time spent at temperatures greater than T' is given by

$$2t' \text{ units} = 7.64\,t' \text{ h} \quad (9)$$

Model responses

Figure 2 provides the means for judging how the model responds to changes in mean nest temperature or changes in the amplitude of diel fluctuations in temperature. An increase in the value of the expression $R/(M - T_0)$ will cause a decrease in the value of δ. Thus greater values of δ will be obtained for a nest that experiences wider fluctuations in temperature (R large) than another nest, even though mean temperatures for both nests may be the same. This response results from both a smaller value of t' for the nest with wider temperature fluctuations (Fig. 2) and the presence of R in the formula for δ.

Conversely, a decrease in mean nest temperatures (M small) will result in a larger value of δ. Unlike the model response to change in R, model response to change in M results solely from a corresponding change in t'. δ will be less affected by changes in mean nest temperature than by changes in the magnitude of temperature fluctuations about that mean.

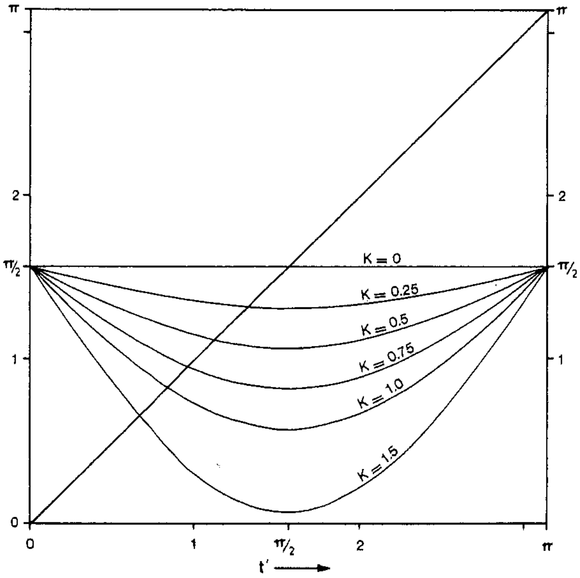

Fig. 2. A graph showing the responses of t' to changes in the parameters R, M and T_0 of the model. The temperature T' above and below which half of embryonic development occurs corresponds to a time t' such that

$$t' = \frac{\Pi}{2} - \frac{R}{M - T_0} \mathrm{Sin}\, t'$$

Solutions to this equation for various values of $K = R/(M - T_0)$ are shown on the graph by the intersection of the diagonal $y = t'$ with the curves $y = \Pi/2 - K\,\mathrm{Sin}(t')$. It is clearly evident that t' declines for increasing values of K

The model is unaffected by changes of scale in the measurement of developmental rates (parameter A is absent from (4)), an observation that is important when applying the model.

Results

Incubation of *Emys orbicularis* in Brenne, France, is about four times as long at 18° C and three times as long at 19.5° C than at 25° C (Pieau 1978). Assuming that average rates of development during incubation reflect rates during the period critical for sex determination, and recalling that the model is unaffected by choice of scale for the measurement of developmental rates, we can set ds/dt equal to 0.25, 0.33 and 1.00 respectively. Using least-squares regression, this yields

$$\frac{ds}{dt} = 0.1109\,T - 1.7835 = 0.1109(T - 16.1)$$

so $T_0 = 16.1°$ C. Pieau (1982) later presented data on fluctuating temperatures and sex ratios for five nests (Table 1). Nest I had a mean temperature of about 24.8° C with fluctuations of 15° C (read from Pieau's Fig. 1). From these data we have

$$T_0 = 16.1 \qquad M = 24.8 \qquad R = 7.5$$

Fourteen iterations of (4) yielded $t' = 0.8980$ with no further improvement at the fourth decimal place. Substituting t' in (2) yielded 29.5° C for the effective nest temperature, 4.7° C higher than the mean nest temperature. *Emys orbicularis* has a threshold temperature of 28.5° C (Pieau 1976). If the outcome of sexual differentiation depends on the relative duration of incubation above and below the threshold we would expect hatchlings from Nest I to be male, as the mean nest temperature is well below the threshold. If the outcome depends on the amount of development that occurs above and below the threshold, we would expect the hatchlings to be female, because the effective nest temperature is above the threshold. Clearly the considerations that led to the development of the model have implications for sex determination in natural nests, and the model's predictions are testable.

Support for the model is drawn from two field studies of sex determination in turtles. Claude Pieau (1982) found that mean temperatures of five nests of the European pond turtle *Emys orbicularis* from Brenne in France, were each well below the threshold temperature of 28.5° C (Table 1), and on that basis the nests were expected to produce predominantly male offspring (Pieau 1973, 1975). Four of the five nests produced predominantly females, a clear demonstration of the inadequacy of mean nest temperatures for predicting hatchling sex. Prediction is much improved using the higher values of T' obtained from the model with $T_0 = 16.1$ calculated in the example above and by substituting the mean temperature and range in temperatures for each nest (Table 1). Only Nest V deviates substantially from the model prediction. T' of 27.8° C for that nest is less than the threshold so it could be expected to produce males when in fact the sex ratio was 10:1 in favour of females. However Nest V was the only one for which diel temperatures did not fluctuate consistently, stabilizing at low temperatures for four of the thirteen days that temperatures were monitored (Pieau 1982). Sex may have been determined in the

Table 1. Nest temperatures for *Emys orbicularis* from Brenne in France (taken from Fig. 1 of Pieau 1982). *E. orbicularis* has a single threshold temperature of 28.5° C (Pieau 1976) so on the basis of mean nest temperatures alone, all nests would be expected to produce males. Abbreviations: *M*, mean nest temperature; *R*, mean deviation in temperature above and below the mean; *T′*, temperature above and below which half of embryonic development occurs

Nest	*M*	*R*	*T′*	Sex			
				Model prediction	Male	Observed intersex	Female
I	24.8	7.5	29.5	female	4	0	17
II	23.9	6.0	27.4	male	9	10	2
III	26.8	5.9	29.6	female	4	3	9
IV	25.8	5.7	28.6	mixed	3	6	17
V	25.5	5.0	27.8	male	1	12	10

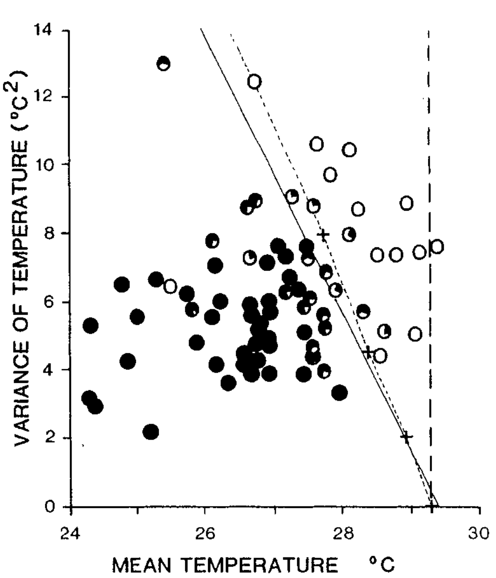

Fig. 3. A plot of male and female nests of *Graptemys ouachitensis* ($n=58$), *G. pseudogeographica* ($n=9$) and *G. geographica* ($n=7$) against the mean and variance of nest temperature in week 4–5 of incubation (after Bull 1985). The proportion of males in the nest is represented by the proportion of the symbol that is black. The solid sloping line was fitted empirically by Bull to separate male and female nests. The dotted line is that predicted by the model – nests to the right of the line have more development occurring at temperatures above the threshold temperature than below it, nests to the left have less development occurring above the threshold than below it. The vertical dashed line would be expected to separate male and female nests if mean nest temperature alone dictated sex

seven days before temperatures stabilized, and the model prediction based on data for those seven days was in agreement with observation. Overall support for the model must also be qualified because nest temperatures were measured at the same depth but in soil adjacent to nests. Metabolic heating has been shown to be of some consequence in turtle nests (Burger 1976; Standora and Spotila 1985) and this, combined with possible differing thermal characteristics of the nest chamber and the soil above it compared to adjacent undisturbed soil, may have resulted in higher nest temperatures than those recorded by the probes.

Stronger support for the model stems from the studies of James Bull and Richard Vogt on map turtles in the genus *Graptemys*. Bull (1985) compared the sex ratios of nests that differed with respect to mean temperature and variance in temperature, and found that nests producing females had higher means or higher variances than nests producing males (Fig. 3). A straight line with negative slope best discriminated between male and female nests in contrast to the vertical line that would be expected if mean temperture alone determined hatchling sex.

In map turtles, development at 31° C is approximately twice as rapid as at 25° C during the stages critical for sexual differentiation (Bull and Vogt 1981). These data yield an estimate for T_0 of 19.0° C. Map turtles have a threshold of about 29.3° C (Bull et al. 1982a), so the model was used to predict mean temperatures that corresponded to an effective nest temperature of 29.3 for R equal to 1, 2, 3, ...6. The variance of the function $T=R\cdot\mathrm{Cos}(t)+M$ is $R^2/2$ so these values of R correspond to variances of 0.5, 2.0, 4.5, 8.0, 12.5 and 18.0 respectively. A plot of the mean/variance pairs with an effective temperature equal to the threshold is remarkably close to the sloping line established empirically by Bull (Fig. 3). The effect noted by Bull can be explained solely by assuming that the threshold temperature for sex determination is 29.3° C with females produced from eggs with embryos that undergo more than half their development above the threshold rather than from those spending more than half their time above it.

Discussion

It is difficult to test models using data collected for some other purpose, notwithstanding the selectivity that might occur, and the model needs to be tested specifically. This could be done in the laboratory using fluctuating temperatures to determine the precise value of the mean temperature that produced both temperatures and comparing it to the threshold temperature obtained in constant temperature experiments. The difference between the two could then be compared to that predicted by the model. Such data are currently unavailable. However the agreement between the "discriminant line" derived from the model and that derived empirically by Bull (1985) is convincing (Fig. 3), and some speculation on the implications the model predictions have for our understanding of temperature-dependent sex determination is justified.

Hours spent at temperatures above the threshold temperature (or above 30° C) have been used for predicting hatchling sex (Wilhoft et al. 1983; Bull 1985; Schwartzkopf and Brooks 1985). However, one hour spent at temperatures up to 1° C above the theshold will not be equivalent to one hour at temperatures up to 5° C above the threshold, if proportion of development is more important than proportion of time spent above the threshold. The threshold value, when expressed in hours required above the threshold temperature to produce females, will depend on the thermal regime used in experiments. This point is also evident from the model. Nests producing mixed sexes will have an effective temperature equal to the threshold temperature. For such nests, the time spent above the threshold will be $7.64t'$ hours, a value dependent on t' and therefore M and R, the mean and variability in temperature.

Threshold temperature appears to be heritable in turtles (Bull et al. 1982b, but see Webb and Smith 1984) and is therefore subject to natural selection. Bull et al. (1982a) predicted that the threshold temperature should be lower at cool latitudes than at warm latitudes for populations of the same species but if anything, the reverse trend was evident for emydid turtles of Wisconsin and Tennessee in North America. The authors argued that under natural conditions, there may be greater potential for evolution of maternal behaviour in choosing nest sites than for evolution of the threshold because when nest temperatures vary widely, variation in the threshold temperature is only of consequence for a small proportion of nests. However, subsequent studies found that sex ratios of *Chrysemys picta* depended more on yearly variation in climate than on variation in site characteristics and that females selected nests to maximize the probability that eggs would complete development, rather than to influence offspring sex (Schwartzkopf and Brooks 1987). The model presented here predicts that changes in the relationship between the developmental rate and temperature and changes in nest depth (since R will decline with depth; Thompson 1988b) each have the potential to compensate for changes in ambient temperatures with latitude. Furthermore, ambient temperatures may fluctuate more widely about lower means at higher latitudes than at lower latitudes, so that the same effective nest temperature can be achieved at both latitudes even though mean nest temperatures are lower at high latitudes. These considerations, coupled with the fact that maximum nest temperatures may depend more on solar radiation (similar at Wisconsin and Tennessee) than on ambient air temperatures, and that turtles at southern warmer latitudes nested two weeks earlier than their northern counterparts (Bull et al. 1982a), may explain the failure of the threshold temperature to vary with latitude in the manner expected.

The consequences of the model, if correct, are greater for freshwater and terrestrial species that deposit eggs in shallow nests where temperatures fluctuate widely (up to 18° C in *Emys orbicularis*; Pieau 1982) than for marine species with deep nests where diel fluctuations in temperature are modest (0.5–1.0° C in *Chelonia mydas*; Morreale et al. 1982). Shallow nesting species may have more scope for varying parameters other than the threshold temperature than do the deep nesting marine species. Bull et al. (1982a) could demonstrate little variation in the threshold temperature among emydid turtles whereas the marine Green Turtle (*Chelonia mydas*) and Leatherback Turtle (*Dermochelys coriacea*) nesting on the same beach had thresholds that differed by ca. 0.5° C (Mrosovsky et al. 1984). Consistent with expectation, the leatherbacks had the higher threshold and nested in relatively greater numbers during the warmer parts of the season.

It has been suggested that developmental rate rather than temperature *per se* is the proximal factor that influences sex (Webb and Smith 1984). The model is unable to distinguish between these two possibilities, but in nests where temperatures fluctuate appreciably, the model predicts that any factor that modifies the relationship between developmental rate and temperature (and hence T_0) will influence hatchling sex ratios when temperatures are in the vicinity of the threshold. Such secondary factors include soil moisture and rates of gas exchange which may act synergistically with temperature to affect embryo metabolism and developmental rates (Miller 1985). Paukstis et al. (1984) found that substratum water potential does modify the influence of temperature on developmental rates in *Chrysemys picta* (see incubation periods listed in their Table 1), and further demonstrated an influence of water potential on sex ratios when temperatures fluctuated between 18 and 31° C. Under this regime, the effective nest temperature T' would have been about 28.4° C which is within the range 28.3 to 29.5° C established as the upper threshold temperature for *C. picta* (Bull et al. 1982a). Again, this is consistent with the model, though it would not have predicted an influence of water potential on sex ratios from experiments at constant temperatures (Gutzke and Paukstis 1983).

Clearly the model presented in this paper, which needs to be verified by controlled experiments with fluctuating temperatures, has important implications for our understanding of temperature-dependent sex determination in natural nests. Further detailed study of the thermal characteristics of nests and of sex determination under natural conditions is also warranted.

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