



A model to predict the thermal reaction norm for the embryo growth rate from field data



Marc Girondot^{a,b,*}, Yakup Kaska^c

^a Laboratoire Écologie, Systématique et Évolution (UMR8079), Faculté des Sciences d'Orsay, Université Paris-Sud, 91405 Orsay, France

^b AgroParisTech, CNRS, 91405 Orsay, France

^c Pamukkale Üniversitesi, Fen Edebiyat Fakültesi, Biyoloji Bölümü, Denizli, Turkey

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ABSTRACT

The incubation of eggs is strongly influenced by temperature as observed in all species studied to date. For example, incubation duration, sexual phenotype, growth, and performances in many vertebrate hatchlings are affected by incubation temperature. Yet it is very difficult to predict temperature effect based on the temperature within a field nest, as temperature varies throughout incubation. Previous works used egg incubation at constant temperatures in the laboratory to evaluate the dependency of growth Prod. Type: FTh rate on temperature. However, generating such data is time consuming and not always feasible due to logistical and legislative constraints. This paper therefore presents a methodology to extract the thermal reaction norm for the embryo growth rate directly from a time series of incubation temperatures recorded within natural nests. This methodology was successfully applied to the nests of the marine turtle *Caretta caretta* incubated on Dalyan Beach in Turkey, although it can also be used for any egg-laying species, with some of its limitations being discussed in the paper. Knowledge about embryo growth patterns is also important when determining the thermosensitive period for species with temperature-dependent sex determination. Indeed, in this case, sexual phenotype is sensitive to temperature only during this window of embryonic development.

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1. Introduction

Virtually all biological rates in ectothermic animals, including development times (Gillooly et al., 2002) and growth rates (Gillooly et al., 2001), are affected by temperature.¹ Egg incubation temperatures affect the duration of embryogenesis (Miller, 1985), probability of embryo survival (Van Damme et al., 1992), sex determination for species with temperature-dependent sex determination (Pieau, 1996), and morphology and body size at hatching (Du and Ji, 2003). In addition, the long-term effects of incubation temperature on the physiology and behavior of hatchlings has been observed (Burger, 1989; Sibly and Atkinson, 1994). Thus, the fitness of developing embryos is strongly dependent on the temperature within the nest during incubation.

The effects of temperature are usually assessed by comparing certain traits that are measured in individuals incubated at different

constant temperatures. However, the temperature within a nest is not constant, varying over several spatial and temporal scales. It is dependent on latitudinal location, seasonal temperature changes, shading by vegetation, sand color, and episodic events such as rain and nest depth (Hays et al., 2001; Matsuzawa et al., 2002). Temperature increases due to the metabolic heating of embryos (Godfrey and Mrosovsky, 1997) or decomposition of organic matter on the beach (Valverde et al., 2010) have also been reported. To deal with such a complex situation, the constant temperature equivalent (CTE) was defined as the constant temperature that generates an effect similar to a complex pattern of changing temperature (Orchard, 1975, 1976). CTEs have, for example, been used in the context of sex determination given the relationship between incubation duration and sex ratio (Godfrey et al., 1996; Kaska et al., 2006). However, CTE mimics only some of the properties of the system, while fluctuating temperatures present certain effects that are not observed with CTE (Delmas et al., 2007). For this reason, the integration of fluctuating temperatures into a conceptual framework of egg incubation is preferable.

The majority of analyses examining the effects of temperature on field incubation in reptiles use rather crude statistics, such as mean temperature during incubation (Valenzuela, 2001). To the best of our knowledge, only three previous studies have modeled

* Corresponding author at: Laboratoire Écologie, Systématique et Évolution (UMR8079), Faculté des Sciences d'Orsay, Université Paris-Sud, 91405 Orsay, France. Tel.: +33 1 69 15 72 30.

E-mail address: marc.girondot@u-psud.fr (M. Girondot).

¹ AICs: Akaike information criteria; CTE: constant temperature equivalent; MCMC: Markov chain Monte Carlo; SCL: straight carapace length.

incubation duration for reptile eggs while taking non-constant temperatures into consideration (Delmas et al., 2008; Georges et al., 2005; Girondot et al., 2010). There are two important components in this type of model: (i) the norm of reaction for the growth rate based on the temperature, and (ii) the change of the embryo size or mass index over time. To model the dependency of growth rate on temperature, the following models were used: the linear degree-hour model (Georges et al., 2005), empirical curvilinear model (Delmas et al., 2008; Georges et al., 2005), biophysical model (Georges et al., 2005; Girondot et al., 2010), and polynomial model (Georges et al., 2005). All of these methods use extensive data on embryo growth at constant temperatures obtained in the laboratory. However, such data are only available for a limited number of species.

We therefore propose a general way to model sigmoidal, linear, or exponential embryo growth with variable incubation temperatures obtained from the field. This general model can be applied to any egg-laying species with some limitations. To test its validity, we use data obtained from 21 nests of the marine turtle *Caretta caretta* that were monitored on Dalyan Beach in Turkey.

2. Materials and methods

The model presented here integrates within a single framework both the dependency of growth rate on temperature—also called the norm of reaction—and embryo growth based on these growth rates. The models for growth rate dependence on temperature and embryo growth are fitted using maximum likelihood and Bayesian Markov chain Monte Carlo (MCMC) methods to best describe the observed hatchling size according to a time series of temperature within the nests. The model was implemented as an R package “embryogrowth” available on Comprehensive R Archive Network (<http://cran.r-project.org>).

2.1. Dependency of growth rate on temperature

Biological temperature-dependent rate models based on the Arrhenius and Eyring equations were formulated by Sharpe and DeMichelle (1977). Subsequently, the original formulation of Sharpe and DeMichelle was modified by Schoolfield et al. (1981) in order to remove the very high correlations of parameter estimators Eq.(1).

$$r(T) = \frac{\rho_{(298\text{ K})} \frac{T}{298} \exp\left[\frac{\Delta H_A^\ddagger}{R} \left(\frac{1}{298} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{\Delta H_L}{R} \left(\frac{1}{T_{1/2L}} - \frac{1}{T}\right)\right] + \exp\left[\frac{\Delta H_H}{R} \left(\frac{1}{T_{1/2H}} - \frac{1}{T}\right)\right]} \quad (1)$$

$r(T)$ is the mean development rate at temperature T (time^{-1}), T is the temperature in K ($298\text{ K}=24.85\text{ }^\circ\text{C}$), R is the universal gas constant ($\text{J K}^{-1} \text{mol}^{-1}$). The original model defined R in $\text{cal K}^{-1} \text{mol}^{-1}$, but is here converted into SI units.

$\rho_{(298\text{ K})}$ is the development rate at $24.85\text{ }^\circ\text{C}$ assuming no enzyme inactivation (time^{-1}), ΔH_A^\ddagger is the enthalpy of activation of the reaction catalyzed by the enzymes (J mol^{-1}), $T_{1/2L}$ is the temperature in K at which the enzymes are 1/2 active and 1/2 low-temperature inactive, ΔH_L is the change in enthalpy associated with the low-temperature inactivation of the enzymes (J mol^{-1}), $T_{1/2H}$ is the temperature in K at which the enzymes are 1/2 active and 1/2 high-temperature inactive, ΔH_H is the change in enthalpy associated with the high-temperature inactivation of the enzymes (J mol^{-1}). To ensure that $T_{1/2H} \geq T_{1/2L}$, a new variable ΔT was introduced with $T_{1/2H} = T_{1/2L} + |\Delta T|$. Thus, the fitted variables were $T_{1/2L}$, ΔT , ΔH_H , ΔH_L , ΔH_A^\ddagger , and $\rho_{(298\text{ K})}$.

This model can be simplified by taking into account only four parameters (Schoolfield et al., 1981). This equation is analogous to the equation developed by Johnson and Lewin (1946):

$$r(T) = \frac{\rho_{(298\text{ K})} \frac{T}{298} \exp\left[\frac{\Delta H_A^\ddagger}{R} \left(\frac{1}{298} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{\Delta H_H}{R} \left(\frac{1}{T_{1/2H}} - \frac{1}{T}\right)\right]} \quad (2)$$

Thus, the fitted variables were $T_{1/2H}$, ΔH_H , ΔH_A^\ddagger , and $\rho_{(298\text{ K})}$.

The original publication (Schoolfield et al., 1981) used the oversimplification $298\text{ K}=25\text{ }^\circ\text{C}$, which has been corrected here.

2.2. Change of embryo size or mass index over time

The development of marine turtle embryos was previously assessed by the measurement of a variety of indicator variables, including total body length (straight or curved), head length and width, straight carapace length (SCL) and width, bridge length (distance across inframarginal scales), tail length, fore and hind flipper length, and plastron length (Blanck and Sawyer, 1981; Caldwell, 1959; Deraniyagala, 1939; Domantay, 1968; Penyapol, 1958). Plots of data obtained from the measurement of most morphological characters follow a more or less sigmoidal shape. Typically, the rate of change is slow at first, but accelerates during a portion of the incubation period only to slow again in the days before hatching (Miller, 1982). This observation invalidates the linear or exponential growth rate previously used to model turtle development (Delmas et al., 2008; Georges et al., 2005; Girondot et al., 2010).

Several sigmoidal equations can be used to describe the early growth of embryos (Gompertz, 1825; Richards, 1959; von Bertalanffy, 1938). The flexibility of these equations makes them behave in a similar manner. We use a modification of the Gompertz model proposed by Laird (1964):

$$X(t) = K \exp\left(\ln\left(\frac{X(0)}{K}\right) \exp(-r(T)t)\right) \quad (3)$$

where $X(0)$ is the size or mass at nesting time ($\text{time}=0$), $r(T)$ is the growth rate at the beginning of the curve, and K is the carrying capacity with $\lim X(t) = K$. Note that hatching generally occurs before the embryo reaches the size or mass K . The K parameter can be viewed here as simply a way of reducing growth at the end of incubation.

The dynamic of $X(t)$ is governed by the Gompertz differential equation (Eq. (4)):

$$X'(t) = r(T) \ln\left(\frac{K}{X(t)}\right) X(t) \quad (4)$$

The exponential growth rate [$X'(t) = r(T)X(t)$] and linear growth rate [$X'(t) = r(T)$] were also tested.

$X(0)$ cannot be fitted from observation data. The early stages of development among turtles are similar, all following the same general pattern of preovipositional development. Development beyond the oviposition stage of middle gastrulation is arrested until the female locates a suitable place to nest (Miller, 1982).

The process of gastrulation has been described for a number of species of turtles, including *Caretta caretta* (Agassiz, 1857; Fujiwara, 1971; Kaska and Downie, 1999; Mitsukuri and Ishikawa, 1886; Nayar, 1958). However, most structures used as an embryo size or mass index do not exist in the gastrula stage. The gastrula is a disk measuring approximately 1.7 mm in diameter; this size is used as $X(0)$ (Kaska and Downie, 1999). This approximation will be discussed in greater detail below.

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