

ON THE TRANSIENT TEMPERATURES OF ECTOTHERMS

J. SCOTT TURNER*

Department of Biology, Franklin and Marshall College, Lancaster, PA 17604, U.S.A.

(Accepted 30 October 1986)

Abstract—Studies of the heating and cooling rates of ectotherms usually report only a time constant for temperature change. This implies that the transient temperatures of ectotherms behave like a first-order physical system. However, the transient temperatures of ectotherms may behave more like an overdamped second-order system. Reporting only a single time constant ignores half of the information in a temperature transient, and severely limits the predictive power of the results gathered to date.

Key Word Index—Ectotherms, heating and cooling rates, birds-eggs, alligators.

INTRODUCTION

Given the important role that rate of change of body temperature may play in the thermal ecology of reptiles (Cowles, 1940, 1941, 1945; Cowles and Bogert, 1944; Colbert *et al.*, 1946; Spotila *et al.*, 1972; Spotila, 1980; McNab and Auffenberg, 1976; Ellis and Ross, 1978; Smith, 1979; Bartholomew, 1982), it is not surprising that body size and how it might affect the rate of change of body temperature has received a lot of attention (see Bartholomew, 1982, for a recent summary).

The usual experimental protocol for this type of work exposes an animal to a sudden change of environmental temperature (a "step change"), and follows body temperature through its transient. From these data, it is then possible to calculate a metric which describes the transient. Data on rates of temperature change currently exist for reptiles of all extant orders, but mostly for lizards, crocodylians and turtles. The body sizes across which comparisons can be made range from 5 g or less to tens or hundreds of kilograms (Smith, 1976; Grigg *et al.*, 1979; Bell, 1980; Bartholomew, 1982; Smith *et al.*, 1984; Fraser and Grigg, 1984).

A reptile living in a complex thermal environment probably is more often than not in some kind of temperature transient. Is it possible, using this substantial data base, to begin to predict how reptiles' body temperatures might behave in such an environment? Unfortunately, there are two problems with the existing data that may subvert any such efforts.

Undoubtedly, there are circumstances where an ectotherm is subjected to something other than a step change in temperature. The first problem, then, is how to generalize from data on how body temperatures respond to a step change in temperature (the so-called forcing function) to predict how body temperatures respond to more complex forcing func-

tions. This normally would not be a problem if it were not for a second, and more serious problem.

A considerable body of theory exists that makes it possible to predict the response of any so-called physical system (which may include body temperature) to a variety of forcing functions, provided the system is adequately described mathematically (e.g. see Trimmer, 1950; Glantz, 1979). The metric that has been used to describe rate of change of body temperature is the so-called time constant (τ, s). Describing a transient temperature using the time constant alone implies that it is governed by a first-order linear differential equation of the form:

$$B_1 dT/dt + T = T_f \quad (1)$$

where T = temperature (K), T_f = forcing temperature (K), B_1 = a first order constant (τ) and t = time (s). However, it is readily seen (Fig. 1) that the transient temperature of reptiles can behave more like a second-order system, so-called because it is best described by a second-order linear differential equation:

$$B_2 d^2T/dt^2 + B_1 dT/dt + T = T_f \quad (2)$$

where B_2 = a second order constant (s^2), and B_1 = a first order constant (s). This, then, brings us to the second problem: the theory that enables us to predict first-order responses to complex forcing functions cannot be extended to second-order systems without knowing both parameters. Yet, all measurements of transient body temperatures to date have reported only a first-order parameter.

It is my purpose in this paper to explore, both theoretically and experimentally, what the second order parameters for an ectotherm's body temperature should be. I begin with a very brief discussion of second-order systems, and present a simple model for the second-order parameters for an "ectotherm". I then show how the second-order parameters should behave with respect to body size. I conclude with data showing the estimated second-order parameters for two sets of data: for cooling of birds' eggs, ranging in mass from about 1 g to about 1500 g, and for warming and cooling of alligators, ranging in mass from less than 1 kg to about 10 kg.

*Present address: Percy FitzPatrick Institute of African Ornithology, Department of Zoology, University of Cape Town, Rondebosch 7700, Republic of South Africa.

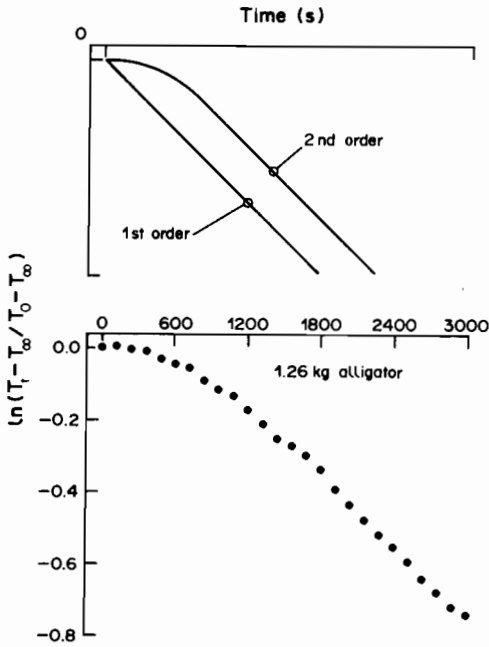


Fig. 1. First-order and second-order responses of body temperature to a step change of environmental temperature. Top panel: Expected first and second order responses compared. Bottom panel: Measured response to a step change of temperature of a 1.26 kg alligator.

SECOND-ORDER SYSTEMS AND THEIR PARAMETERS

The details of second-order systems and their analysis may be found in several places: the treatment by Trimmer (1950) is particularly lucid. The account that follows relies heavily on it and is presented as a convenient summary of the relevant aspects of the theory.

The usual parameters that describe a second-order system like equation (2) are (a) the damping ratio ζ (dimensionless) and (b) the natural frequency ω_n (rad s^{-1}). With reference to equation (2), these parameters are:

$$\zeta = B_1 / (2\sqrt{B_2}) \quad (3a)$$

$$\omega_n = 1/\sqrt{B_2} \quad (3b)$$

Equation (2) can thus be rewritten:

$$\ddot{T}/\omega_n^2 + 2\zeta\dot{T}/\omega_n + T = T_f \quad (4)$$

Equation (4) is in the so-called standard form of a second-order linear differential equation, and is solved using readily available methods (Trimmer, 1950; Glantz, 1979).

Of the two parameters, the damping ratio is the most important for the present. If $\zeta < 1$ the system is said to be underdamped—the response to a step change is a decaying oscillation. If $\zeta = 1$, the system is said to be critically damped—the response to a step change is not an oscillation, but a response with a strong second-order component. If $\zeta \cong 1$, the system is near-critically damped. If $\zeta > 1$, the system is said to be overdamped, and the behavior of the system approximates a first-order system. Larger values of ζ result in a closer approximation. For example, a

second-order system with $\zeta > 5$ may be approximated as a first-order system, with a resulting error of about 1% at most, and this only for a short time at the beginning of the transient (Trimmer, 1950).

SECOND ORDER PARAMETERS FOR AN "ECTOTHERM"

Derivation

A standard "core-shell" model is used to calculate the second-order parameters for a model ectotherm (Porter and Gates, 1969). The assumptions used in the model are outlined in the Appendix. The morphology is a sphere. The following equations are the results of a standard derivation, so many details have been omitted in the interests of brevity. Details of derivation may be found elsewhere (e.g. Glantz, 1979). Alternative treatments may be found in Porter and Gates (1969), Porter *et al.* (1973), and in Stevenson (1985).

Starting with an energy balance for the core and shell nodes of the model, it is readily shown that temperature of two nodes results in two first-order linear differential equations. For the core:

$$dT_c/dt = (T_s - T_c)/R_i C_c \quad (5)$$

and for the shell:

$$dT_s/dt = [(T_e - T_s)/R_e C_s] - [(T_s - T_c)/R_i C_s] \quad (6)$$

These equations are readily expressed in terms of core temperature alone as a single second-order linear differential equation:

$$(R_e R_i C_s C_c) \ddot{T}_c + (R_i C_c + R_e C_c + R_e C_s) \dot{T}_c + T_c = T_e \quad (7)$$

and so by equation (4):

$$\zeta = (R_i C_c + R_e C_c + R_e C_s) / (2\sqrt{R_e R_i C_s C_c}) \quad (8a)$$

$$\omega_n = 1/\sqrt{R_e R_i C_s C_c} \quad (8b)$$

Estimation

The internal resistance to heat transfer is comprised of the parallel resistances to heat transfer for conduction and blood flow (Turner, 1987a). For lizards, the core radius appears to be about 3/4 the outer radius over all body sizes (Tracy *et al.*, 1980), and for such a sphere, conduction resistance is:

$$R_k = 1/12\pi r_o k \quad (9)$$

and blood flow resistance is:

$$R_b = 1/\dot{m}_b V_s c_b = 48/37\dot{m}_b \pi r_o^3 c_b \quad (10)$$

The external resistance is considered to be comprised of the parallel resistances to heat transfer for convection and radiation. Convection resistance is estimated using the Nusselt-Reynolds correlation for spheres from Thomas (1980):

$$\text{Nu} = 2 + (0.4 \text{Re}^{0.5} + 0.06 \text{Re}^{0.67}) \text{Pr}^{0.4} \quad (11)$$

where $\text{Pr} \cong 0.71$. Convection resistance then is:

$$R_{cv} = 1/h_c A \quad (12)$$

Radiation resistance is simply:

$$R_r = 1/\epsilon\sigma A(T_s + T_e)(T_s^2 + T_e^2) \quad (13)$$

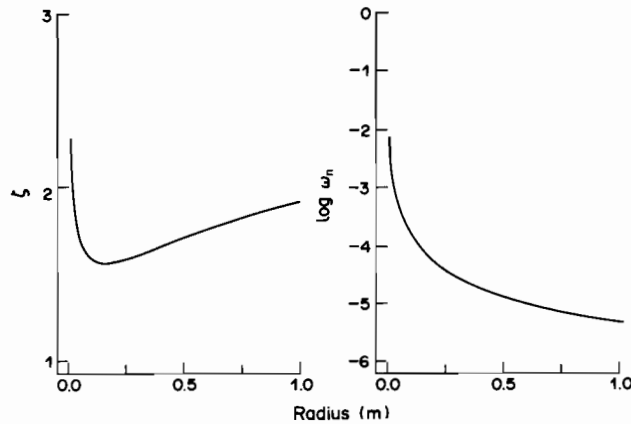


Fig. 2. Expected scaling of second-order parameters for a spherical "ectotherm" from 0.01 to 1 m radius. Left panel: damping ratio (ζ). Right panel: Natural frequency (ω_n).

Finally capacitances for the core and shell are estimated:

$$C_c = 9\pi r_0^3 \rho c p / 16 \quad (14a)$$

$$c_s = 37\pi r_0^3 \rho c p / 48 \quad (14b)$$

Simulations

The second order parameters obviously will vary with both internal resistance and external resistance [equations [8a] and (8b)]. Thus, there are no such things as "the" parameters for an organism of a certain size. Likewise, there is no single relationship describing how these parameters vary with body size.

I present a single simulation, using a wind speed of 1.5 m s^{-1} , an environment temperature of 50°C , an assumed surface temperature of 25°C , and "normal" blood flow in the shell, as determined by Smith *et al.* (1978). The results of the simulation are depicted in Fig. 2, to show in a general way how the parameters should vary with size.

In general, small organisms should be overdamped. As "body size" increases, the damping ratio goes down, reaching some minimum value. Further increases of "body size" result in a slow increase of ζ , but ζ does not appear to reach the large values found at the low end of the "body size" range.

I have done other simulations using different environmental conditions. I do not report their results graphically, for their conclusions are readily summarized in a few sentences. In general, any decline in total resistance will push ζ to higher values. As expected from the scaling relationships of convection and radiation heat transfer (Porter and Gates, 1969; Spotila *et al.*, 1973; Spotila, 1980; Turner, 1987a, b), changes in wind speed have their greatest effect on ζ at small sizes, while changes in the radiative environment have their greatest effect at larger sizes. Changes in blood flow also will affect ζ , but only if internal resistance is a significant component of the total resistance (Turner, 1987a, b). In general, this should not occur at either very small or very large body sizes (Turner, 1987a, b).

The natural frequency, ω_n , declines with increasing size, and increases with decreasing resistance to heat exchange (Fig. 2).

EMPIRICAL ESTIMATES OF SECOND-ORDER PARAMETERS

Second order parameters are readily estimated from empirical data, provided certain criteria are met. The most straightforward way is to estimate both parameters simultaneously by subjecting the system to a sinusoidal forcing function. The second order parameters are then readily estimated from the amplitude and phase delay of the forced response (Trimmer, 1950). Imposing a sinusoidal forcing is easy in some circumstances (such as for voltage), but it is technically difficult to sinusoidally force temperature. In any event, I know of no instance in which temperature transients have been measured in this way.

It is possible, however, to estimate the second order parameters from the body temperature response to a step function in environmental temperature. It is a "bootstrap" solution which requires solving for one term, and then using it in the solution for others (Trimmer, 1950). Two conditions must be met before such a method can be employed. First, the animal must be in thermal equilibrium at the start of the transient. Second, the transient response must be complete, that is one must have measurements from the moment environmental temperature is changed.

I have used this method to estimate the second order parameters for two of my own sets of data. One set of data are for cooling of birds' eggs of various sizes, originally reported in Turner (1985c). The other set of data are for both heating and cooling of alligators of various sizes, originally reported in Turner and Tracy (1985). Undoubtedly, the method could be employed for other data that currently exist in the literature. From their reports, it is not easy to be sure that the necessary conditions have been met, and so I have not attempted to analyze these. However, I am reasonably confident the necessary conditions have been met for my own data.

Estimating second order parameters

This method is outlined in Trimmer (1950). In my judgement, some important details were omitted from Trimmer's treatment, and so I present a brief summary of the treatment here.

The method centers around another way of writing the second order equation specifically for a step change:

$$(T_1 - T_\infty)/(T_0 - T_\infty) = [\tau_1/\tau_1 - \tau_2] \times e^{-t/\tau_1} + [\tau_2/\tau_1 - \tau_2] e^{-t/\tau_2} \quad (15a)$$

where:

$$\tau_1 = 1/[\zeta\omega_n - \omega_n\sqrt{\zeta^2 - 1}] \quad (15b)$$

and:

$$\tau_2 = 1/[\omega_n\sqrt{\zeta^2 - 1} - \zeta \cdot \omega_n] \quad (15c)$$

Equation (15a) is resolved into two first-order curves, which graphically appear on a semi-logarithmic plot as two lines, with one having a slope of $-1/\tau_1$, and the other having a slope of $-1/\tau_2$ (Fig. 3). Unlike true first-order curves, these lines do not intercept the y-axis at (0, 0), but at (0, $\ln\alpha$) and at (0, $\ln\beta$), respectively (Fig. 3). From equation (15a):

$$\alpha = \tau_1/(\tau_1 - \tau_2) \quad (16)$$

As the transient proceeds, it will approximate a first-order response, with $\tau_1 = \tau$. The value of τ_1 is readily estimated from empirical data by analyzing only that portion of the transient that mimics a first-order response. Once this is done, α is readily estimated, and τ_2 calculated:

$$\tau_2 = \tau_1(\alpha - 1)/\alpha \quad (17)$$

The damping ratio is then estimated by solving the equation:

$$\tau_1/\tau_2 = [\zeta + \sqrt{\zeta^2 - 1}]/[\zeta - \sqrt{\zeta^2 - 1}] \quad (18)$$

and the natural frequency is solved from ζ :

$$\omega_n = 1/[\tau_1 - \sqrt{\zeta^2 - 1}] \quad (19)$$

Second order parameters for birds' eggs

In this experiment, eggs were filled with scrambled, uncooked hen's egg, and cooled under conditions of free convection (see Turner, 1985 for details). The variation of both τ_1 and τ_2 with egg mass are shown on a double-log plot in Fig. 4. Regression analysis of

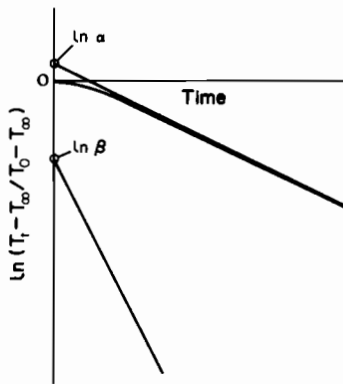


Fig. 3. The resolution of a second-order response to a step change in temperature (heavy line) into two first-order responses with time constants τ_1 (upper light line) and τ_2 (lower light line), and intercepts (0, $\ln\alpha$) and (0, $\ln\beta$), respectively.

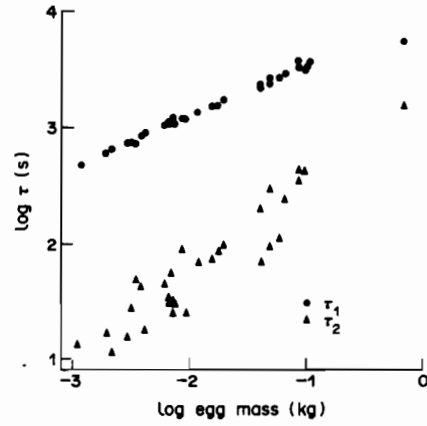


Fig. 4. Relationships of τ_1 (circles) and τ_2 (triangles) with egg mass for eggs cooling from 37 to 25°C.

the data yields the following equations:

$$\tau_1 = 7962 M^{0.397} \quad r^2 = 0.99 \quad (20a)$$

$$\tau_2 = 2443 M^{0.832} \quad r^2 = 0.93 \quad (20b)$$

where M = egg mass (kg). Clearly, τ_2 will become larger with respect to τ_1 as egg mass increases. Consequently, very small eggs will be overdamped and will approach critical damping as size increases. This is shown explicitly in Figs 5a and 5b. Damping ratio goes down with increasing mass: over the range of egg masses reported here:

$$\zeta = 1.15 M^{-0.176} \quad r^2 = 0.76 \quad (21a)$$

For the natural frequency:

$$\omega_n = 2.28 \cdot 10^{-4} M^{-0.614} \quad r^2 = 0.97 \quad (21b)$$

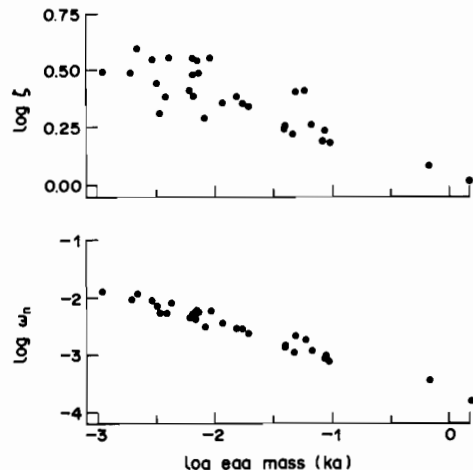


Fig. 5. Relationships of damping ratio (ζ ; top panel) and natural frequency ω_n ; bottom panel) with egg mass for eggs cooling from 37 to 25°C.

Second order parameters for alligators

In this experiment, alligators were warmed and cooled in a temperature-controlled wind tunnel, exposed to a head-on wind of 1.5 m s^{-1} . These data were originally reported in Turner and Tracy (1985).

For warming (Fig. 6), the time constants from equation (15a) are:

$$\begin{aligned} \tau_1 &= 3090 M^{0.360} \\ r^2 &= 0.88 \end{aligned} \tag{22a}$$

and:

$$\begin{aligned} \tau_2 &= 501 M^{0.572} \\ r^2 &= 0.66 \end{aligned} \tag{22b}$$

As with the eggs (Fig. 4), τ_2 becomes larger with respect to τ_1 as body size increases, with similar consequences for the second-order parameters. However, theory also predicts (see above) that as body size increases, ζ should decline, reach a minimum at some body size, and then increase again. This may be the case for alligators warming (Fig. 7). Consequently, I have fitted a second-order polynomial to the data in this case and:

$$\begin{aligned} \log \zeta &= 0.190 - 0.446 \log M + 0.398 (\log M)^2 \\ r^2 &= 0.45 \end{aligned} \tag{23a}$$

and for the natural frequency:

$$\begin{aligned} \omega_n &= 8.07 \cdot 10^{-4} M^{0.466} \\ r^2 &= 0.84 \end{aligned} \tag{23b}$$

For alligators cooling, the time constants (Fig. 8) are:

$$\begin{aligned} \tau_1 &= 3715 M^{0.278} \\ r^2 &= 0.54 \end{aligned} \tag{24a}$$

and:

$$\begin{aligned} \tau_2 &= 631 M^{0.506} \\ r^2 &= 0.84 \end{aligned} \tag{24b}$$

The second-order parameters (Fig. 9) therefore are:

$$\begin{aligned} \zeta &= 1.422 M^{0.075} \\ r^2 &= 0.34 \end{aligned} \tag{25a}$$

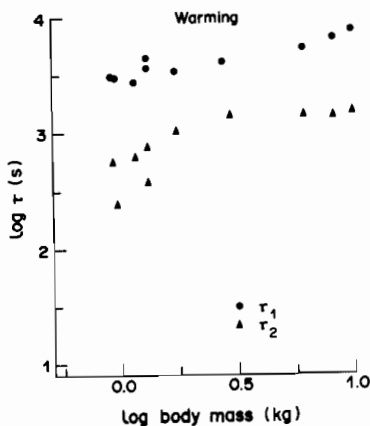


Fig. 6. Relationships of τ_1 (circles) and τ_2 (triangles) with body mass for alligators warming from 20 to 35°C.

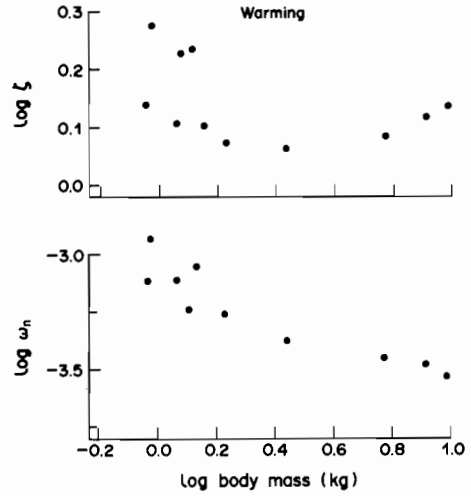


Fig. 7. Relationships of damping ratio (ζ ; top panel) and natural frequency ω_n ; bottom panel) with body mass for alligators warming from 20 to 35°C.

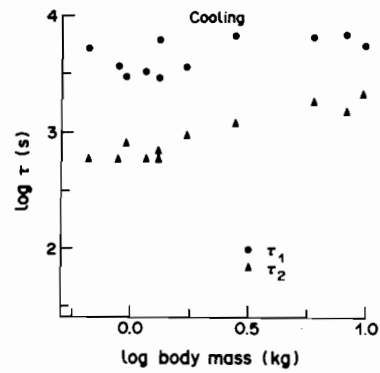


Fig. 8. Relationships of τ_1 (circles) and τ_2 (triangles) with body mass for alligators cooling from 35 to 20°C.

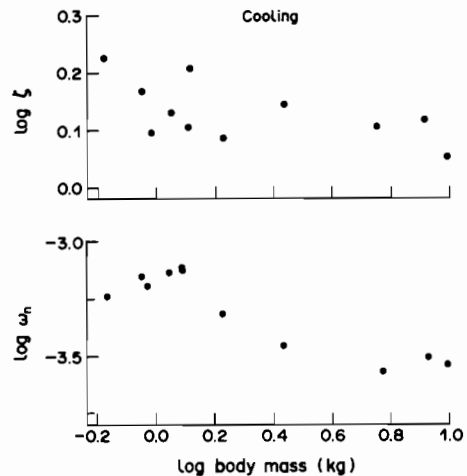


Fig. 9. Relationships of damping ratio (ζ ; top panel) and natural frequency ω_n ; bottom panel) with body mass for alligators cooling from 35 to 20°C.

and:

$$\begin{aligned}\omega_n &= 6.53 \cdot 10^{-4} M^{0.392} \\ r^2 &= 0.82\end{aligned}\quad (25b)$$

DISCUSSION

The data for cooling of bird's eggs and for warming and cooling of alligators broadly support the predictions for how the second-order parameters for body temperature should behave with respect to body size. That is, small ectotherms should be over-damped, and their body temperatures should behave very much like first-order systems (see below). As body size increases, body temperatures approach critical damping. There is no reason to suggest that ectotherms ever are under-damped.

There are considerable data on the temperature transients of animals, and invariably, these have reported time constants only (Smith, 1976; Smith and Adams, 1979; Smith, 1979; Grigg *et al.*, 1979; Bell, 1980; Turner and Tracy, 1985; Turner, 1987a, b.). I would suggest that future studies of transient temperatures of ectotherms use the parameters appropriate to a second-order or higher-order system. This suggestion goes against current practice, and so requires some justification.

The fact that organisms appear to behave more like second-order systems does not mean that time constants are without value. A second-order system will approximate a first-order system if the transient continues for a long enough time (Fig. 3). If the time constant is measured late enough in the transient, as usually is done, then it is a valuable description of the transient thermal properties of the animal. There also may be circumstances in which a first-order approximation is quite good. Nevertheless, relying solely on the time constant essentially discards half the information available in the transient. Moreover, the predictive power that can be gained from the data may be severely compromised.

As an example, consider the problem of predicting the body temperature of an ectotherm in response to a complicated variation of environmental temperature. It is possible to resolve any complex forcing temperature into a series of simpler forcing temperatures, such as a Taylor series, or a Fourier series. If the body temperature response to each term of the forcing series can be calculated, then the body temperature will be simply the sum of the responses to each term (Trimmer, 1950). Theoretically then, it should be possible to predict the complete transient response of an animal to any forcing temperature. If we assume that the animal's transient temperature is governed by a second-order equation, but is described by time constant only, what will the likely errors be? Let us focus on Fourier series, although the point I will make applies to any way of resolving the resulting variation of body temperature.

Fourier series are useful for estimating any periodic function, and it is possible to extend the method to non-periodic functions as well. A Fourier series for any periodic variation in environmental temperature is:

$$T_c = T_0 + \sum_{n=1}^{\infty} A_n \cos(n\omega_1 t + \theta_n) \quad (25)$$

where T_0 = the average temperature, A_n = the amplitude of the sinusoid for harmonic n , ω_1 = the angular frequency of the first harmonic, and θ_n = the phase delay for harmonic n . For the moment, we consider the simplest case: what will the variation of body temperature be in response to a sinusoidal environmental temperature that completes one cycle in 24 h ($\omega_1 = 2\pi/24h \cong 72.7 \mu\text{rad s}^{-1}$)?

The body of an animal subjected to a sinusoidal forcing temperature will behave like a low-pass filter, that is, body temperature also will be a sinusoid that will differ in amplitude and in phase from the forcing temperature. Given the forcing temperature, it is possible to estimate the body temperature at any time in the cycle by using two numbers; the gain ratio, G , which is the ratio of the amplitudes of the body temperature and environmental temperature oscillations, and a phase delay, ϕ , which is the phase angle between the body temperature oscillation and the environmental temperature.

It is possible to estimate both these numbers for a first-order system and a second-order system (see Trimmer, 1950; Glantz, 1979), and from these, estimate the likely deviation that would result from using a first-order approximation. For a first-order system:

$$G_1 = 1/\sqrt{1 + \omega_1^2 \tau^2} \quad (26a)$$

$$\phi_1 = -\tan^{-1}(\omega_1 \tau) \quad (26b)$$

and for a second-order system:

$$G^2 = 1/\sqrt{(1 - \beta^2)^2 + (2\zeta\beta)^2} \quad (27a)$$

$$\phi_2 = -\tan^{-1}(2\zeta\beta/1 - \beta^2) \quad (27b)$$

where:

$$\beta = \omega_1/\omega_n \quad (27c)$$

The proportional deviation, D , for each parameter is calculated:

$$D_G = (G_1 - G_2)/G_2 \quad (28a)$$

$$D\phi = (\phi_1 - \phi_2)/\phi_2 \quad (28b)$$

The expected deviations with respect to "body size" are plotted in Fig. 10.

We see (Fig. 10) that a first-order approximation sometimes will be quite good. For small animals, the expected deviations are small, and for the most part, negligible. However, the expected deviations increase with respect to body size. For a 24 h cycle, the gain ratios, and hence amplitudes of body temperature, predicted by a first-order approximation may be many times that for the second-order prediction. The deviations for the phase-delay are similarly great at larger body sizes.

It is likely that animals will be subjected to sinusoidal variations of shorter period than 24 h. A small lizard shuttling in and out of sunlight may experience very rapid fluctuations of environmental temperature. Also, using a Fourier series to predict body temperature requires predicting the response to sinusoids with periods much shorter than 24 h. If the forcing temperature has abrupt changes (such as a series of step alterations), these high-frequency oscillations become extremely important. How large will

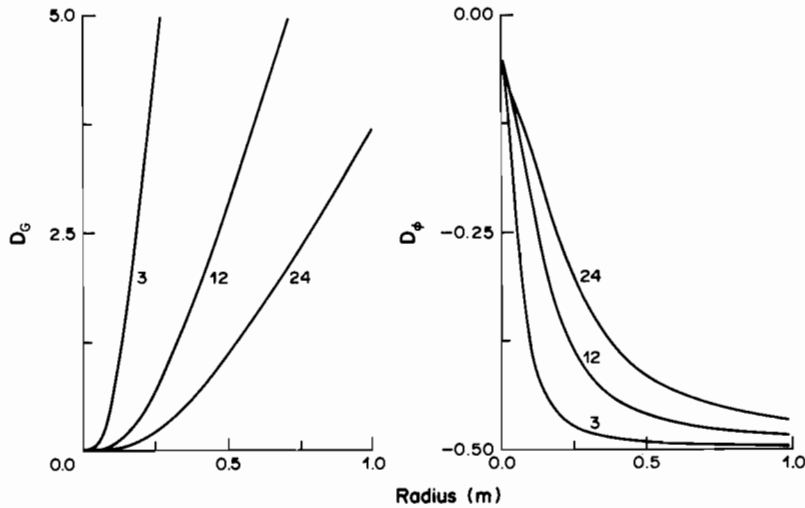


Fig. 10. Estimated deviations [see equations (28a) and (28b)] in gain ratio (D_G ; left panel) and phase delay (D_ϕ ; right panel) for a spherical "ectotherm", subjected to sinusoidally-fluctuating environmental temperatures with periods of 24, 12 and 3 h.

the deviations be when a first-order approximation is used at these higher frequencies?

In Fig. 10, I also have plotted the expected deviations for cycles with periods of 12 and 3 h. Clearly, the deviations become more severe over all body sizes as the frequency of oscillation increases. Another consequence of this is that the maximum body size for which a first-order approximation might be adequate is forced to smaller and smaller size as frequency increases.

The usefulness of this approach in predicting transient temperatures of ectotherms awaits empirical test, of course. However, there are good reasons to suggest it would be useful. It is now possible to predict body temperature of ectotherms fairly reliably, using physical and mathematical models of heat exchange. However, these methods, while quite powerful, have their own potentially serious sources of error (e.g. see Tracy *et al.*, 1984). Also, applying them to field situations can be cumbersome, requiring extensive quantitative description of microclimate, and of various properties of the animals, such as surface area, reflectivity, absorptivity, all of which are subject to their own errors. In addition, because many of the most accurate models are solved numerically rather than analytically, their use often requires having computing power at hand.

Unfortunately, these very sophisticated methods have developed more or less in isolation from the wealth of experimental data on heating and cooling rates. There are many reasons for this, but at least one is that time constants alone are not very useful as predictive tools when the organism clearly behaves like a second-order system.

Direct measurements of second-order parameters for ectotherm's body temperatures, rather than the time constants that currently are standard practice, may unify these two currently disparate lines of inquiry. It also may enable biologists to make robust predictions of field body temperatures, while circumventing some of the currently intimidating complexity of the "biophysical" approach to thermal ecology.

REFERENCES

- Bartholomew G. A. (1982) Physiological control of body temperature. In *Biology of the Reptilia* (Edited by F. H. Pough and C. Gans), Vol. 12, pp. 167–211. Academic Press, London.
- Bell C. J. (1980) The scaling of the thermal inertia in lizards. *J. exp. Biol.* **86**, 79–86.
- Colbert E. H., Cowles R. B. and Bogert C. M. (1946) Temperature tolerances of the American alligator, and their bearing on the habits, evolution and extinction of the dinosaurs. *Bull. Am. Mus. Nat. Hist.* **86**, 333–373.
- Cowles R. B. (1940) Additional implications of reptilian thermal tolerance. *Am. Nat.* **74**, 542–561.
- Cowles R. B. (1941) Winter activities of desert reptiles. *Ecology* **22**, 125–140.
- Cowles R. B. (1945) Surface-mass ratio, paleoclimate and heat sterility. *Am. Nat.* **79**, 561–567.
- Cowles R. B. and Bogert C. M. (1944) A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* **83**, Article 5.
- Ellis H. I. and Ross J. P. (1978) Field observations of cooling rates of Galapagos land iguanas (*Conolophus subcristatus*). *Comp. Biochem. Physiol.* **59A**, 205–209.
- Fraser S. and Grigg G. C. (1984) Control of thermal conductance is insignificant to thermoregulation in small reptiles. *Physiol. Zool.* **57**, 392–400.
- Glantz S. A. (1979) *Mathematics for Biomedical Applications*, 423 pp. University of California Press, Berkeley.
- Grigg G. C., Drane C. R. and Courtice G. P. (1979) Time constants of heating and cooling in the eastern water dragon, *Physignathus lesueurii*, and some generalizations about heating and cooling in reptiles. *J. therm. Biol.* **4**, 354–360.
- McNab B. K. and Auffenberg W. (1976) The effects of large body size on the temperature regulation of the Komodo dragon, *Varanus komodoensis*. *Comp. Biochem. Physiol.* **55A**, 345–350.
- Porter W. P. and Gates D. M. (1969) Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* **39**, 227–244.
- Porter W. P., Mitchell J. W., Beckman W. A. and DeWitt C. B. (1973) Behavioral implications of mechanistic ecology. Thermal and behavioral modelling of desert ectotherms and their microenvironment. *Oecologia* **13**, 1–54.

- Smith E. N. (1976) Heating and cooling rates of the American alligator, *Alligator mississippiensis*. *Physiol. Zool.* **49**, 37–48.
- Smith E. N. (1979) Behavioral and physiological thermoregulation of crocodylians. *Am. Zool.* **19**, 239–247.
- Smith E. N. and Adams S. R. (1978) Thermoregulation of small American alligators. *Herpetologica* **34**, 406–408.
- Smith E. N., Robertson S. and Davies D. G. (1978) Cutaneous blood flow during heating and cooling in the American alligator. *Am. J. Physiol.* **235**, R160–R167.
- Smith E. N., Standora E. A. and Robertson S. L. (1984) Physiological thermoregulation of mature alligators. *Comp. Biochem. Physiol.* **77A**, 189–193.
- Spotila J. R., Soule O. H. and Gates D. M. (1972) Biophysical ecology of the alligator. Heat energy budgets and climate spaces. *Ecology* **53**, 1094–1102.
- Spotila J. R., Lommen P. W., Bakken G. S. and Gates D. M. (1973) A mathematical model for body temperatures of large reptiles. Implications for dinosaurian ecology. *Am. Nat.* **107**, 391–404.
- Spotila J. R. (1980) Constraints of body size and environment on the temperature regulation of dinosaurs. *A Cold Look at the Warm-Blooded Dinosaurs* (Edited by Thomas R. D. K. and Olson E. C.), pp. 233–252. Westview Press, Boulder, CO.
- Stevenson R. D. (1985) Body size and limits to the daily range of body temperature in terrestrial ectotherms. *Am. Nat.* **125**, 102–117.
- Thomas L. C. (1980) *Fundamentals of Heat Transfer*, 702 pp. Prentice-Hall, Englewood Cliffs, NJ.
- Tracy C. R., Christian K. A., Turner J. S. and Porter W. P. (1980) A new transient state energy budget of a reptile (*Conolophus pallidus*) which employs physiological control of energy exchange. *Bull. Ecol. Soc. Am.* **61**, 93.
- Tracy C. R., van Berkum F. H., Tsuji J. S., Stevenson R. D., Nielson J. A., Barnes B. M. and Huey R. B. (1984) Errors resulting from linear approximations in energy balance equations. *J. therm. Biol.* **9**, 261–264.
- Trimmer J. D. (1950) *Response of Physical Systems*, 268 pp. Wiley, New York.
- Turner J. S. (1987a) The cardiovascular control of heat exchange. Consequences of body size. *Am. Zool.* **27**, 69–79.
- Turner J. S. (1987b) *Embryonic Blood Flow and the Heat Exchange of Avian Eggs*. Privately published, 9 pp.
- Turner J. S. (1985c) Size and cooling rate of birds' eggs—a natural isomorphic body. *J. therm. Biol.* **10**, 101–104.
- Turner J. S. and Tracy C. R. (1985) Body size and the control of heat exchange in alligators. *J. therm. Biol.* **10**, 9–11.

APPENDIX

Symbols and Constants

A	Surface area of sphere (m^2)
B_1	First order parameter (s)
B_2	Second order parameter (s^2)
C_c	Capacitance of core (JK^{-1})
C_s	Capacitance of shell (JK^{-1})
c_b	Specific heat of blood ($4187 JK^{-1} kg^{-1}$)
cp	Specific heat of tissue ($4187 JK^{-1} kg^{-1}$)
D_G	Deviation in gain ratio
$D\phi$	Deviation in phase angle
G_1	First-order gain ratio
G_2	Second-order gain ratio
h_c	Convection coefficient ($WK^{-1} m^{-2}$)
k	Thermal conductivity ($0.5 W m^{-1} K^{-1}$)
\dot{m}_b	Blood mass flow rate ($1.15 kg s^{-1} m^{-3}$)
n	Harmonic in Fourier series
R_b	Blood flow heat transfer resistance (KW^{-1})
R_{cv}	Convection heat transfer resistance (KW^{-1})
R_c	External heat transfer resistance (KW^{-1})
R_i	Internal heat transfer resistance (KW^{-1})
R_k	Conduction heat transfer resistance (KW^{-1})
R_r	Radiation heat transfer resistance (KW^{-1})
r_0	External radius (m)
T	Temperature (K)
T_c	Temperature of core (K)
T_e	Environmental temperature (K)
T_f	Forcing temperature (K)
T_s	Temperature of shell (K)
T_∞	Equilibrium temperature (K)
T_0	Temperature at start of transient (K), average temperature in Fourier series
t	Time (s)
V_s	Shell volume (m^3)
Nu	Nusselt number
Pr	Prandtl number
Re	Reynolds number
α	Intercept of first-order component (Fig. 3)
β	Intercept of second-order component (Fig. 3), ratio of natural and forcing frequencies
ϵ	Emissivity
θ_n	Phase delay of n th harmonic in Fourier series (rad)
ω_f	Angular velocity of forcing function ($rad s^{-1}$)
ω_n	Natural frequency ($rad s^{-1}$)
ϕ_1	First-order phase angle (rad)
ϕ_2	Second-order phase angle (rad)
ρ	Density ($1000 kg m^{-3}$)
σ	Stefan-Boltzmann constant ($5.67 \cdot 10^{-8} W m^{-2} K^{-4}$)
τ	Time constant (s)
ζ	Damping ratio