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# Predicting body temperature of endotherms during shuttling

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## Abstract

This paper presents two models that can be used to predict the temporal dynamics of body temperature in endotherms. A first-order model is based on the assumption that body temperature is uniform at all times, while a second-order model is based on the assumption that animals can be divided in a core and a shell, the temperature being uniform within each compartment. According to the second-order model, animals may be able to maintain their internal organs at almost constant temperature during shuttling despite large variations in the temperature of peripheral tissues. © 2002 Elsevier Science Ltd. All rights reserved.

*Keywords:* Core-shell models; Second-order models; *Octodon degus*; Patch use

## 1. Introduction

The body temperature of animals may be subject to long- and short-term fluctuations. Some of this variability is unrelated to environmental conditions: birds and mammals kept under constant conditions of light and temperature retain a number of endogenous circadian rhythms. Activity and body temperature, among other parameters, follow regular oscillations with a periodicity close to 24 h (Aschoff, 1982). Furthermore, the periodicity of body temperature is not induced by the activity pattern itself (Hiddinga et al., 1997; Strijkstra et al., 1999). Nevertheless, body temperature is affected by environmental factors. The relationship between body temperature and environment is well known in ectotherms, many of which have little thermoregulatory abilities beyond the behavioural choice of favourable microclimates. In many cases, body temperature has a large impact on the locomotor abilities of ectotherms: they are unable to forage efficiently and/or avoid predators unless their body temperature is sufficiently high. Because of the clear ecological implications of body temperature for

ectotherms, the effects of ambient temperature on their body temperature has been carefully studied at the empirical (reviews in Avery, 1982; Huey et al., 1989) and theoretical levels (Turner, 1987; O'Connor, 1999).

Ambient temperature can affect body temperature of endotherms in at least two ways. Endotherms exposed to low temperatures may go into hibernation, torpor or hypothermia, reducing their body temperature to save energy consumption. Diurnal animals (both ecto- and endotherms) living in arid environments face the risk of death by hyperthermia if they are exposed to the sun and high temperatures during long periods. In principle, evaporative cooling can be used to maintain body temperature below ambient temperature. In practice, water is so scarce in arid environments that individuals can make little use of it for thermoregulation. An alternative strategy is to allow body temperature to increase during periods of exposure to the sun, and to cool down by passive heat transfer when ambient temperature decreases. Large animals, such as camels, can allow their body temperature to fluctuate following the day–night cycle of ambient temperature. Because of their big thermal inertia and good insulation, large animals can spend a full day in the sun making moderate use of evaporative water-cooling. Body temperature decreases again during the cooler night (Schmidt-Nielsen, 1997).

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Unlike their larger neighbours, desert rodents cannot stand long periods of exposure to the sun and heat. Their thermal inertia and insulation are so small, that in order to keep their body temperature within physiological limits they would need to evaporate each day an amount of water several times their body weight (Schmidt-Nielsen, 1997). Small diurnal animals, therefore, cannot accumulate heat throughout the day and release it to the environment at night. But they can use a similar principle, in a shorter time scale. Small animals can remain in the sun for a few minutes. They accumulate heat and their body temperature increases sharply. When body temperature approaches the lethal threshold, small animals must search a thermal refuge (normally a shade or burrow) where ambient temperature is lower than body temperature and heat can be dissipated with little or no use of precious water. The resulting continuous movement between a hot foraging patch and a cool thermal refuge (or, in species such as sea-feeding iguanas, between a cold foraging patch and a warm thermal refuge; Bartholomew and Lasiewski, 1965) is referred to as “shuttling” (Chappell and Bartholomew, 1981; Bennett et al., 1984; Byman, 1985; Vispo and Bakken, 1993; Hainsworth, 1995).

In order to study the ecology of desert animals, we need a reasonable understanding of how ambient temperature affects body temperature. The models developed for reptiles (Turner, 1987; O'Connor, 1999) are insufficient because they ignore the effect of metabolic heat production (but see Spotila et al., 1973). Specific models developed for humans (Werner and Webb, 1993) are of little practical use because they require the input of a large number of parameters to make predictions. Hainsworth (1995) has developed a simple model that incorporates metabolic heat production. Hainsworth's model was originally applied to antelope ground squirrels, *Ammospermophilus leucurus*, and later extended to other small desert mammals (Degen, 1997; Bozinovic et al., 2000).

If the distinction between ecto- and endotherms is somewhat artificial, it becomes painfully blurred when we consider the problem of shuttling. In effect, a shuttling antelope ground squirrel has given up any hope to thermoregulate in the usual sense. Most mammals, disregarding the daily pattern of temperature variation, keep their body temperature within very narrow ranges through changes in their metabolic rates and evaporative water-cooling. Shuttling mammals do not use these mechanisms to keep their body temperature fixed. Indeed, a shuttling antelope ground squirrel is (from this point of view) like a lizard with high metabolic rate. The models developed here can thus be applied to ectotherms by using the appropriate parameter values.

In a laboratory study of shuttling between heated food patches and cooler habitat, Bozinovic et al. (2000) conclude that degus, *Octodon degus*, “used food patches

during shorter bouts of time than predicted” by their simulations. As ever so often, this deviation from expectations can be explained in a number of ways. Among others: (a) as a safety measure. Degus need not stay in the food patch so long as their body temperature is below the lethal threshold (about 42°C; Bozinovic et al., 2000). It may be safer to leave when temperature is 1° or even 2° below the threshold. (As there is bound to be some stochasticity: the lethal threshold is more a heuristic concept than a physiological entity. It would be more realistic to assume that the probability of entering hyperthermia increases as body temperature increases. With this assumption, models of optimal patch use would have to be cast within a framework that would be mathematically equivalent to signal detection theory.) (b) Physiological costs. A high body temperature, even well below the lethal “threshold” may be physiologically costly. For instance, a high body temperature might be energetically costly if it is associated with a higher turnover of cell machinery.

There is, however, another reason why degus might stay in the patches shorter than expected: body temperature in a heated patch might increase faster than predicted. Bozinovic et al. (2000) use an equation derived by Hainsworth (1995) to predict the temporal course of body temperature in a heated patch. A more rigorous treatment of Hainsworth's model produces somewhat different results. In this paper, I first reanalyse Hainsworth's (1995) model (the “first-order” model). Later, I consider the implications of using a core-shell model (“second-order” model) with metabolic heat production. The second-order model is an extension of Turner's (1987) core-shell model.

## 2. First-order models

The model presented in this section was already developed by Bakken and Gates (1975). The formalism they use is rather daunting and it appears that their work has escaped the attention of field biologists. Eppley (1994) uses a special case of this model to study cooling rates in developing endotherms. The purpose of this section is to present the model in a way that can be easily understood by researchers lacking a thorough biophysical training and to explain why Hainsworth's (1995) model is inappropriate.

First, we consider an inert body in thermal disequilibrium with its environment. Assuming that the temperature of the body,  $T_b$  (°C), is homogeneous and that the operative temperature is  $T_e$  (°C), we have that the derivative of the body temperature with respect to time,  $t$ (s), is given by

$$\frac{dT_b}{dt} = \frac{T_e - T_b}{RC} \quad (1)$$

where  $C$  is the thermal capacitance of the body ( $J^{\circ}C^{-1}$ ) and  $R$  is the heat-transfer resistance between the body and its environment ( $^{\circ}C W^{-1}$ ). (For a discussion of operative temperature, see Bakken, 1992.) The physical interpretation of Eq. (1) is as follows: the rate of increase of body temperature is equal to the rate of heat influx divided by the thermal capacitance of the body (the amount of heat required to increase body temperature by  $1^{\circ}C$ ). Heat influx is itself equal to the difference between ambient and body temperature divided by the heat-transfer resistance (a measure of how difficult it is for heat to enter the body).

Eq. (1) can be integrated to obtain the temporal dynamics of temperature in an inert body. Live animals, however, differ from inert bodies in two important respects: (1) they produce heat internally as the result of activity and metabolic processes and (2) they can induce water evaporation for cooling. These processes have important effects on body temperature and must be incorporated to Eq. (1).

Let  $M(W)$  be the total rate of metabolic heat production and  $E(W)$  the rate at which metabolic heat is dissipated through evaporative cooling. The rate of increase of body temperature due to metabolic heat production (corrected for evaporative cooling) is then the net heat production in the body divided by its heat capacitance

$$\frac{M - E}{C} \tag{2}$$

and therefore the rate of change of body temperature is given by the sum of two terms; one representing heat influx (as in Eq. (1)) and another representing internally produced heat

$$\frac{dT_b}{dt} = \frac{T_e - T_b}{RC} + \frac{M - E}{C} \tag{3}$$

(The precise form of this equation will depend on the site where evaporative cooling takes place; see Bakken and Gates, 1975. A detailed discussion of the effects of evaporative cooling for second-order models is given in Appendix A.)

After rearrangement, we can express Eq. (3) as

$$\frac{dT_b}{dt} = \frac{T_{\infty} - T_b}{RC} \tag{4}$$

where the asymptotic body temperature,  $T_{\infty}$ , is

$$T_{\infty} = T_e + (M - E)R. \tag{5}$$

Assuming that all parameters in (4) are independent of body temperature, integration of Eq. (4) is straight forwards and leads to

$$T_b = T_{\infty} + (T_0 - T_{\infty})e^{-t/(RC)}, \tag{6}$$

where  $T_0$  is body temperature ( $^{\circ}C$ ) at time  $t = 0$ . Comparison of Eqs. (1) and (4) shows that the metabolic heat production changes the asymptotic body

temperature, but not the exponential time constant. The thermal capacitance and heat-transfer resistance of the body determine the time constant independently of metabolic heat production.

Eq. (6) is formally different from the expressions developed by Hainsworth (1995), who integrated Eq. (1) first and then added as a correction the metabolic heat production. The most relevant question, however, is whether the actual time courses of heating and cooling predicted by Eq. (6) and by Hainsworth's model are sufficiently different to be biologically meaningful. To explore this possibility, we can compare the predictions of both models for degus (Fig. 1) in the experimental conditions used by Bozinovic et al. (2000). According to the data provided by Bozinovic et al. (2000), the time required for *O. degus* to reach a body temperature of  $42^{\circ}C$  starting from  $37^{\circ}C$  with  $T_e = 50^{\circ}C$  would be 4.98 min according to Eq. (6) and 7.89 min according to Hainsworth's model. For  $T_e = 60^{\circ}C$ , this times become 2.82 and 3.63 min, respectively. Hence, for *O. degus*, Hainsworth's model overestimates maximum patch residence time by 58% and 29% at  $50^{\circ}C$  and  $60^{\circ}C$ , respectively. It is not surprising, then, that degus

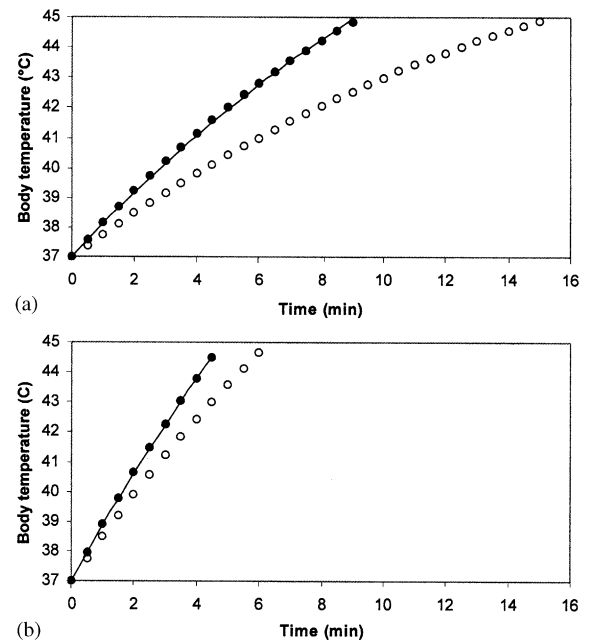


Fig. 1. Heating curves showing the increase in body temperature of degus foraging at different ambient temperatures: (a)  $T_e = 50^{\circ}C$ , (b)  $T_e = 60^{\circ}C$ . Black circles represent the predictions according to Eq. (6), empty circles according to Hainsworth's (1995) model.  $C = 686.2 J^{\circ}C^{-1}$ ,  $R = 1.14^{\circ}C W^{-1}$  and  $M = 2.434 W$  (Bozinovic et al., 2000). The line represents body temperature when metabolic rate depends on body temperature ( $Q_{10} = 2$ ). The section "body temperature effects on metabolic rate" explains how this line is calculated.

remain in the foraging patch shorter than predicted by Bozinovic et al. (2000).

The accuracy of Hainsworth’s approximation, however, depends on the parameter values. For the antelope ground squirrel, the approximation is excellent for practical purposes. Using the parameter values measured by Chappell and Bartholomew (1981) we can compare the predictions of Eq. (6) and Hainsworth’s model (Fig. 2). Although Hainsworth’s model

underestimates asymptotic body temperatures of ground squirrels exploiting patches by 11°C (not shown in the figure), body temperatures predicted by both models are almost indistinguishable in the physiological range. In general, when the operative temperature is much higher than the maximum body temperature, Hainsworth’s model will provide a good approximation unless metabolic heat production is very large. On the other hand, if operative temperature is similar to the maximum body temperature (as was the case with degus at 50°C), the approximation will be poor. Since Hainsworth’s model is not mathematically simpler than Eq. (6), there seems to be no reason to use his approximation.

2.1. Body temperature effects on metabolic rate

In deriving Eq. (6), we have assumed that the different parameters (thermal capacitance and heat-transfer resistance, metabolic rate and evaporative cooling) are independent of body temperature. The assumption is justified for the thermal capacitance, which is a physical property of the organism, not under its direct control, and relatively constant unless body temperature approaches the freezing or boiling points of water. Evaporative cooling and heat-transfer resistance are, to a large extent, under the control of the organism. They are not temperature independent, but it will often be the case that they are adjusted to meet environmental conditions and that they remain somewhat independent of body temperature. The assumption that is less likely to be justified, however, is that metabolic rate is independent of body temperature (Bakken and Gates, 1975; Eppley, 1994). The rate of physiological processes increases with temperature in a roughly exponential way, rates increasing two- to three-fold when temperature increases by 10°C. If metabolic rate increases with body temperature exponentially, how will the predictions of Eq. (3) be affected? Let us start by rewriting (3) as

$$\frac{dT_b}{dt} = \frac{T_e - T_b}{RC} + \frac{M_0 e^{qT_b} - E}{C}, \tag{7}$$

where  $q$  ( $^{\circ}\text{C}^{-1}$ ) is the exponential rate of increase in metabolic rate (with  $Q_{10} = e^{10q}$ ) and  $M_0$  is metabolic rate at 0°C. We can now study the steady states of this differential equation. Let

$$M^* = \frac{e^{qRE - qT_c - 1}}{Rq}. \tag{8}$$

A bit of algebra shows that if  $M_0 > M^*$  there is no steady state for (7) and body temperature increases to infinity. If  $M_0 = M^*$  there is an unstable steady state, and if  $M_0 < M^*$  there are two steady states, at  $T_1$  and  $T_2$  ( $T_1 < T_2$ ). The steady state at  $T_1$  is stable, but the steady state at  $T_2$  is unstable: if the initial temperature is

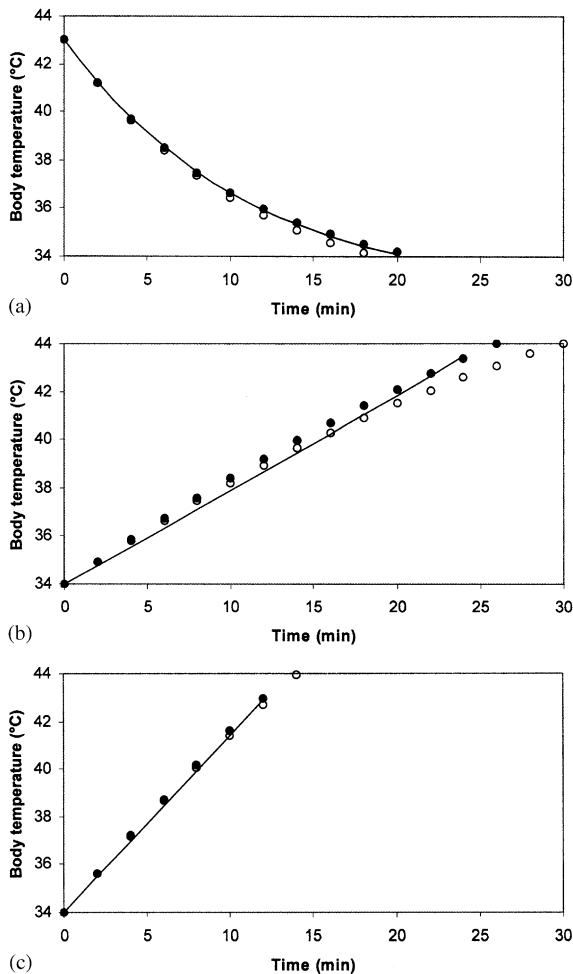


Fig. 2. Cooling (a) and heating (b, c) curves showing the time course of body temperature of antelope ground squirrels foraging at different ambient temperatures: (a)  $T_e = 32^{\circ}\text{C}$ , (b)  $T_e = 50^{\circ}\text{C}$ , (c)  $T_e = 70^{\circ}\text{C}$ . Black circles represent the predictions according to Eq. (6), empty circles according to Hainsworth’s (1995) model. During cooling,  $C = 343.1 \text{ J } ^{\circ}\text{C}^{-1}$ ,  $R = 1.82^{\circ}\text{C W}^{-1}$ ,  $M = 0.55 \text{ W}$  and  $E = 0.165 \text{ W}$ ; during heating,  $C = 343.1 \text{ J } ^{\circ}\text{C}^{-1}$ ,  $R = 10.0^{\circ}\text{C W}^{-1}$ ,  $M = 1.7 \text{ W}$  and  $E = 0.561 \text{ W}$  (Hainsworth, 1995). The line represents body temperature when metabolic rate depends on body temperature ( $Q_{10} = 2$ ). The section “body temperature effects on metabolic rate” explains how this line is calculated.

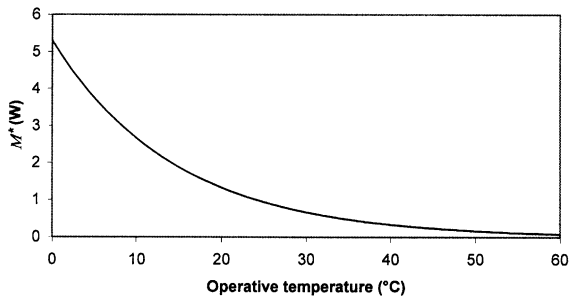


Fig. 3. Relationship between  $M^*$  and  $T_c$  assuming that  $R=1^\circ\text{C W}^{-1}$  and  $Q_{10}=2$ . Eq. (7) has a stable steady state in the region below the curve.

$T_0 < T_2$ , temperature tends to  $T_1$ . But if  $T_0 > T_2$  body temperature increases to infinity. Fig. 3 shows the relationship between  $M^*$  and  $T_c$  assuming that  $R=1^\circ\text{C W}^{-1}$  and  $Q_{10}=2$ . (Notice that  $M^*=1$  implies a metabolic rate of 13 W at  $37^\circ\text{C}$ .)

To study the quantitative effect of (7), I have integrated this equation with the parameters corresponding to degus and antelope ground squirrels. I have chosen the values of  $M_0$  so that metabolic rate is equal for (3) and (7) at the midpoint of the temperature range considered. (The integration can be done numerically using Runge-Kutta's method, Press et al., 1992.) The predictions of (7) appear as a solid line in Figs. 1 and 2: clearly, there is little difference between the predictions of (3) and (7). For these particular cases, the effect of body temperature on metabolic rate can be ignored. The reason why the two models agree for these examples is that the derivative of body temperature in (7) can be decomposed in two terms: a linear and an exponential term. Where the linear term dominates, Eqs. (3) and (7) make similar predictions. It would seem that, for those ambient temperatures such that (7) has a stable equilibrium, the effect of body temperature on metabolic rate could be ignored as a first approximation.

### 3. Second-order models

I will consider now second-order models of temperature dynamics. Eq. (6) itself is an approximation. It assumes that body temperature is homogeneous. If temperature gradients are present within an animal's body, more complicated models must be used. The degree of sophistication required for an application will depend on the magnitude of the errors that can be tolerated. It is possible to model the dynamics of body-temperature fluctuations with a great deal of detail (see e.g., Spotila et al., 1973; Werner and Webb, 1993; O'Connor, 1999), but the more sophisticated the model the larger the number of parameters that must be

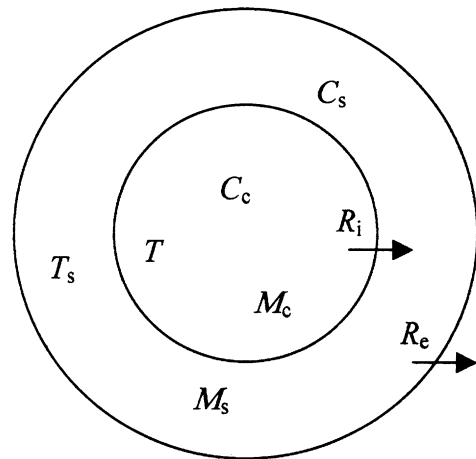


Fig. 4. Basic components of the core-shell model with metabolic heat production. The animal is divided in two thermal compartments. The inner core has a uniform temperature of  $T_c$  ( $^\circ\text{C}$ ), thermal capacitance  $C_c$  ( $\text{J } ^\circ\text{C}^{-1}$ ) and metabolic heat production  $M_c$  (W). The outer shell has a uniform temperature of  $T_s$  ( $^\circ\text{C}$ ), thermal capacitance  $C_s$  ( $\text{J } ^\circ\text{C}^{-1}$ ) and metabolic heat production  $M_s$  (W). The internal (core-shell) heat-transfer resistance is  $R_i$  ( $^\circ\text{C W}^{-1}$ ), and the external (shell-environment) heat-transfer resistance is  $R_e$  ( $^\circ\text{C W}^{-1}$ ).

included. For well-studied systems where the relevant parameters are known, this needs not be a problem. Most often, however, the thermal capacitance of and heat-transfer resistance between the different components of the model will not be known. If these parameters must be estimated (or even worse, guessed), the predictive value of the models will be severely reduced. It is unclear that we gain anything from using a high-order model with unreliable parameters rather than a first-order model (Eq. (6)) with more reliable parameters. In this paper, I will not consider anything beyond second-order models.

To understand the physical processes behind a second-order model, we will consider a simple extension of Turner's (1987) core-shell model. The core-shell model assumes that the body can be divided in two thermal compartments (the inner core and the outer shell) and that temperature is homogeneous within each compartment. Core and shell are conceptual idealisations and, in practice, it will seldom be possible to partition an animal's body in such compartments in any clear-cut fashion. Let us denote by  $T_c(T_s)$ ,  $C_c(C_s)$  and  $M_c(M_s)$  the temperature ( $^\circ\text{C}$ ), thermal capacitance ( $\text{J } ^\circ\text{C}^{-1}$ ) and metabolic heat production (W) of the core (shell), respectively. Let  $R_i$  be the heat-transfer resistance ( $^\circ\text{C W}^{-1}$ ) between core and shell, and  $R_e$  the heat-transfer resistance between the shell and the environment (Fig. 4). With the assumption of temperature homogeneity, the dynamics of core and shell

temperatures are determined by

$$\begin{aligned} \frac{dT_c}{dt} &= \frac{T_s - T_c}{R_i C_c} + \frac{M_c}{C_c}, \\ \frac{dT_s}{dt} &= \frac{T_e - T_s}{R_e C_s} - \frac{T_s - T_c}{R_i C_s} + \frac{M_s}{C_s}. \end{aligned} \tag{9}$$

The first equation in (9) is equivalent to Eq. (3), if we recognise that the thermal “environment” of the core is the shell. (Surface evaporative cooling has been neglected for simplicity:  $M_c$  should be understood as net rate of heat production at the core. For a full discussion of evaporative cooling at the skin and fur, see Appendix A.) The second equation is similar, but it includes two flux terms: heat exchange between the environment and the shell and heat exchange between the shell and the core.

For a constant environmental temperature, this system of differential equations can be solved using standard techniques (e.g. McCann, 1982), leading to

$$\begin{aligned} T_c &= Ae^{-t/\tau_1} + Be^{-t/\tau_2} + T_{\infty,c}, \\ T_s &= A \frac{a\tau_1 - 1}{a\tau_1} e^{-t/\tau_1} + B \frac{a\tau_2 - 1}{a\tau_2} e^{-t/\tau_2} + T_{\infty,s}, \end{aligned} \tag{10}$$

where

$$\begin{aligned} T_{\infty,c} &= T_e + (R_i + R_e)M_c + R_e M_s, \\ T_{\infty,s} &= T_e + R_e(M_c + M_s), \\ \tau_1 &= \frac{2}{a + d + \sqrt{(a - d)^2 + 4ac}}, \\ \tau_2 &= \frac{2}{a + d - \sqrt{(a - d)^2 + 4ac}}, \\ a &= \frac{1}{R_i C_c}, \\ c &= \frac{1}{R_i C_s}, \\ d &= \frac{R_i + R_e}{R_i R_e C_s}. \end{aligned} \tag{11}$$

The expressions for the asymptotic temperatures change somewhat if surface evaporative cooling is considered (see Appendix A). When the parameters in the right-hand side of (9) are piecewise constant (i.e., they are constant between  $t_0$  and  $t_1$ ,  $t_1$  and  $t_2$ ... but change discontinuously at  $t_1, t_2$ ...), as it happens (approximately) during shuttling, the solution is the same but the time exponential constants  $\tau_1$  and  $\tau_2$  must be calculated according to (11) for each interval and the integration constants  $A$  and  $B$  must be determined between  $t_0$  and  $t_1$  according to some boundary conditions and for each subsequent interval imposing the continuity of core and shell temperature at each transition. It is probably easiest (if somewhat unorthodox) to reset time to zero at each transition and calculate the values of the integration constant between  $t_i$  and  $t_{i+1}$

from

$$\begin{aligned} T_c(t = t_i) &= A_i + B_i + T_{\infty,c}, \\ T_s(t = t_i) &= A_i \frac{a\tau_1 - 1}{a\tau_1} + B_i \frac{a\tau_2 - 1}{a\tau_2} + T_{\infty,s}. \end{aligned} \tag{12}$$

All parameters in Eq. (12) can be calculated from Eq. (11), so if we calculate  $T_c(t = t_i)$  and  $T_s(t = t_i)$  from Eq. (10) with the values of  $A_{i-1}$  and  $B_{i-1}$  previously calculated and substitute them in Eq. (12) we obtain a system of two equations with two unknowns:  $A_i$  and  $B_i$ . (The coefficients of  $A_i$  and  $B_i$  in Eq. (12) are such that the system of equations always has a unique solution.) The values of  $A_0$  and  $B_0$  can be obtained, for example, from Eq. (12) substituting in the left-hand side the initial values of core and shell temperature.

With respect to the calculation of integration constants, it must be pointed out that Turner’s (1987) equation (15a) and Voss and Hainsworth’s (2001) Eq. (10) were derived on the assumption that at  $t = 0$  core temperature has a certain value ( $T_{0,c}$ ) and that its time derivative equals zero. This condition is normally not met during shuttling, since the derivative of core temperature equals zero only at the steady state and shuttling is all about preventing steady states. (If an animal could forage in a patch when its body temperature reached the steady state it would not need to shift to a thermal refuge, and hence there would be no shuttling.) With our notation, Turner’s (1987) equation becomes

$$\begin{aligned} T_c &= (T_{0,c} - T_{\infty,c}) \\ &\times \left( -\frac{\tau_1}{\tau_2 - \tau_1} e^{-t/\tau_1} + \frac{\tau_2}{\tau_2 - \tau_1} e^{-t/\tau_2} \right) + T_{\infty,c}. \end{aligned} \tag{13}$$

Fig. 5 shows the discrepancies in the predictions of using Eqs. (12) and (13) to predict an animal’s core temperature during shuttling. We consider an antelope ground squirrel shuttling between a foraging patch with temperature  $T_e = 60^\circ\text{C}$  and a thermal refuge with  $T_e = 30^\circ\text{C}$ . Our hypothetical ground squirrel spends, at each shuttling cycle, 4 min in the thermal refuge and two and a half minutes in the patch. After a certain number of cycles, its body temperature reaches a steady state, in the sense that the animal always has the same temperature when it reaches the thermal refuge. (This steady state depends on the amount of time spent in each patch.) Fig. 5a shows the predictions calculated in two different ways. For the empty circles we calculate  $A_i$  and  $B_i$  according to Eq. (12). For the black circles, we calculate  $A_i$  and  $B_i$  disregarding shell temperature and assuming that core temperature is continuous and that its derivative equals zero at the start of each phase of the cycle. (Eq. (13): this is what equation (15a) from Turner (1987) and Eq. (10) from Voss and Hainsworth (2001) amount to.) As we can see from Fig. 5a, Eq. (13) underestimates core temperature at the steady state by

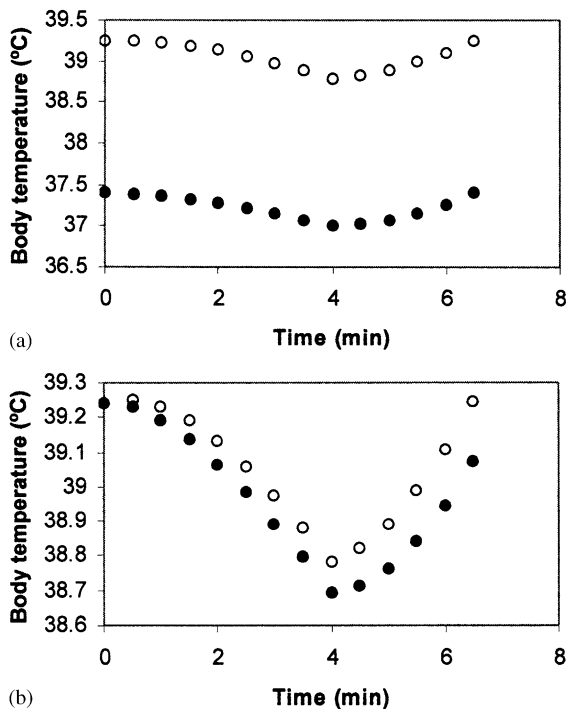


Fig. 5. Core temperature of shuttling antelope ground squirrels when the integration constants of Eq. (10) are calculated according to Eq. (12), empty circles, or Eq. (13), black circles. (a) A shuttling cycle at the steady state predicted by each model. (b) The data from Eq. (12) correspond to the steady state, but those from (13) represent a single shuttling cycle starting at the same temperature as the steady state of Eq. (12). Parameter values are those provided by Hainsworth (1995) and used for Fig. 1, except that heat capacitance is divided in two components (35% shell, 65% core), and the same is done for metabolic rate (20% shell, 80% core). The compartmentalisation of heat capacitance and metabolic rate is arbitrary. During cooling,  $C_c = 223.0 \text{ J } ^\circ\text{C}^{-1}$ ,  $C_s = 120.1 \text{ J } ^\circ\text{C}^{-1}$ ,  $R_i = 4.00^\circ\text{C W}^{-1}$ ,  $R_e = 1.82^\circ\text{C W}^{-1}$ ,  $M_c = 0.44 \text{ W}$  and  $M_s = 0.11 \text{ W}$ ; during heating,  $C_c = 223.0 \text{ J } ^\circ\text{C}^{-1}$ ,  $C_s = 120.1 \text{ J } ^\circ\text{C}^{-1}$ ,  $R_i = 4.00^\circ\text{C W}^{-1}$ ,  $R_e = 10.0^\circ\text{C W}^{-1}$ ,  $M_c = 1.36 \text{ W}$  and  $M_s = 0.34 \text{ W}$ .

almost  $2^\circ\text{C}$  relative to Eq. (12). In Fig. 5b we look at the same phenomenon from a different perspective. The empty circles give the same data as in Fig. 5a. The black circles are calculated from Eq. (13), but looking at a single shuttling cycle that starts at the same temperature as for the empty circles. With the parameter values that we have used, we notice that cooling proceeds faster according to Eq. (13) than to Eq. (12), while heating proceeds faster according to Eq. (12) than to Eq. (13). This is because the derivative of core temperature is positive at the start of the cooling and heating phases, due to the effect of the shell. The net effect of these effects is that, when core temperature is calculated according to Eq. (13), core temperature is lower at the end than at the beginning of the shuttling cycle. In other

words, according to Eq. (13) the animal is above the steady state (as could be seen from Fig. 5a).

Fig. 5 shows that using Eqs. (12) and (13) to calculate the integration constants leads to markedly different results. But which method is better and why? When we solve a differential equation, we end up with a number of integration constants that must be calculated from some boundary conditions. We often derive these constants from “initial” conditions: the state of our system at time  $t = 0$ . The name “initial” conditions gives the misleading impression that the system has no prior history. If we build an animal we can select its core and shell temperature whichever way we wish, and we could potentially have individuals satisfying either Eq. (12) or (13). With a shuttling animal, we have to calculate  $A$  and  $B$  in Eq. (10) every time that the animal moves from one patch to another. But we are no longer able to select the state of the animal. Even if, for convenience, we reset time to  $t = 0$  at the start of every phase (as implicitly do Turner, 1987, and Voss and Hainsworth, 2001), we cannot delete the history of the animal, and hence we cannot choose the initial conditions: they will be given by the state of the animal at the end of the previous phase. Because core and shell temperatures (according to Eq. (9)) are continuous in time even if the environmental parameters are discontinuous (provided that the discontinuity is finite: if ambient temperature became equal to infinity things would be otherwise—but this is clearly of no biological relevance), we must enforce that core and shell temperatures at the beginning of the cooling phase are the same as at the end of the foraging phase, and vice versa. For this, we must use Eq. (12). Indeed, if we calculate  $A$  and  $B$  as in Eq. (13) and we go back to (10), we can see that shell temperature is discontinuous. Voss and Hainsworth (2001) present a second-order model that does not include shell temperature. This, however, does not imply that we gain a degree of freedom for the calculation of the integration constants. In their model, we start with a single second-order differential equation for body temperature. If we have an animal shuttling between times  $t = 0$  and  $t = t_{\text{end}}$ , and if the animal changes habitat at times  $t_1, t_2, \dots$  then we can safely use Eq. (13) (Eq. (10) in Voss and Hainsworth, 2001) to predict body temperature between  $t = 0$  and  $t = t_1$ . Between  $t_1$  and  $t_2$ , however, this is no longer correct. Their model is formulated as

$$a \frac{d^2 T}{dt^2} + b \frac{dT}{dt} + cT = f(t) \quad (14)$$

and according to this model, when  $f(t)$  presents a discontinuity at time  $t_1$ , then  $T(t)$  is continuous at  $t_1$  and its derivative presents a discontinuity of fixed magnitude. In other words,  $T'(t)$  cannot be calculated for  $t_1$ , but we can calculate its limiting values for  $t < t_1 (T'(t_1^-))$  and for  $t > t_1 (T'(t_1^+))$ , and the value of  $\Delta T' = T'(t_1^+) - T'(t_1^-)$  can be calculated from the magnitude

of the step in  $f(t)$ . Now, we know  $T'(t_1-)$  because it is the value of the derivative of body temperature at the moment when the animal *leaves* one patch and we can calculate  $\Delta T'$  from  $f(T)$ . Hence, we can calculate the value of the derivative of body temperature at the moment when the animal *reaches* the new patch,  $T'(t_1+) = \Delta T' + T'(t_1-)$ . This (and not  $T'(t_1+) = 0$ ) is the second boundary condition that we must use if we want to apply Voss and Hainsworth's (2001) model to shuttling.

Eq. (11) gives the asymptotic core and shell temperatures ( $T_{\infty,c}$  and  $T_{\infty,s}$ ), and the exponential time constants ( $\tau_1$  and  $\tau_2$ ), as a function of six physical parameters (Fig. 4). In practice, however, it is possible to measure the time constants and the asymptotic temperature without having to measure the heat-transfer resistance, heat capacitance and metabolic rates of the core and shell components (remember that  $A$  and  $B$  are integration constants that must be determined from the initial conditions: they don't need to be measured). The time constants and asymptotic temperatures can be derived from cooling and heating curves, as described by Turner (1987) and Voss and Hainsworth (2001). Hence, the relationships given by Eq. (11) can be used to predict the effect of increasing or decreasing the value of a certain parameter (such as the metabolic rate of the core) on the temporal dynamics of body temperature. But if we want to predict the temporal dynamics of a real animal's body temperature, it is easier to measure the time constants and the asymptotic temperature from heating and cooling curves.

### 3.1. Comparison of first- and second-order models

Consider two animals with the same mass, same total heat capacitance and net metabolic heat production and with the same heat-transfer resistance between the animal and its environment. Let us assume that one animal has uniform temperature throughout its body while the other has two compartments at different temperature (the core and the shell). The temperature gradient between core and shell can be obtained if there is limited blood flux between the two compartments and/or if there are counter current heat exchangers (Scholander and Schevill, 1955). A first-order model will be appropriate to describe the dynamics of body temperature in the first animal, but a second-order model will be required for the second one. Let us now consider how a certain shuttling regime affects both animals. (For simplicity, we will refer to these hypothetical animals as first- and second-order animal.)

We first notice that a first-order model is a limiting case of a second-order model: if, in a core-shell model the heat-transfer resistance between core and shell decreases, heat flow between the two compartments is enhanced and their temperatures become more and

more homogeneous. In the limiting case when  $R_i = 0$ , there is no difference between core and shell temperature. When this happens, of the two exponential time constants that appear in Eq. (10), one tends to zero and the other becomes equal to  $R_e \cdot (C_c + C_s)$ . This is precisely the value of the time constant in a first-order model, Eq. (6), as the total heat capacitance of a body is the sum of the heat capacitance of its parts.

The presence of a heat-transfer resistance between core and shell ( $R_i > 0$ ) has two effects. On the one hand it retards the dissipation of the heat generated at the core. This implies that the asymptotic core temperature of a second-order animal is higher than the asymptotic body temperature of a first-order animal when they are in the same environment. Comparison of Eqs. (5) and (11) shows that the difference in asymptotic temperatures is the product  $R_i \cdot M_c$ , and hence it tends to zero with  $R_i$ . Besides, the heat-transfer resistance between core and shell introduces a time lag in the response of the core to changes in environmental temperature. During shuttling, core and shell temperatures oscillate. But the magnitude of the oscillations is larger for the shell than for the core. Limiting the heat flow between core and shell thus provides animals with a mechanism to control the temperature of sensitive internal organs even when the skeletal muscles and peripheral tissues are exposed to wide temperature fluctuations.

Animals shuttling between inhospitable foraging patches and thermal refuges try to minimise heat exchange with their environment in the foraging patch and to maximise it in the refuge. The heat-transfer resistance between the animal and its environment,  $R_e$ , should be as high as possible in the foraging patch (to minimise heat exchange and maximise the amount of time that the patch can be exploited) and as low as possible in the refuge (to maximise heat exchange with the environment and minimise the time spent in the refuge). These expected differences between heat-transfer resistance in foraging patches and thermal refuges do correspond to empirical observations (e.g., Chappell and Bartholomew, 1981; Bozinovic et al., 2000). The heat-transfer resistance between core and shell,  $R_i$ , on the other hand, should follow a different pattern. Let us consider a desert rodent shuttling between a cool burrow and a hot foraging patch. To maximise the time spent in the foraging patch, the animal must reduce the rate of increase of core temperature. When it first enters the foraging patch, shell temperature is lower than core temperature. A low  $R_i$  will have a cooling effect for the core (see Eq. (9)). When the shell becomes warmer than the core, on the other hand, a low  $R_i$  will maximise heat influx into the core and will lead to an increase in its rate of heating. As a result, then, animals should have a low  $R_i$  when they arrive to the foraging patch and a high  $R_i$  when shell temperature becomes higher than core temperature. In the thermal refuge,  $R_i$  should remain



high until shell temperature drops below core temperature, and then it should decrease to facilitate cooling.

The differences between the predictions of first- and second-order models help us understand why the development of second-order models is important. The presence of internal heat-transfer resistances introduces important changes in the temporal dynamics of body temperature. Because animals can and do modify these heat-transfer resistances for thermoregulatory purposes, we need to be able to predict the effect of these changes if we are to understand how animals react to different environmental challenges. Second-order models constitute the simplest approximation to this study. It is important to realise, however, that the distinction between core and shell is a heuristic one. It is not possible to divide an animal a priori between its core and its shell compartments. Indeed, the most useful division between core and shell may be a function of ambient temperature, since it depends on the presence of heat-transfer barriers that can be adjusted by modifying the pattern of blood flux.

#### 4. Discussion

This paper has considered two mathematical models that can be used to predict the temporal dynamics of body temperature as a function of environmental conditions. The models can help us understand the ecological limits of different species faced with temperature constraints and water limitations.

The first-order model, originally derived by Bakken and Gates (1975), can be used with relatively little information. To apply it, we need three parameters: the heat-transfer resistance of the animal, its thermal capacitance and its metabolic heat production. Of these three, only the metabolic heat production needs to be measured. This is because heat-transfer resistance can be obtained from the metabolic rate of animals at rest (McNab, 1980), and the thermal capacitance is the product of the animal's mass (g) by its (average) specific heat capacity ( $\text{J g}^{-1} \text{ } ^\circ\text{C}^{-1}$ ). The specific heat capacity of rodents is  $3.431 \text{ J g}^{-1} \text{ } ^\circ\text{C}^{-1}$  (Hainsworth, 1995), and the same value can probably be used for most birds and mammals.

Second-order models require more information before they can be applied. The relevant information (two time constants and asymptotic temperatures for each ambient temperature) is not difficult to obtain, but it cannot be readily estimated and must be measured for each species of interest. The investment of time and resources into measuring the relevant time constants will be only worthwhile if the predictions from the first-order model deviate substantially from the experimental data. This is indeed the case in reptiles (Turner, 1987) and in bird eggs (Voss and Hainsworth, 2001), but there is, to my

knowledge, no relevant data to ascertain the merits of first- and second-order models in endotherms. In view of the formal similarities between the models for ecto- and endotherms, it seems likely that the second-order correction provides a substantial improvement for endotherms as well.

Theoretical models of temperature regulation can be used to predict variations in body temperature, but they also have heuristic value, since they can help us understand the consequences of changing certain parameters that are associated with biophysical properties of the organism. In this sense, the second-order model shows that precise thermoregulation of sensitive internal organs can be achieved despite wide fluctuations in the temperature of peripheral tissue. It also suggests a physiological mechanism (control of the heat-transfer resistance between core and shell) that can be used to achieve this goal.

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#### Appendix A

The second-order model, as described in the main body of this article, does not take into account where evaporative cooling takes place. When, for whatever reason, one wants to distinguish between respiratory and surface evaporative cooling, the heat-flux process must be modelled in more detail. Here we consider the second-order version of what Bakken and Gates (1975) call an "animal with pelage and significant conductance to the ground". (If one wants to consider a simpler animal, it will be sufficient to choose the corresponding parameter values. For instance, we obtain an animal with no conductance to the ground by setting the heat-transfer resistance between the animal and the ground equal to infinity.) This model animal differs from the one represented in Fig. 4 in the way it dissipates heat to the environment:

- There is a direct path of heat flux between the animal's shell and the ground. The ground is at temperature  $T_g$  ( $^\circ\text{C}$ ) and the heat-transfer resistance between shell and ground is  $R_g$  ( $^\circ\text{C W}^{-1}$ ).
- There are two interfaces between the shell and the environment: the skin and the fur. Their temperatures are  $T_{r0}$  and  $T_{r1}$  ( $^\circ\text{C}$ ), respectively. We assume (Bakken and Gates, 1975) that they have zero heat

capacity (they cannot store heat), which in turn implies that any heat they receive from the outside is transferred inwards. We denote by  $R_s$  and  $R_f$  the heat-transfer resistances ( $^{\circ}\text{C W}^{-1}$ ) between shell and skin and skin and fur, respectively. The rates of evaporation at skin and fur are  $E_s$  and  $E_f$  (W), respectively.

The equation describing heat exchange at the fur (Bakken and Gates, 1975) is

$$H(T_{r1} - T_a) + \sigma\epsilon T_{r1}^4 + E_f = \frac{T_{r0} - T_{r1}}{R_f} + Q_a. \quad (\text{A.1})$$

In the left-hand side we have heat losses to the environment. The first term represents convection ( $H$  is the convection coefficient,  $\text{W }^{\circ}\text{C}^{-1}$  and  $T_a$  the air temperature,  $^{\circ}\text{C}$ ), the second thermal radiation (the Stefan-Boltzmann constant is  $\sigma = 5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$  and the emissivity  $\epsilon$  ranges from 0 to 1) and the third water evaporation. In the right-hand side, the first term represents heat gains through conductance from the skin and the second absorbed radiation (in W). To simplify the model we assume that thermal radiation is linear in fur temperature (Bakken and Gates, 1975), leading to the following equation:

$$H(T_{r1} - T_a) + \rho T_{r1} + E_f = \frac{T_{r0} - T_{r1}}{R_f} + Q_n, \quad (\text{A.2})$$

where

$$\rho = 4\sigma\epsilon\bar{T}_{r1}^3, \quad (\text{A.3})$$

$$Q_n = Q_a + 3\sigma\epsilon\bar{T}_{r1}^4 \quad (\text{A.4})$$

and  $\bar{T}_{r1}$  is the mean surface temperature.

Heat exchanges at the skin takes place through evaporation and conductance between fur and skin or shell and skin, leading to

$$E_s = -\frac{T_{r0} - T_s}{R_s} - \frac{T_{r0} - T_{r1}}{R_f}. \quad (\text{A.5})$$

Finally, the equations for shell and core are very similar to the ones already used, except that the shell equation incorporates direct conductance to the ground

$$C_s \frac{dT_s}{dt} + \frac{T_s - T_{r0}}{R_s} = M_s - \frac{T_s - T_c}{R_i} - \frac{T_s - T_g}{R_g} \quad (\text{A.6})$$

and the equation for the core includes respiratory evaporative cooling ( $E_c$ , in W)

$$C_c \frac{dT_c}{dt} + \frac{T_c - T_s}{R_i} = M_c - E_c. \quad (\text{A.7})$$

Of these equations, only two are differential equations, while (A.2) and (A.5) are algebraic equations. Hence, the entire set can be reduced with some algebra to a set of two differential equations: Eq. (A.7) and

$$C_s \frac{dT_s}{dt} = M_s - \alpha_s E_s - \alpha_r E_r - \frac{T_s - T_c}{I} - \frac{T_s - T_c}{R_i}, \quad (\text{A.8})$$

where

$$\begin{aligned} T_c &= \frac{R_g(HT_a + Q_n) + [1 + (H + \rho)(R_s + R_f)]T_g}{(R_s + R_f + R_g)(H + \rho) + 1}, \\ I &= \frac{[1 + (H + \rho)(R_s + R_f)]R_g}{(R_s + R_f + R_g)(H + \rho) + 1}, \\ \alpha_s &= \frac{1 + (H + \rho)R_f}{1 + (H + \rho)(R_s + R_f)}, \\ \alpha_r &= \frac{1}{1 + (H + \rho)(R_s + R_f)}. \end{aligned} \quad (\text{A.9})$$

Notice that Eqs. (A.7) and (A.8) are formally identical to Eq. (9) with  $I$  taking the role of  $R_c$  and when the metabolic rates are substituted by “net” values to correct for evaporative cooling. In the case of the core, the net metabolic rate that must be used is just metabolic heat produced minus heat used for evaporation in the lungs and mouth cavity (Eq. (A.7)), but in the case of the shell evaporative cooling at skin and fur must be “discounted” by multiplicative factors  $\alpha_s$  and  $\alpha_r$  (Eq. (A.8)) that are always less than one (Eq. (A.9)). In particular, this implies that respiratory water evaporation is more efficient for cooling than surface evaporation.

When this model is solved for constant ambient temperature, we obtain once again Eq. (10) as solution except that now

$$\begin{aligned} T_{\infty,c} &= T_c + (R_i + I)(M_c - E_c) + I(M_s - \alpha_s E_s - \alpha_r E_r), \\ T_{\infty,s} &= T_c + I(M_c - E_c + M_s - \alpha_s E_s - \alpha_r E_r), \\ \tau_1 &= \frac{2}{a + d + \sqrt{(a - d)^2 + 4ac}}, \\ \tau_2 &= \frac{2}{a + d - \sqrt{(a - d)^2 + 4ac}}, \\ a &= \frac{1}{R_i C_c}, \\ c &= \frac{1}{R_i C_s}, \\ d &= \frac{R_i + I}{R_i I C_s}. \end{aligned} \quad (\text{A.10})$$

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