Modeling energetic and theoretical costs of thermoregulatory strategy

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(Received 30 July 2010; final version received 11 May 2011)

Poikilothermic ectotherms have evolved behaviours that help them maintain or regulate their body temperature ($T_b$) around a preferred or ‘set point’ temperature ($T_{set}$). Thermoregulatory behaviors may range from body positioning to optimize heat gain to shuttling among preferred microhabitats to find appropriate environmental temperatures. We have modelled movement patterns between an active and non-active shuttling behaviour within a habitat (as a biased random walk) to investigate the potential cost of two thermoregulatory strategies. Generally, small-bodied ectotherms actively thermoregulate while large-bodied ectotherms may passively thermoconform to their environment. We were interested in the potential energetic cost for a large-bodied ectotherm if it were forced to actively thermoregulate rather than thermoconform. We therefore modelled movements and the resulting and comparative energetic costs in precisely maintaining a $T_{set}$ for a small-bodied versus large-bodied ectotherm to study and evaluate the thermoregulatory strategy.

Keywords: animal behaviour; ecology and evolutionary biology

AMS 2010 Mathematics Subject Classification codes: 92-08; 34C60

1. Introduction

An ectotherm’s body temperature ($T_b$) fluctuates with ambient environmental temperatures. Thus, ectothermic animals such as invertebrates, fishes, amphibians, and reptiles do not generate internal or physiological heat and must rely on adaptations of behavioural and physiological mechanisms to regulate and maintain $T_b$ [5]. Although these animals are commonly and mistakenly referred to as ‘cold-blooded’, many ectotherms can thermoregulate and maintain a high preferred $T_b$ [22]. Thermoregulatory behaviours may include shuttling between sun and shade and using body positioning for solar and radiant heat gain [41].

Thermoregulatory strategies are known to influence habitat use [1,28,29,39,41] and foraging tactics [10,37]. Some ectotherms thermoregulate more actively than others to maintain a relatively constant or narrow range of $T_b$ (stenothermic) while others may be able to function and perform efficiently over a wide range of $T_b$ (eurythermic). Two known thermobehavioural
strategies associated with stenothermic versus eurythermic $T_b$ are active thermoregulation and thermoconformity, respectively. Thermoconformity allows an animal to conserve energy by not actively seeking a preferred body temperature, thus thermally conforming to environmental temperature ($T_e$).

Here we model the movement of two ectotherms as a random walk with directional bias [15,20,45] to explore the potential energetic cost differences between active behavioural thermoregulation and passive thermoconformity. We consider only the simple case of an animal moving left or right a fixed number of units $\Delta x$ in a fixed unit of time $\Delta t$. Although animals in the field are not restricted to one-dimensional movement, many experimenters commonly use shuttle boxes or linear thigmothermal gradients [26] in investigating thermoregulatory behaviour [12,24,27,29,46]. Furthermore, such a simple one-dimensional model that uses fixed movement lengths (over $\Delta t$) allows for a proportional $\Delta x$ with respect to velocity and direct comparison of thermoregulatory strategies.

Thermal biologists commonly measure the thermal quality of an ectotherm’s microhabitat to understand thermoregulatory behaviour [28,38,39,41], and habitat quality is a general way to include directional bias in mechanistic models of animal movement [17,20]. Our movement model utilizes a specific functional form for the thermal quality of habitat. Experimental evidence suggests that physiological performance depends on $T_b$ and can be described by a thermal preference curve [4,6,21,30]. This curve depicts the degree of performance with respect to a life history trait such as metabolic rate, sprint speed, or reproductive capacity as a function of $T_b$. In general, thermal performance is minimal at a lower critical $T_b$, increases monotonically to an optimal performance at a preferred $T_b$ or set temperature ($T_{set}$), and decreases monotonically to its minimal performance at an upper critical $T_b$. Figure 1 depicts a typical performance curve [21]. Our model will use the thermal fitness function and its general form given by Martin and Huey [30] to quantify thermal quality.

Body temperature $T_b$ is related to $T_e$ (or more accurately, operative temperature [8]) in which habitat quality influences $T_e$ and is a function of position and time. We assume that movement is biased on both the thermal quality of the habitat and the thermoregulatory strategy.

![Figure 1](image_url)  
**Figure 1.** An example of a relative performance function for an ectotherm [21]. The degree of performance with respect to a life history trait such as metabolic rate, sprint speed, or reproductive capacity are plotted as a function of body temperature.
thermoregulating versus thermoconforming). A thermoconformer has a lower probability of moving (in general) for any habitat quality than does a thermoregulator. A thermoregulator will have a relatively high probability of moving (especially under low thermal quality of habitat) in the direction for which the gradient of habitat quality is largest.

The benefit of thermoregulation is the ability to maintain preferred $T_b$, thereby maximizing fitness and performance. The costs associated with thermoregulation include both energy and time expenditure. Huey and Slatkin [22] used a qualitative mathematical model to determine the thermoregulatory strategy of a lizard. They created theoretical benefit and cost functions to quantify energy budgets as a function of environmental temperature and computed the optimal thermoregulatory strategy by maximizing the net benefit (i.e. the integral of the difference between benefit and cost) over the set of available environmental temperatures that exist within a habitat. Many conclusions are drawn from Huey and Slatkin’s [22] model, including that the physiologically optimal temperature is not always the ecologically optimal temperature and that thermoregulation is beneficial only when associated costs are low. There has since been experimental evidence which both corroborate [19,46] and refute [9] Huey and Slatkin’s model.

We use general life history data for a small-bodied lizard and large-bodied rattlesnake to investigate the potential cost of thermoregulatory strategy by both small-bodied and large-bodied ectotherms. Unlike small-bodied lizards, rattlesnakes use a sit-and-wait foraging strategy [37] and therefore passively thermoconform to their environment [25,28] while foraging. Lutterschmidt et al. [28] further speculate why this rattlesnake species may be able to sacrifice preferred $T_b$ and thermally conform within selected microhabitats. The ectothermic ability to function over a wide range of $T_e$ (as depicted in Figure 2) may offset the energetic costs associated with the thermoregulatory movements of such a large-bodied ectotherm.

Generally, small-bodied ectotherms (e.g. whiptail lizards) actively thermoregulate with shuttling behaviour and movements to maintain $T_{set}$ while more large-bodied ectotherms (e.g. timber rattlesnakes) sacrifice $T_{set}$ to passively thermoconform to their environment [28]. The use of an active (rather than non-active) thermoregulatory strategy is most likely tied to the increased

![Figure 2. Frequency distribution of field body temperatures ($^\circ$C) for a rattlesnake (Crotalus horridus) modified from [25]. This rattlesnake demonstrates a eurythermic ability to function over a wide range of $T_e$.](image-url)
energetic costs of movement and locomotion for a large-bodied ectotherm. To evaluate the theoretical benefits and costs between these two different thermoregulatory strategies for each ectotherm, we modelled movement patterns between active versus non-active thermoregulation and the potential theoretical costs associated with switching thermoregulatory strategies between these ectotherms (i.e. forcing the lizard to thermoconform and the rattlesnake to thermoregulate). Such a theoretical investigation is possible with the use of a biased random walk model and may allow for discussion on how thermoregulatory strategies may be tied to the life histories of body size and foraging tactics.

We compute a theoretical benefit and cost of thermoregulatory strategy in maintaining a preferred $T_b$ as it is dependent on average $T_b$ and distance moved. Benefit is measured by the degree to which an animal is able to maintain $T_b$ at its preferred temperature. We assume that cost is due to metabolic cost of physiological maintenance (basal metabolism) and cost of locomotion. We determine how the benefit–cost ratio for each thermoregulatory strategy depends on movement defined by each of the thermoregulatory strategies. The lizard uses an active foraging strategy and behaviourally thermoregulates in order to maintain its $T_b$ at a preferred $T_b$ [3]. The temperature relations for this actively thermoregulating species were used with forced thermoconformity to generate the critical benefit to cost ratio at which the thermoregulatory strategies are equivalent.

The paper is outlined as follows. In Section 2 we describe the equations which govern the movement model and $T_e$. In Section 3, we describe the simulation algorithm and use our simulations to compute the benefits and costs of thermoregulation (with shuttling behaviour) for a given thermoregulatory strategy. Two sets of parameters Table 1 are modelled in our investigations for a lizard (thermoregulator) and rattlesnake (thermoconformer). These parameters were either referenced, inferred, or estimated to best reflect the comparative natural histories of these two ectotherms.

2. Model description

2.1. Movement model

We use a mathematical model for ectothermic fitness [30]

$$b(T_b) = \exp\{-\exp(\beta(T_b - T_{set}) - 8) - \alpha(T_b - T_{set})^2\},$$

where $T_b$ is the body temperature and $T_{set}$ is the preferred body temperature. As described in [30], this particular formulation of $b(T_b)$ typically provides a reasonable empirical fit to data near $T_{set}$ and is easy to modify by manipulating the parameters $T_{set}$, $\alpha$ and $\beta$ which are species-specific. Here we consider relative fitness where maximum fitness is equal to one. Example fitness functions and of movement probabilities for a lizard and rattlesnake are plotted (Figure 3).

Temperature parameters must be specified to determine movement probabilities. Let $P_0(T_b)$ and $P_1(T_b)$ denote the movement probabilities of the thermoregulator and thermoconformer,
Figure 3. The fitness function (1) and movement probability function (2) for a thermoregulating lizard (left) and a thermoconforming rattlesnake (right). The parameters in Table 1 were used (as described in Section 3.1) to compute the parameters in Equations (1) and (2). Fitness functions $b(T_b)$ are depicted as solid curves, whereas movement probability functions $P_0(T_b)$ and $P_1(T_b)$ are depicted as dashed curves.

respectively. Let $CT_{\text{max}}$ denote the upper critical (lethal) temperature and $CT_{\text{min}}$ denote the lower critical (lethal) temperature. For the thermoregulator, we assume that

(r1) $P_0(T_{\text{set}}) = 0$ and $P_0(T_b) > 0$ if $T_b \neq T_{\text{set}}$,
(r2) $P_0(T_b) \uparrow 1$ as $T_b \downarrow T_{\text{PL}}$ or $T_b \uparrow T_{\text{PU}}$,
(r3) $P_0(T_b) = 1$ for $T_b < T_{\text{PL}}$ or $T_b > T_{\text{PU}}$,

and for the thermoconformer, we assume that

(c1) $P_1(T_b) = 0$ for $CT_{\text{min}} + 1.5^{\circ} < T_b < CT_{\text{max}} - 1.5^{\circ}$,
(c2) $P_1(T_b) \uparrow 1$ as $T_b \downarrow CT_{\text{min}}$ or $T_b \uparrow CT_{\text{max}}$,
(c3) $P_1(T_b) = 1$ for $T_b < CT_{\text{min}}$ or $T_b > CT_{\text{max}}$.

These properties are motivated by Huey and Slatkin’s [22] model which relates body temperature to environmental temperature based on a thermoregulatory strategy. In particular, a perfect thermoregulator maintains body temperature at its optimal physiological temperature ($T_b = T_{\text{set}}$) independent of environmental temperature, whereas a perfect thermoconformer’s body temperature tracks the environmental temperature ($T_b = T_e$). The specific movement probability functions that we use are

$$P_0(T_b) = 1 - b(T_b), \quad P_1(T_b) = 1 - \exp\{-0.5(|T_b - a|/\phi)^{\kappa}\}. \quad (2)$$

Proper choices for $\alpha$ and $\beta$ in Equation (1) will yield a function $P_0(T_b)$ which approximates (r1), (r2), and (r3). The parameters $a, \phi, \kappa$ in $P_1(T_b)$ are

$$a = (CT_{\text{min}} + CT_{\text{max}})/2, \quad \phi = (CT_{\text{max}} - CT_{\text{min}} - 1.5)/2, \quad \kappa \gg 1,$$

which yields a function $P_1(T_b)$ which approximates (c1), (c2), and (c3). Examples are plotted (dashed) in Figure 3. The functions (2) were chosen so that the movement probabilities as they depend on $T_b$ may be easily computed using a small number of parameters and are not necessarily motivated by empirical data.

$T_b$ depends on the environmental temperature which in general may be space dependent. Thus, the fitness function is also space-dependent with gradient $\partial b/\partial x$. Movement direction
Environmental temperature function is given by the sign value of a random draw from a normal distribution with
\[
\text{mean} = \gamma \frac{\partial b}{\partial x} \quad \text{and} \quad \text{variance} = \frac{1}{|\gamma \frac{\partial b}{\partial x} + \epsilon|},
\]
(3)
where \(\epsilon\) and \(\gamma\) are positive constants. Depending on the constants \(\gamma\) and \(\epsilon\), when \(\partial b/\partial x\) is small and the animal is moving, the movement (i.e. searching behaviour) will be relatively unbiased. However if the gradient of \(b\) is large the movement (i.e. seeking behaviour) will be heavily biased towards the direction of increasing \(b\). This bias in movement is similar to \([17]\). The constant \(\epsilon\) is small and the variance is defined if \(\partial b/\partial x = 0\). The scaling constant \(\gamma\) is used to control movement sensitivity to small gradients in the fitness function. Larger values of \(\gamma\) increase the tendency of the animal to engage in seeking rather than searching behaviours. We discuss the method of choosing \(\gamma\) in the following section.

Ectotherms typically have different heating and cooling rates \([18,32]\) and a model relating body temperature to environmental temperature should account for these differences. Many species-specific heating and cooling models can be found in the literature \([8,14,16,18,32,42,44]\). We use two models to most accurately compute body temperatures based upon experimental data for both the lizard and rattlesnake (Table 1). Specifically, they are
\[
\left(\frac{dT_b}{dt}\right)_{x=x_0} = F(T_e(x_0, t), T_b(x_0, t)) = R_b H(z) - R_c H(-z),
\]
(4)
and
\[
\left(\frac{dT_b}{dt}\right)_{x=x_0} = F(T_e(x_0, t), T_b(x_0, t)) = z[R_b H(z) + R_c H(-z)],
\]
(5)
where \(z = T_e(x_0, t) - T_b(x_0, t)\) and \(H(z) = \tan^{-1}(\kappa z)/\pi + 1/2\) with \(\kappa \gg 1\). The function \(H(z)\) is a continuously differentiable approximation of the step function \(H(z) = 1\) if \(z > 0\) and \(H(z) = 0\) if \(z < 0\). Equation (4) is essentially the linear model of heating and cooling with \(F = R_b\) for \(T_e(x_0, t) > T_b(x_0, t)\) and \(F = R_c\) for \(T_e(x_0, t) < T_b(x_0, t)\). The constants \(R_b > 0\) and \(R_c > 0\) are the heating and cooling rates (°C/min) respectively. Equation (5) is essentially the exponential model of heating and cooling with time constants \(1/R_b\) and \(1/R_c\) with units min⁻¹, respectively. Equations (4) or (5) is integrated at each time step to find \(T_b\) as a function of \(t\). In our simulations we use Equation (4) for the rattlesnake and Equation (5) for the lizard in order to be consistent with the experimental methodology used (e.g. [7,25], respectively) to determine the parameter values displayed in Table 1.

### 2.2. Environmental temperature equations

The environmental temperature function is
\[
T_e(x, t) = K_{T_e}(t) + m_e x, \quad x \in \mathbb{R}, \ t \in \mathbb{R}^+,
\]
(6)
so that \(T_e(x, t)\) is a temperature gradient which varies homogeneously with time as \(K_{T_e}(t)\). Here \(K_{T_e}(t)\) and \(m_e\) are parameters with units of temperature and temperature per unit distance respectively. The parameter \(K_{T_e}(t)\) controls \(T_e(0, t)\) while the parameter \(m_e\) controls the rate of change of \(T_e\) with respect to position \(x\). This (relatively) simple formulation of available environmental temperatures is a straightforward way to simulate an experimental apparatus known as a shuttle box or laboratory thermal gradient \([12,24,27,29,46]\). In Section 3.1, we model \(K_{T_e}\) as randomly fluctuating to investigate the movement model in a time-dependent \(T_e\). In Section 4, we fix \(K_{T_e}\) and use the parameter \(m_e\) to control the locomotory cost of thermoregulation in a time-independent \(T_e\).
3. Simulations of the movement model

3.1. Simulation algorithm

All computations and simulations for the random walk were performed using MATLAB [31]. The position is described by real-valued \( x \in \mathbb{R} \), time by \( t \in \mathbb{R}^+ \), and we disregard boundaries. Discretized time and space are denoted \( t_n \) and \( x_n \) with fixed increments \( \Delta t \) and \( \Delta x \). The algorithm for the simulation is as follows.

(i) Prescribe environmental temperature \( T_e(x,t) \). Use parameter sets from Table 1 to prescribe fitness \( b(T_b) \), constants for heating and cooling rates, and velocity. Initialize the position.

(ii) Update the time as \( t_{n+1} = t_n + \Delta t \) and compute the environmental temperature at the new time and current position. Compute the body temperature by integrating heating and cooling model (4) or (5) from \( t_n \) to \( t_{n+1} \).

(iii) Calculate fitness \( b(T_b) \) from Equation (1). Use \( b(T_b) \) to compute movement probability as described in Section 2.1 and determine whether to move or not by a random draw from the Bernoulli distribution with probability of success \( P_0(T_b) \) and \( P_1(T_b) \) from Equation (2).

(iv) If not moving, set \( \Delta x = 0 \). If moving, compute position change using \( \Delta x = v \cdot \Delta t \) where the velocity is from Table 1 and the sign of the velocity \( v \) is chosen by the sign value of a random draw from a normal distribution with mean and variance from Equation (3). We approximate \( \partial b/\partial x \) as follows. First, we approximate the time rate of change in body temperature using Euler’s method

\[
T_b(x, t_{n+1}) \approx T_b(x, t_n) + F(x, t_n) \Delta t,
\]

where \( \Delta t = t_{n+1} - t_n \) and \( F(x, t) \) is as in Equation (4) for the rattlesnake and Equation (5) for the lizard. Then use the chain rule to see that

\[
\frac{\partial b}{\partial x} = \frac{\partial b}{\partial T_b} \cdot \frac{\partial T_b}{\partial T_c} \cdot \frac{\partial T_c}{\partial x} \approx \frac{\partial b}{\partial T_b} \cdot \frac{\partial F}{\partial T_c} \cdot \Delta t \cdot \frac{\partial T_c}{\partial x}.
\]

(v) Update the position as \( x_{n+1} = x_n + \Delta x \) and re-iterate the algorithm.

The parameters \( \alpha \) and \( \beta \) that determine \( b(T_b) \) in Equation (1) and \( P_0(T_b) \) in Equation (2), and \( \partial b/\partial x \) in Equation (3) were numerically approximated. To compute \( P_0(T_b) \), \( \alpha \) and \( \beta \) were determined so that \( |b(T_{PL})| < 10^{-3} \) and \( |b(T_{PL})| < 10^{-3} \) and for \( b(T_b) \), \( \alpha \) and \( \beta \) were determined so that \( |b(C_T_{\text{max}})| < 10^{-3} \) and \( |b(C_T_{\text{min}})| < 10^{-3} \) where \( T_{PL}, T_{PU}, C_T_{\text{min}}, \) and \( C_T_{\text{min}} \) are from Table 1. The scaling constant \( \gamma \) in Equation (3) was chosen as \( 3 \times 10^{-6} \) for the lizard and \( 5 \times 10^{-6} \) for the rattlesnake. This choice of \( \gamma \) ensured sensitivity to gradients in the benefit function \( b \) at thermal extremes \( C_T_{\text{min}} \) and \( C_T_{\text{max}} \). The constant \( \kappa = 100 \) for \( P_1 \) in Equation (2) and for the heating and cooling models in Equations (4) and (5) so that \( H(z) \) is essentially a step function. We used randraw.m (Efficient Random Variates Generator, mathworks.com) to perform the random draws from the Normal and Bernoulli distributions.

3.2. Simulation results

Initially, we consider an environmental temperature (6), where \( K_{T_e}(t) \) is given by

\[
K_{T_e}(t) = \rho_n F_1(t) + \left\{ \frac{\rho_{n+1} - \rho_n}{\theta} (t - t_n - \tau - \theta) + \rho_{n+1} \right\} F_2(t) \tag{7}
\]
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Figure 4. A simulation of the movement and body temperature of a thermoconforming rattlesnake (top) and a thermoregulating lizard (bottom) with time and space dependent $T_e(x,t)$. The parameters that define Equations (6) and (7) are $\mu_{T_e} = T_{set}$, $\sigma^2_{T_e} = 3$, and $m_e = 0.05$. The plots in the left column depict position $x$ of the ectotherm (solid) and the position of $T_{set}$ (dashed). The plots in the right column depict body temperature $T_b$ (solid), environmental temperature $T_e$ at the ectotherm’s position (dash-dot), and preferred body temperature $T_{set}$ (dashed). The initial temperature of each ectotherm is $T_b(x_0,0) = T_e(x_0,0) = C T_{\text{max}} - 1$.

where

$$F_1(t) = \begin{cases} 1, & t_n \leq t < t_n + \tau \\ 0, & \text{otherwise} \end{cases} \quad F_2(t) = \begin{cases} 1, & t_n + \tau \leq t < t_n + \tau + \theta \\ 0, & \text{otherwise} \end{cases}$$

and $t_n = n(\tau + \theta)$, $n = 0, 1, 2, 3, \ldots$. Here $\tau$ and $\theta$ are fixed and $\rho_n$ is chosen by a random draw from a normal distribution with mean $\mu_{T_e}$ and variance $\sigma^2_{T_e}$ to simulate random fluctuations in $T_e$. Here $T_e$ has gradient $m_e$ for all $t$. At the $n$th iteration, the parameter $K_{T_e}(t) = \rho_n$ on a time interval of duration $\tau$, but at $t_n + \tau$ the entire gradient varies (linearly) over a time interval $\theta$ from $\rho_n$ to a randomly selected value $\rho_{n+1}$. Simulations are shown for the lizard and rattlesnake with $\tau = 100$, $\theta = 2\tau$, $\mu_{T_e} = T_{set}$ and $\sigma^2_{T_e} = 2^\circ{\text{C}}$ in Figure 4. The rattlesnake exhibits very little movement with $T_b$ relatively far from its $T_{set} = 32.7^\circ{\text{C}}$ while the lizard thermoregulates, moving often to maintain $T_b$ at its preferred temperature $T_{set} = 40.5^\circ{\text{C}}$.

A simple way to investigate how thermoregulatory strategy is affected by $T_e$ is to use an environmental temperature function that is time-independent. In particular, we use a thermal gradient of the form (6) where both $K_{T_e}$ and $m_e > 0$ are constant. By increasing or decreasing $m_e$, we manipulate the distance over which a thermoregulating animal must travel in order to arrive at its preferred body temperature as depicted in Figure 5. The locomotory cost of $T_e$ is inversely related to the environmental temperature gradient ($m_e$) and we use the quantity $1/m_e$ to define the locomotory cost of $T_e$. 
may be computed from Equation (6) as $x = \frac{T_e}{m_e x + 20^\circ C}$ and $T_{set} = 32.7^\circ C$ (preferred $T_b$ for the rattlesnake). When $m_e = 0.6^\circ C m^{-1}$ a rattlesnake at $x = 15 m$ will have $T_e = 29^\circ C$ and must move a distance $d_1 = 6.1 m$ to arrive at $T_e = T_{set}$. When $m_e = 0.4^\circ C m^{-1}$, a rattlesnake at $x = 15 m$ will have $T_e = 26^\circ C$ and must move a distance $d_2 = 16.6 m$ to arrive at $T_e = T_{set}$. The quantity $1/m_e$ defines the locomotory cost of $T_e$ (as $d_1 < d_2$ and this cost increases with $1/m_e$).

Figures 6–8 compare the locomotory cost of $T_e$ for both a low ($1/m_e = 10$) and high ($1/m_e = 100$) cost. Two hundred simulations resulted in the frequency distributions shown for body temperature and distance moved. We use $\Delta t = 1$ min per iteration over a 12 h photophase (720 iterations). If the ectotherm moves, the velocities from Table 1 then yield distances of 3.0 m per iteration for the lizard data depicted in Figure 6 and 1.67 m per iteration for the rattlesnake data depicted in Figures 7 and 8. The environmental temperature is as in Equation (6). The temperature gradient $m_e$ is held constant in each simulation. The preferred temperature $T_{set}$ is fixed at $x = 0$ and $K_T = T_{set}$ so that $T_e(0,t) = T_{set}$ for all $t$. The changes in $T_e$ per iteration are $\Delta T_e = 3.00 \Delta m_e = 3.00m_e$ for the lizard and $\Delta T_e = 1.67 \Delta m_e = 1.67m_e$ for the rattlesnake and an ectotherm’s precision in maintaining $T_{set}$ will obey $|T_b - T_{set}| \geq \Delta T_e$.

At the start of each simulation, the position of the ectotherm is $x = x_0$ and $T_e(x_0,0)$ is randomly selected as $T_e(x_0,0) = \chi \cdot CT_{min} + [1 - \chi] \cdot CT_{max}$ where $\chi$ is the MATLAB function rand(1) which returns a pseudorandom value drawn from the standard uniform distribution on the open interval (0,1). In each of Figures 6–8, we compare the low cost and high cost $T_e$ using the same set of randomly generated starts $T_e(x_0,0)$. In general, we assume that $T_b(x_0,0) = T_e(x_0,0)$ (i.e. the ectotherm has a body temperature which has been initially equilibrated to $T_e$) so that $x_0$ may be computed from Equation (6) as $x_0 = (T_b(x_0,0) - T_{set})/m_e$. If $T_e(x_0,0)$ was less than $CT_{min} + 1$ or greater than $CT_{max} - 1$, we set $T_b(x_0,0) = CT_{min} + 1$ and $T_b(x_0,0) = CT_{max} - 1$, respectively. This was done to increase the probability that $T_b$ did not reach its lower thermal limit $CT_{min}$ or its upper thermal limit $CT_{max}$ when $T_b$ was initially close to these limits. Any data sets for which $T_b$ exceeded its thermal limits when $T_e(x_0,0)$ was close to $CT_{max}$ or $CT_{min}$ were not used.

In Figures 6 and 7, the natural thermoregulatory strategies for the lizard and rattlesnake with movement probabilities shown in Figure 3. In addition, Figure 8 shows the simulation results when a rattlesnake is forced to thermoregulate by altering its movement probability to obey (r1), (r2),
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Body Temperature ($^\circ$C)

Frequency \times 10^{-2}

Distance Moved (m)

Frequency \times 10^{-2}

Figure 6. Frequency distributions of body temperature ($T_b$) and distance moved for a thermoregulating lizard with low cost (top) and high cost (bottom) $T_c$ from Equation (6) with $m_c$ as indicated and $K_T \equiv T_{set} = 40.5^\circ$C. Here the natural thermoregulatory strategy for the lizard with movement probability $P_0(T_b)$ as shown on the left in Figure 3 is used.

and (r3) in Section 2.1 and using $P_0(T_b)$ from Equation (2) and the parameters for the rattlesnake in Table 1. All of the histograms were generated using the software R version 2.10.1 [34].

4. Theoretical benefit and cost of thermoregulatory strategy

For each simulation, the thermoregulatory costs are computed at each iteration as a maintenance cost (independent of movement) and a locomotory cost. In particular, if the distance moved is $\Delta x$ with an average body temperature $\overline{T_b}$, then the cost is

$$c(\Delta x, \overline{T_b}) = \alpha_S e^{\beta_S \overline{T_b}} \Delta t + d_M \Delta x.$$  \hspace{1cm} (8)

The parameters $\alpha_S = 0.0033$ ml O$_2$ min$^{-1}$, $\beta_S = 0.0847$, and $d_M = 0.0461$ ml O$_2$ m$^{-1}$ are computed from Anderson and Karasov [3]. The benefits of thermoregulation are computed using the average body temperature and the fitness function in Equation (1) as $b(\overline{T_b})$. The total benefit to cost ratio for a simulation is then determined by summing $b(\overline{T_b})/c(\Delta x, \overline{T_b})$ over the entire simulation.

Figure 9 depicts benefit to cost ratio as a function of $m_c$ using the lizard parameters from Table 1. Both behaviours, thermoregulation (the natural strategy of the lizard) and thermoconformity, were simulated using the lizard parameters from Table 1. The benefit $b(T_b)$ from Equation (1) and $P_0(T_b)$
Figure 7. Frequency distributions of body temperature ($T_b$) and distance moved for a thermoconforming rattlesnake with low cost (top) and high cost (bottom) $T_e$ from Equation (6) with $K_T \equiv T_{set} = 32.7^\circ C$. Here the natural thermoregulatory strategy for the snake with movement probability $P_1(T_b)$ as shown on the right in Figure 3 is used. For high cost $T_e$, there were a small number of distances that were greater than 100 m while for the low cost $T_e$, there were no distances more than 70 m.

from Equation (2) are as shown in Figure 3 while $P_1(T_b)$ was computed as described in Section 3.1. Each data point corresponds to the averaged total benefit to cost ratio (averaged over 200 simulations) with cost computed as in Equation (8). The simulations were performed just as those described in the previous section to generate the data for the frequency distributions in Figures 6–8. The locomotory cost increases with $1/m_e$ as depicted in Figure 5. The thermoconforming lizard rarely moves and its benefit to cost ratio is essentially constant. The thermoregulating lizard moves often and its benefit to cost ratio decreases monotonically with $1/m_e$. At low cost, the optimal strategy (highest benefit to cost ratio) is to thermoregulate and at high cost the optimal strategy is to thermoconform. Our model supports Huey and Slatkin’s [22] model and experimental evidence [46].

Figure 10 depicts the averaged total benefit to cost ratio as a function of average body temperature using the lizard parameters from Table 1. The benefit $b(T_b)$ from (1) and $P_0(T_b)$ from Equation (2) are as shown in the left in Figure 3. The thermal gradients were fixed at either $m_e = 0.005$ or $m_e = 0.01$. The initial position of the ectotherm was randomly selected to vary the distance from the position at $x = 0$ of its preferred body temperature $T_{set} = T_e(0, t)$ (with $K_T \equiv T_{set}$ in Equation (6)). Specifically, we initially placed the ectotherm at a position $x_0 = (T_0 - T_{set})/m_e$ obtained by setting the left-hand side of Equation (6) to $T_0$ and solving
Figure 8. Frequency distributions of body temperature \( T_b \) and distance moved for a thermoregulating rattlesnake with low cost (top) and high cost (bottom) \( T_e \) from Equation (6) with \( K_e \equiv T_{\text{set}} = 32.7^\circ \text{C} \). Here the rattlesnake is forced to thermoregulate by altering its movement probability to obey (r1), (r2), and (r3) in section 2.1 and using \( P_0(T_b) \) from Equation (2) and the parameters for the rattlesnake in Table 1.

for \( x = x_0 \). Here the initial temperature \( T_0 = T_e(x_0,0) \) was randomly selected from a normal distribution with mean

\[
\mu_k = T_\ell + (k - 1) \cdot \frac{T_r - T_\ell}{14}, \quad k = 1, \ldots, 15,
\]

where \( T_\ell = T_{\text{set}} - 5^\circ \) and \( T_r = T_{\text{set}} + 2^\circ \) and fixed variance \( 1^\circ \text{C} \). The duration and step lengths used in each simulation was as described previously. At the end of each simulation the total benefit to cost ratio and the average body temperature were computed. Each of the 15 data points depicted in Figure 10 were obtained after averaging these over 200 simulations with \( \mu_k \) fixed at one of the values in Equation (9).

The total distance travelled and the range of environmental temperatures encountered by the ectotherm over the time course of a simulation increased as the difference between \( T_0 \) and \( T_{\text{set}} \) increased. Martin and Huey [30] used the benefit function (1) and determined that optimal body temperature (the body temperature that maximizes total fitness over time) in a fluctuating environment will be below the body temperature \( T_{\text{set}} \) which maximizes instantaneous fitness \( b(T_b) \) from Equation (1). (They conjecture that this is due to the skewness in \( b(T_b) \)). Thermoregulatory costs are ignored in [30]. Maximal benefit to cost ratio in Figure 10 is below \( T_{\text{set}} \). Thus our model, which accounts for cost as well as benefit, is consistent with [30].
Figure 9. The averaged total benefit to cost ratio (averaged over 200 simulations) versus the inverse of the environmental temperature gradient $m_e$. The dashed horizontal line with ◦ data points is the thermoconforming lizard while the monotonically decreasing curve fit to the * data points is the thermoregulating lizard. The locomotory cost is inversely related to $m_e$ as depicted in Figure 5. The optimal strategy for low cost $T_e$ ($1/m_e$ small) is to thermoregulate while the optimal strategy for high cost $T_e$ ($1/m_e$ large) is to thermoconform.

Figure 10. The averaged (total) benefit to cost ratio as it depends on the average body temperature using the lizard parameters in Table 1. The data points * are for $m_e = 0.005$ and ◦ are for $m_e = 0.01$. The vertical dashed line is at $T_b = T_{set}$. The optimal body temperature (the body temperature that maximizes total fitness over time) is below the body temperature $T_{set}$ which maximizes instantaneous fitness $b(T_b)$ at $T_b = T_{set}$ for both $m_e = 0.005$ and $m_e = 0.01$. 
5. Conclusions

Here we have introduced a simple biased random-walk model with fixed movement lengths and fixed time increments to investigate the theoretical costs associated with thermoregulatory strategy of an ectotherm. We simulate our model on a one-dimensional spatial domain and model both a time- and space-dependent environmental temperature gradient. The probability an ectotherm will move depends on both \( T_b \) and thermoregulatory strategy where thermoconformers are least likely to move (wide tolerance of \( T_b \)) and thermoregulators are most likely to move (narrow tolerance of \( T_b \)). Movement is biased on thermal quality of habitat (i.e. thermotaxis) which is measured by the fitness function, a function of \( T_b \) which is optimal at \( T_{set} \). In our model, an ectotherm will tend to move in a direction which increases its fitness function and reduce \( |T_{set} - T_b| \). Simulated ectotherm movements are consistent with thermoregulatory strategy (Figure 4).

Our model indicates that thermoconformity as a thermoregulatory strategy may provide an energetic advantage in reduced exploratory movements of the thermal environment with minimal cost to \( T_b \) for eurythermic species. However, many stenothermic species [7] must actively thermoregulate and require the precise regulation of \( T_b \) to maintain optimal physiological performance. Although both of these thermoregulatory strategies have associated benefits and costs, these thermoregulatory strategies have phylogenetic constraints that may be associated with species-specific performance traits and life histories. For example, the behaviours used to actively thermoregulate and maintain a preferred \( T_b \) are tied to the energy intake and expenditure of an active foraging strategy [3]. Similarly, sit-and-wait foragers such as the timber rattlesnake (\( \textit{Crotalus horridus} \)) must remain sedentary in a hunting posture [37] and thermally conform to a particular microhabitat to ensure foraging success.

There is no doubt that physiologies [32], life histories (e.g. maximum body size), and behaviours (e.g. modes of foraging) have influenced or have provided a selective force on the thermoregulatory requirements and the thermal dependence of physiological performance among ectothermic species. Thus, more temperature tolerant or eurythermic species have different associated benefits and costs than stenothermic species allowing for ecological differences such as habitat utilization [38,39].

Here we demonstrate how the associated increase in thermoregulatory costs influence the distribution of \( T_b \) and movement in a thermoregulating lizard (e.g. \( \textit{Cnemidophorus tigris} \)) and a thermoconfoming rattlesnake (e.g. \( \textit{Crotalus horridus} \)). The model indicates that a precise and effective regulation of \( T_b \) is possible by a lizard with minimal movement at a low thermoregulatory cost (Figure 6). This thermoregulatory accuracy and effectiveness [41] is defined as the lizard’s ability to effectively maintain its \( T_b \) near \( T_{set} \). However, thermoregulatory effectiveness decreases as thermoregulatory cost increases from \( 1/m_e = 10 \) to 100. With increased thermoregulatory cost, the difference between operative \( T_e \) and \( T_{set} \) also increases (defining low thermal quality [38]) and the lizard must move greater distances to reach and maintain \( T_{set} \) (Figure 5). We can see the result of increased thermoregulatory cost as the frequency distributions of \( T_b \) and movements for the lizard dramatically changes from \( 1/m_e = 10 \) to 100. The greater distribution of \( T_b \) indicate a reduction in thermoregulatory precision and effectiveness and the lizard expends much greater energy (indicated by the now wide distribution of movement distances for \( 1/m_e = 100 \)) in an attempt to regulate its \( T_b \) around 41° C as shown in Figure 6.

Conversely and comparatively, we see little consequence to \( T_b \) or movement with an increased thermoregulatory cost for the thermoconforming rattlesnake. Such a eurythermic species may experience a wide range of body temperatures (Figure 2) but expends little energy in movement for both thermoregulatory costs of \( 1/m_e = 10 \) and 100 (Figure 7). The model indicates that there is little consequence to increasing thermoregulatory costs or changes in thermal quality under the non-thermoregulatory strategy of thermoconforming to \( T_e \). However, we wished to investigate
how the potential costs of a thermoconforming rattlesnake would change if it were behaviourally forced to actively thermoregulate as a lizard. The utility in this simulation model is that we may manipulate parameters of physiological performance traits that are outside the natural behaviours of large-bodied rattlesnakes and observe how these forced behaviours may be maladaptive for the species. With the same physiological performance parameters, we forced the rattlesnake to thermoregulate and observed a dramatic difference in both its thermoregulatory effectiveness and movement pattern for $1/m_e = 10$ thermoregulatory costs between a conforming (Figure 7) and regulating (Figure 8) rattlesnake. Although the rattlesnake now maintains a precise $T_b$, the consequence is an increase in movement non-indicative of a sit-and-wait forager. This effect is exacerbated with the increased thermoregulatory cost of $1/m_e = 100$ (Figure 8, top panels) where there is now no thermoregulatory precision and even greater energetic cost of movement.

Here we specifically demonstrate that a rattlesnake would experience a significant metabolic cost associated with movement and an attempt to thermoregulate $T_b$. Although thermal regulation and maintenance of an optimal $T_b$ may indirectly influence fitness [21], some ecologists further stress the importance of other biotic factors [35,36,40,43] and that under field conditions, activities such as foraging may take precedence over thermoregulation [28,33]. Thus, temperature may not always be the central concern of ectotherms, especially of those species living in moderate thermal environments or having the physiological ability to tolerate wide ranging $T_e$. Both the physical environment and species-specific traits may set fundamental constraints upon activity and behaviour, including those involving thermoregulation. We hope that our simulation model and theoretical investigation for thermoregulatory benefits and costs helps support the idea that eurythermic species with broad tolerances and physiological performance may sacrifice optimal $T_b$ to ultimately conserve energetic costs [25,28].

Our model, as with any mathematical model, has inherent limitations. We use a fixed stepsize to model average speed. Many random walk models include a variable stepsize, which is consistent with actual movement patterns [45]. A natural way to include variable stepsize in our model is to let the movement speed depend on $T_b$ (since time steps are fixed and stepsize is proportional to speed). We ran simulations and collected data using the speed $v$ from Table 1 scaled by the fitness function $b(T_b)$ shown in Figure 3 for the lizard. Thus, the maximum speed is $v = 3.00$ at $T_b = T_{set}$ and speed decreases to zero at the lower and upper thermal limits $CT_{min} = 17.0$ and $CT_{max} = 46.0$. The simulation results show that the frequency distributions are not qualitatively different than those depicted in Figure 6. The lizard is able to maintain $T_b$ near $T_{set}$ in both a low cost and high cost $T_e$ (with more variability in the high cost $T_e$). Similarly, after computing benefit to cost ratio as in Figure 9 as a function of cost of $T_e$ and for a given thermoregulatory strategy, the benefit-cost ratio decreases monotonically as the cost of $T_e$ increases and the optimal strategy for low cost $T_e$ is to thermoregulate while the optimal strategy for high cost $T_e$ is to thermoconform. Another limitation of our model is that simulated movement paths are not verified experimentally. Laboratory or field data related to thermotaxis in reptiles could be used for a quantitative analysis of movement [2,45]. Finally, our model accounts for thermotaxis in one spatial dimension, but discounts other environmental affects on movement (e.g. predator–prey interactions) and multiple spatial dimensions. These limitations suggest that future work on this model and other models of thermotaxis in small- and large-bodied ectotherms are necessary to understand thermoregulatory strategy in a wider context.

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