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Net energy gain as a function of body mass and temperature

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Abstract

Empirical studies have reported that fitness first increases but eventually decreases as temperature increases, at least for ectotherms. Although body mass is a key intrinsic factor that influences fitness, its role in shaping such hump-shaped thermal performance curves remains an open question. In this work, we ask whether performance as a function of temperature broadens, shrinks, or shifts when body mass increases. We build a model that integrates ecological (foraging), physiological (metabolism), and thermodynamic (warm-up) processes and asks how their interplay shapes the daily net energy gain, which we use as a proxy for performance. We found that there is no single expected relationship of how the thermal performance curve changes with body mass, but foraging shapes its upper limit and warm-up ability determines its lower limit. More generally, the model aims to fuel feedback between empirical and theoretical work by identifying important parameters and relationships amenable to empirical investigations, and by proposing how the three types of processes may influence species' geographic distribution.

Introduction

16 Temperature is a crucial abiotic factor that influences performance, including growth, fecundity, mortality, and other components of fitness (Birch 1953; Angilletta et al. 2002; Huey and

18 Stevenson 1979; Savage et al. 2004). The thermal performance curve describes how performance changes as a function of temperature (Huey and Stevenson 1979; Angilletta 2009; Amarasekare

20 and Savage 2012). In addition to its intrinsic ecological and evolutionary importance, the thermal performance curve of a species is a critical factor in assessing its vulnerability to climate change

22 (Calosi et al. 2008; Deutsch et al. 2008; Kingsolver et al. 2011). For instance, species in the tropics seem to have narrower thermal performance breadth and consequently are more vulnerable to

24 an increase in temperature (Deutsch et al. 2008).

A classical empirical result—at least for ectotherms—is that the thermal performance curve

26 is non-monotonic and skewed to the left, meaning that the optimal temperature (the peak of the curve) is closer to the critical maximum temperature than to the critical minimum temperature

28 (Barlow 1962; Huey and Berrigan 2001; Angilletta 2009). The theory underlying this observation has been explored from several angles. One explanation focuses on how enzyme reaction

30 rates depend on temperature. The models combine the denaturation of enzyme, which is typically a unimodal function of temperature, with the catalytic reaction rate, which increases expo-

32 nentially with temperature, to explain the left-skewed curve (Van der Have and De Jong 1996; Van der Have 2002; Ratkowsky et al. 2005; Kingsolver 2009). A more inclusive approach is to

34 break down thermal performance into three components: development, fecundity, and mortality (Amarasekare and Savage 2012). The functional shapes of each of those components and how

36 they intersect thus determine the basic properties of the curve (the optimium, minimum, maximum, and skewness). A different framework, called Dynamic Energy Budget (DEB) modeling,

38 describes performance based on how energy (from food) is assimilated and then allocated to different needs such as growth, maintenance, and reproduction (Kooijman 2009). DEB models are

40 not specifically constructed to investigate the hump-shaped pattern, but when detailed species-specific data are available, DEB models have the power to reproduce patterns such as how the

42 body size of an individual or the number of offspring it produces changes over its lifetime (Nisbet

et al. 2000).

Such models describe the qualitative and quantitative shapes of performance curves and how they differ among individuals, but they are not designed to probe the traits that underlie those differences. One intrinsic trait that might underlie variability in thermal performance curves is body size, which influences many physiological and ecological processes (Calder 1984; Schmidt-Nielsen 1984; Peters 1986). Empirical data show that body size is associated with temperature in a variety of contexts. At the global scale, Bergmann's rule states that body size tends to increase with decreasing temperature (Bergmann 1847; Blackburn et al. 1999). At the physiological level, an individual grows larger under a colder thermal regime (Van Voorhies 1996), and the resting metabolic rate scales simply with body size and temperature (Kleiber et al. 1947; Peters 1986; Gillooly et al. 2001; Brown et al. 2004). Despite the intimate relationship between body size and temperature, theoretical studies that link body size and performance do not yet account for the explicit effect of temperature (e.g., Yodzis and Innes 1992; Brown et al. 1993). A key open question thus remains, how does the thermal performance curve change with body size?

When considering thermal performance, the role of behavioral thermoregulation is often overlooked (Kearney et al. 2009). A particular example is the warm-up phase for ectotherms, especially insects. Because muscle needs to be above a certain temperature to function properly, when the environment is below that temperature, warm-up is necessary (e.g., Heinrich 1975). In some species, like dung beetles, the duration and completion of warm-up is important because it is crucial to arrive on site before resources are degraded or depleted (Hanski and Cambefort 1991). The ability to warm up has further been hypothesized to cause diel partitioning, which facilitates coexistence (Viljanen 2009). Intuitively, large ectotherms warm up more slowly than smaller ones because large individuals have a smaller surface area-to-body size ratio and thus a reduced capacity to transfer heat from the environment to the body. The warm-up aspect of thermoregulation, its dependence on body size, and especially its role in shaping thermal performance has not been explored.

Here, we build a theoretical model to investigate how the thermal performance curve varies with body size. We define performance as net energy gain, which is the difference between

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total energetic gain and energetic cost. We look at the effects of three processes in shaping net energy gain: physiological processes of metabolism, ecological processes of resource availability and foraging, and behavioral thermodynamic processes of warm-up. The model is conceptually valid for heterotherms, but to include more explanatory detail, we narrow our taxonomic scope to insects. In particular, the model is best suited for fully-grown, adult insects that are income breeders, such as dung beetles and bees. In general, we find that metabolism plays only a secondary role in shaping thermal performance. Instead, resource availability and allometric scaling of foraging are key in defining the upper thermal limit, whereas the ability to warm-up sets the lower thermal limit.

Model Description

The model investigates the daily performance of an adult insect with fixed body size. We define performance as net energy gain, which is the difference between energetic gain and loss during the day. The energetic gain is the amount of energy acquired during solitary foraging, whereas the energetic loss is the sum of metabolic costs incurred while resting and during foraging activity. The model contains a thermoregulation phase that precedes activity. It thus applies to insects that must complete warm-up because muscles are only operational when they are above a certain temperature. The model is built by describing relationships among several variables (fig. 1a). First, we describe the external properties of the environment. Second, we use empirically derived relationships to model the rate of energetic loss and gain as a function of body size and temperature. Third, we use thermodynamic principles to describe changes in body temperature during warm-up. Finally, we integrate these components to define net energy gain. We then further justify the functional forms and parameters employed by our model.

Environment

We consider three properties of the environment: the temperature, the intensity of solar radiation, and the amount of available resource. We define environmental temperature T_e as the temperature felt by the individual while inactive. Because insects are small, we assume that environmental temperature does not depend on body size. Our model derivation here does

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not account for temperature variation during the day, but we show in the Appendix that daily temperature changes do not affect the qualitative results.

We assume that at any given time of the day, the intensity of solar radiation is $S_R = S_0 \cos(\psi)$, where ψ is the zenith angle and $S_0 = 1361\,\mathrm{Wm}^{-2}$ is the maximum solar radiation at noon. Solar radiation is needed to generate heat during the warm-up phase of the model. See the Appendix and Campbell and Norman (2012) for more details on how ψ depends on latitude and the day of the year as well as how we obtained the time of sunrise.

We denote by R the daily quantity of resource available. The energy density per unit of resource mass is ρ. Poor environments in terms of resource can thus be obtained by low quantity R or low quality ρ.

Energetic cost

Resting metabolic rate

Following Brown et al. (2004), we assume that resting metabolic rate increases with body size and temperature such that

$$e_b(z,t) = a_1 z^{b_1} \exp\left(\frac{-E}{k(T_b(t) + 273.15)}\right), \tag{1}$$

where z is body mass, $T_b(t)$ is the body temperature at time t in Celsius, E and k are respectively the activation energy and the Boltzman constant (this is the Arrhenius equation), and a_1 and b_1 are constants which we call respectively the coefficient and exponent. At rest, the body temperature of the individual matches that of the environment (e.g., Bartholomew and Heinrich 1978) so that $T_b(t)$ in equation (1) can be replaced by $T_e(t)$.

Active metabolic rate

For simplicity and because it is poorly characterized empirically, we assume that the functional form of the active metabolic rate is the same as that of the resting metabolic rate, i.e.,

$$e_a(z,t) = a_2 z^{b_2} \exp\left(\frac{-E}{k(\max[T_w(z_{th}), T_e(t)] + 273.15)}\right), \tag{2}$$

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where T_w is the minimum thoracic temperature that would permit foraging. The warm-up phase (see section Warm-up below) determines whether an individual is able to warm up and eventually forage. Large-bodied individuals often have higher temperature during activity, so we allow T_w to depend on z_{th}, as in Bartholomew and Casey (1977*b*):

$$T_w(z_{th}) = c_0 + c_1 z_{th}. \tag{3}$$

Here, z_{th} is the mass of the thorax, and c_0 and c_1 are two free parameters. Thus, unlike resting metabolic rate (eq. [1]), the effect of temperature on active metabolic rate depends on body size. The use of the function 'maximum' (max) is a rough approximation such that when the environmental temperature is too high, there is an additional cost of foraging, such as the additional energy used to avoid overheating. To ensure that the cost of activity exceeds that of resting, we assume that the parameters of the active metabolic rate are not less than the parameters of the resting metabolic rate, i.e., $a_2 \geq a_1$ and $b_2 \geq b_1$.

Energetic gain: foraging

We define foraging rate $g(z)$ as the average amount of resource an individual collects per unit of time. Here, given that absolute metabolic cost increases with body size (eq. [2]), we assume that foraging rate also increases with body size, and for simplicity, we assume a power law,

$$g(z) = a_3 z^{b_3}. \tag{4}$$

This equation pools together different activities such as searching for and handling the resource. We will not assume any particular value for b_3, and our results explore its role in shaping thermal performance. If small individuals are more agile, equation (4) takes a concave shape (fig. 1b). Alternatively, if large individuals have better searching ability (e.g., they find more distant resources), equation (4) takes a convex shape. Finally, the rate of energy gain includes both foraging rate and resource quality:

$$e_g(z) = g(z)\rho = a_3 z^{b_3} \rho. \tag{5}$$

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Warm-up

When environmental temperature is low, an individual needs to reach sufficient internal temper-

ature to be active for foraging. In general, warm-up behavior would include the when, where,

and how of warming up. Here, however, we focus on whether or not warm-up can be com-

pleted, and if so, the duration of warm-up. Furthermore, insects do not need to warm up the

entire body, only the thorax where most of the muscles are (Kammer and Heinrich 1974; Heinrich

1975; Bartholomew and Heinrich 1978; Verdú et al. 2012). Therefore, we track the temperature of

the thorax, T_w (eq. [3]), and so focus on thoracic mass, z_{th}, rather than body mass.

The most common strategy for warming up is to absorb solar radiation. Heat is transfered to

the thorax from the surface of the body by passive conductance (Bakken 1976). A second strategy

is to endogenously generate heat by contracting muscles against each other, similar to shivering

(e.g., Kammer and Heinrich 1974). We assume that the frequency of contraction increases linearly

with thoracic temperature: $f(T_{th}) = a_w T_{th}$ for $T_{th} > 0$ and 0 otherwise. We loosely use the term

"endotherm" for insects that have the ability to generate heat endogenously during warm-up

($a_w > 0$), and "ectotherm" for insects that do not generate heat ($a_w = 0$).

Coupled differential equations track changes in the thoracic temperature and non-thoracic

temperature (i.e., the rest of the body) during warm up. For geometrical simplicity, we assume

that the body is half of a sphere and the thorax constitutes half of the body. The surface of the

thorax and the non-thorax can be easily calculated given the mass and the density of the insect

(see Appendix).

Change in thoracic temperature, T_{th}, is based on heat exchange between the thorax and the

non-thorax. We have

$$\frac{dT_{th}}{dt} = \frac{1}{s z_{th}} \left[z_{th} e f(T_{th}) + A_{th} K_1 (T_r - T_{th}) \right], \tag{6}$$

where s is the specific heat capacity, e is the calories generated per contraction and per gram

of muscle (Kammer and Heinrich 1974), A_{th} is the total surface of the thorax, and K_1 is the

conductance between the thorax and the non-thorax.

Change in the non-thorax temperature (T_r; the subscript r is to remind us it is the rest of

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the body) is based on thermal exchange between the surface of the individual and the external environment. We have

$$\frac{dT_r}{dt} = \frac{1}{sz_r} \left[-A_{th}K_1(T_r - T_{th}) \right] + \frac{1}{sz_r} \left(A_r \left[-c_p K_2 h(T_r - T_e, V) - \sigma\varepsilon T_r^4 + \sigma\varepsilon T_e^4 + r_3 S_R \right] \right), \quad (7)$$

where $\varepsilon = 0.935$ is the emissivity of a gray body, u is wind speed, V is the volume of the insect, and A_r is the surface area of the non-thorax (simply the surface of the whole body). We consider two forms of convection here, with $h(T_r - T_e, V) = (T_r - T_e)^{1.25}(1/V)^{1/12}$ for free convection (no wind) and $h(T_r - T_e, V) = 1.4 \times 0.135\sqrt{u/V^{1/3}}(T_r - T_e)$ for laminar convection (Campbell and Norman 2012). The conductance K_1 is defined above, and c_p is the specific heat capacity of the air. The constant K_2 controls convection between the body and the air (Campbell and Norman 2012).

The last term of equation (7) is an approximation of more the detailed equation in Campbell and Norman (2012). Here, we ignore view factors, reflected radiation and so on, and pool every source of radiation into $\sigma\varepsilon T_e^4$ and S_R. The parameter r_3 is used to scale and summarize the quantity of absorbed solar radiation.

We solve the ODE system (equations (6)–(7)) numerically using the function NDSolve in Mathematica. By solving the equations through time, we can find if the minimum temperature required for activity (T_w) is reached. If it is, we can also solve for the duration of the warm-up τ_w from $T_{th}(\tau_w) = T_w$.

Net energy budget

We now integrate all the components above to calculate the energy budget during a 24-hour period. Daily activity consists of resting, warming up, and foraging activity. We assume activity occurs in one block of time and thus require only one warm-up phase. We use t to denote the time of the day and τ for duration. Total foraging time, τ_f, can be fixed, or it can be a function of resource availability R, with $\tau_f = R/g(z)$. (We always assume that an individual can gather at most 50 times its body mass.) If warm-up cannot be completed, foraging does not occur and $\tau_f = 0$. If warm-up is completed, we penalize the individual by subtracting the duration of

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warm-up τ_w from the total foraging time τ_f. Referring to equation (5), the total daily energetic gain is given by

$$E_g(z, \tau_f - \tau_w) = (\tau_f - \tau_w)e_g(z).$$ (8)

If we assume that warm-up starts at t_i the total daily energetic cost is

$$E_d(z, \tau_f) = \int_0^{t_i} e_b(z, t)dt + \int_{t_i + \tau_w}^{t_i + \tau_f} e_a(z, t)dt + \int_{t_i + \tau_f}^{24} e_b(z, t)dt,$$ (9)

where e_b is defined in equation (1) and e_a in equation (2). The first and the last term on the right hand side calculate the total energetic cost when the individual is at rest from $t = 0$ to $t = t_i$ (before foraging) and from $t = t_i + \tau_f$ to $t = 24$ (after foraging). The middle term calculates the total energetic cost of foraging from $t = t_i + \tau_w$ to $t = t_i + \tau_f$. Our calculations show that the energetic cost while warming up from $t = t_i$ to $t = t_i + \tau_w$ is negligible, for both endotherms (actively shivering) and ectotherms (passively basking). We thus omit it from equation (9), in accord with empirical findings (Heinrich 1975).

Daily net energy gain is obtained from the difference between energy gain from foraging (eq. [8]) and total energy expended (eq. [9]), i.e.,

$$E_n(z, \tau_f) = E_g(z, \tau_f - \tau_w) - E_d(z, \tau_f).$$

Power law and parameter justifications

Our model assumes that the relationships between body size, metabolic rate, and foraging rate are represented by power laws. A general pattern is that resting metabolic rate scales with body size with an exponent $b_1 = 0.75$ (eq. [1]), which has been reported from unicellular organisms to mammals (Kleiber et al. 1947; Peters 1986; Gillooly et al. 2001; Brown et al. 2004). Although there is a debate about the actual values (e.g., Isaac and Carbone 2010), we adopt that value to diminish the number of free parameters, allowing us to explore the values of other exponents that are less-well established.

The power law relationship for active metabolic rate has much less empirical grounding, with

few studies measuring it for a range of body sizes. A notable exception is work by Bartholomew

and Heinrich (1978), who found a power law with exponent $b_2 = 1.17$. More studied is metabolic

scope, which is the ratio of maximum active metabolic rate to resting metabolic rate. Many

factors such as foraging mode (flying vs. walking) yield a substantial variation in metabolic scope.

Oxygen consumption during activity can range from 2 to 100 times that of resting (Bartholomew

and Heinrich 1978; Bartholomew et al. 1981, 1985; Chown and Nicolson 2004; Niitepõld 2010)

although a typical value would be between 10 to 40-fold increase (Bartholomew et al. 1981;

Niitepõld 2010).

Recent studies of the rate of energetic gain have recovered a power law relationship to body

size (Pawar et al. 2012; Maino and Kearney 2015). There seems to be no single exponent b_3.

For instance, the exponent can depend on the dimension of the search space, with a value of

0.85 in two dimensions or 1.06 in three dimensions (Pawar et al. 2012). Body size can further

influence other processes. For instance, walking speed can scale with a power 0.29 (Peters 1986),

or dominance competition exerted by larger individual can yield an exponent greater than one.

Our goal, however, is not to assert the homogeneity of these values but instead to explore the

consequences of their heterogeneities.

The effect of temperature could be modeled by multiplying the body mass scaling metabolic

rate with a factor Q_{10}, which denotes the change in metabolic rate with a 10°C increase in the

body temperature (Precht et al. 1973). We however opted for the Arrhenius equation (eq. [1]) used

by Brown et al. (2004) because it reduces the number of free parameters, and it also approximates

the temperature effect for $Q_{10} = 2.45$.

The model parameter values will of course vary across organisms and environments. For

instance, the coefficient of resting metabolic rate or exponent of foraging rate might be different

for ants and dung beetles. Our goal is not to predict specific energetic values, however, but to

explore the effects of these general processes on thermal performance curves. Our conclusions

are thus best interpreted as applying across individuals within species, or across species that are

closely related. Table 1 summarizes the range of parameter values considered in our analyses.

Results

Our main interest is how net energy gain varies as a function of body mass and temperature.
We investigate how the thermal performance curve differs—in width, location, and shape—for
individuals of different body mass. We start by exploring the role of scaling with body mass,
temperature, and resource availability, without considering warm-up. We then focus on warm-
up only. Finally, we report the combined effects of all processes on the thermal performance
curve. Throughout, we emphasize the diverse outcomes that are possible from our model rather
than provide an exhaustive description of the effects of each parameter.

Does net energy gain increase or decrease with body mass?

Larger individuals expend less energy per unit mass (they have a lower mass-specific resting
metabolic rate; $b_1 < 1$ in eq. [1]), so it is intuitive that net energy gain increases with body mass.
Our model indeed shows this behavior, at least when resources are abundant and foraging time
is not constrained (fig. 2a). In contrast, when resource quantity is more limited, net energy gain
peaks at intermediate body mass (fig. 2b) because not enough energy can be obtained to sustain
the high absolute metabolic cost of large-bodied individuals. The scaling of foraging rate, b_3,
does not affect these qualitative patterns.

Alternatively, when foraging time is limited, resource quality determines the form of net
energy gain. Net energy gain increases monotonically with body mass when resource quality
is high (fig. 2d), as when resource quantity is high (fig. 2a). Net energy gain may peak at
intermediate body mass, however, when resource quality is not too high (fig. 2c). Furthermore,
the foraging exponent b_3 affects these qualitative patterns. Our analytical results show that net
energy gain peaks at intermediate body mass if and only if $b_3 < b_2$ and resource quality is within
a certain range (see Appendix).

Net energy gain can also peak at intermediate body mass if the active metabolic rate is in-
creased, because larger individuals are penalized more strongly (fig. 2e, cf. fig. 2a). This effect is
exaggerated at higher temperatures, where again larger individuals pay a higher price (fig. 2f).
The exponent b_3 now dictates whether net energy gain always increases or eventually decreases

with body mass. Even if resources are unlimited, a concave foraging rate ($b_3 < 1$) means that foraging time increases with body mass. Consequently, larger individuals are active for a longer period of time and therefore pay a higher metabolic cost.

When foraging time is fixed, higher active metabolic rate again penalizes larger individuals (fig. 2g, cf. fig. 2d). Higher temperature does not change the qualitative pattern in this case, but net energy gain peaks at lower body mass (fig. 2h).

Overall, we find that there may or may not be an intermediate optimal body mass when considering only how metabolic costs and resource acquisition scale with body mass and temperature. Small individuals generally have low net energy gain because they gather little resource. Large individuals may also have low net energy gain when resource quality and quantity are low or their metabolic costs are high. Otherwise, larger body mass allows greater net energy gain.

When is warm-up completed?

We now set aside the metabolic and foraging processes in order to focus on the warm-up phase. The first component we look at is how the minimum temperature required for the completion of warm-up depends on body mass. With sufficient solar radiation, an individual can always warm up successfully (Appendix). In cold environments with limited solar radiation, however, it might not be possible for an individual to elevate its body temperature to the level needed for activity. Here, we explore how the ability to complete warm-up depends on body mass. For ectotherms and in the absence of wind, smaller mass is advantageous because decreasing body mass increases the surface area-to-body mass ratio and thus increases the ability to absorb more heat from the environment per unit of mass (fig. 3a, dashed line). Unlike the wind-free case, ectotherms of intermediate mass are able to complete warm-up under colder temperatures because individuals with small body mass are penalized due to increasing laminar convection (h in eq. [7]; fig. 3a). Large individuals are penalized because they have higher operative temperatures (eq. [3]). For endotherms, the minimum temperature for completing warm-up decreases with increasing body mass because more of the heat generated endogenously is retained within the body due to smaller surface area-to-body mass ratio (fig. 3a, thick line). In fact, there is a threshold body mass where endogenous heat production entirely cancels heat dissipation (for

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reasonable environmental temperatures), above which the ability to complete warm-up becomes independent of body mass (fig. 3a, thick line).

The second component of the warm-up phase we look at is the duration of warm-up. For ectotherms, the duration of warm-up always increases with body mass and decreases with temperature, as expected (fig. 3b). A exception is for small endotherms: warm-up can be much slower because a high rate of heat dissipation results in a positive but low warm-up rate (fig. 3b, thick lines). We found that the duration of warm-up is longer and more sensitive to body mass and temperature for ectotherms than for endotherms (fig. 3b). We show in the Appendix that these results are robust for a range of parameter values.

We thus learn that small ectotherms can warm up at lower temperatures than small endotherms, except in wind. When endotherms are able to warm up, however, they do so more quickly, especially for large individuals.

How does the thermal performance curve change with body mass?

We integrated the components above to see how they shape thermal performance and how thermal performance varies with body mass. First, we looked at how the inclusion or exclusion of warm-up can affect thermal performance. When the environmental temperature is high, warm-up is not needed and thus does not influence the net energy gain at high temperature, nor by extension the upper thermal limit (fig. 4abc). When the environmental temperature is low, warm-up can reduce the net energy gain because a portion of time that could be spent foraging is expended on warm-up (eq. [9]). Therefore, we focus here on cases where foraging time is limited.

The colder it gets, the longer it takes to warm up, the less time is left for foraging, and thus the lower the net energy gain (fig. 4bc, contrasted with fig. 4a). Because the variation in warm-up duration is more important for ectotherms than for endotherms (for different body mass and temperature, fig. 3b), the reduction in net energy gain as temperature decreases is more significant for ectotherms than for endotherms. In fact, warm-up time can be sufficiently long for large ectotherms that for low temperature, intermediate body mass is better (fig. 4c).

The most notable effect of resource acquisition is that the foraging exponent b_3 shifts the

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upper thermal limit in a size-specific manner. If foraging rate is a convex function of body
mass (fig. 5ac), performance breadth increases with body mass and larger individuals perform
better than smaller ones at any temperature. However, if foraging rate is a concave function of
body mass (fig. 5bd), larger individuals do not gather enough resource at high temperature to
offset their high metabolic costs, so smaller size is advantageous. These findings are generally
the same for endotherms and ectotherms, except that at low temperature, the warm-up process
favors large endotherms and small ectotherms (cf. fig. 4bc).

Finally, we looked at the effect of a reduction in resource availability, for example, due to
habitat loss. We found that the negative effect of resource limitation increases with body mass
(fig. 5e–h; see also fig. 2b). Reduction in resource availability not only shrinks the breadth of the
thermal performance curve for large individuals, but it also decreases their performance such
that small size can be advantageous along the entire temperature gradient.

Overall, our results show that no single relationship describes how thermal performance
curves change with body mass. Different conditions for resource acquisition can generate cases
where larger individuals have broader, shifted, or narrower thermal performance curves relative
to smaller individuals. Although we did not aim to present an exhaustive description of our
model's behavior, our results show the importance of the combined effects of thermoregulation,
metabolism, and ecology on the energy budget.

Discussion

We have developed a model to investigate how the thermal performance of a foraging adult insect
varies with body size. There is a dearth of theoretical work showing clearly how performance
(e.g., optimal temperature, critical minimum or maximum temperature) changes with body size.
We take a first step by exploring the role of metabolism, foraging, and thermoregulation, which
all scale allometrically with body size and all depend on temperature in shaping the net daily
net energy gain of an individual. We work up from basic physiological and ecological processes,
and we additionally put a strong emphasis on the role of thermoregulation for heterotherms
in shaping performance by analyzing in detail the temporal process of warm-up. We identify
several key parameters that have not been measured but which have important roles in shaping

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thermal performance across body size. We quantify how warm-up can decrease performance in cold environments. We further find that the performance curve in warm environments is limited by physiological and ecological processes such as resource availability, foraging, and metabolism. We do not claim that these are the only processes that shape thermal performance—other factors like competition, heat stress, and cold tolerance can be just as important—but net energy gain can be a first proxy for the actual (realized) thermal performance.

In this study, we compared performance across body sizes by calculating net energy gain. Clearly, net energy gain is a very simplistic approximation of performance or fitness. Kozłowski (1996) has pointed out that an energetic definition of fitness is incomplete, and adding size-dependent mortality shifts optimum body size. The energy currency in hand can be converted to, for instance, fecundity, by using additional power law relationships (Kooijman 2009). A notable missing component is the growth and development rate, but such questions have been investigated heavily (Van der Have and De Jong 1996; Kozłowski et al. 2004; Kooijman 2009). Another interesting extension would be to explicitly include competition in the model, as well as finding the optimal time to start warm-up and foraging, or to integrate net energy gain for a longer time span. Using energy as a core currency for understanding species performance is appealing, and many studies have embraced this approach. Energy budget models are now used to predict future species distributions (e.g., Buckley 2008), but the extreme detail and large number of parameters in DEB models (Kooijman 2009) prevents wide application. At the other end of the spectrum, there are parameter-poor models that can generate general insight, but their interpretation and application are hindered because the meanings of the parameters are unclear (e.g., Brown et al. 1993). Our model is situated in the middle of this so-called tactical-strategic spectrum (Holling 1966). Our main goal is to use parameters that are measurable with clear biological meaning yet not too specific to allow us to get general insight when integrating the role of physiology, ecology, and behavior into one framework.

Warm-up

Our work is unique in examining the thermodynamic features of insects to classify quantitative and qualitative patterns of warm-up. The warm-up process was investigated empirically during

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the 1970's and 80's for endothermic insects such as dung beetles, bees, and moths (Heinrich 1975; Bartholomew and Heinrich 1978; Bartholomew et al. 1981), but to the best of our knowledge no other model describes the entire warm-up phase let alone the effect of body size. In general, our model validates intuition about the effect of surface area-to-body mass ratio in heat absorption and heat retention: the ability to complete warm-up increases with decreasing size for ectotherms and with increasing size for endotherms. Our model also quantifies these relationships and thus provide a blueprint for empirical testing. Further, we found an unintuitive intermediate scenario in which warming up ability (in terms of completion and not duration of warm-up) is best attained at intermediate body size. Although the surface area-to-body mass ratio can benefit small ectotherms, it also acts against them in the presence of wind because convection becomes more effective as the ratio increases. Thus, even though the intuition is true in the simplest situation, we show that the addition of the influence of wind, which should be prevalent in many natural conditions, can generate a more subtle pattern.

An important model parameter is conductance, which controls heat exchange between the thorax and the surface. Data about conductance for insects are scare. Bartholomew and Heinrich (1978) found that even though conductance is controlled by very different layers for dung beetles, moths, and bees, they have similar cooling rates. In spite of those data, the homogeneity of such a quantity would be surprising. If warm-up is crucial, endotherms can face a trade-off between low conductance that improves the ability to retain endogenously generated heat when solar radiation is weak, and high conductance that favors heat absorption when solar radiation is strong. Low conductance can be a problem because insects also need to dissipate heat during activity. Yet, other studies on bees and beetles revealed that the process of cooling often happens through different mechanisms such as abdominal pumping or evaporative cooling (Heinrich 1979; Verdú et al. 2012). A different possibility that we have not explored here is whether conductance changes with body size. However at this stage, we believe that the need for more empirical work supersedes the need for additional modeling complexity.

A central question is whether these thermodynamic features are actually important in real systems. Large endothermic insects have been reported to have the ability to thermoregulate.

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Studies on endothermic dung beetles have shown that below a certain mass (about 2 g), individuals become thermoconformers, i.e., not capable of endogeneous thermoregulation (Bartholomew and Heinrich 1978; Verdú et al. 2006). This tipping point can actually occur when endogenous heat production, which increases with body size, equals dissipation of that heat, which decreases with surface area-to-body mass ratio. The completion of warm-up thus becomes independent of temperature when an individual reaches a certain size (dashed line figure 3a). The same ability to warm up is known to allow large individuals to forage during colder periods of the day (May 1985). Furthermore, we found that the inverse relationship occurs for ectothermic insects such that smaller individuals can forage at lower temperature. We are not aware of any dataset that documents foraging time or temperature as a function of body size for ectotherms and endotherms. We hope that our model predictions can eventually be tested both in controlled and natural conditions.

Broader ecological context

Metabolic rate, especially resting rate, has been the subject of intense empirical and theoretical investigation with a major focus on the possible universality of the exponent—known as the 3/4 law (Peters 1986; West et al. 1997; Kozłowski and Weiner 1997; Brown et al. 2004; Isaac and Carbone 2010). Whereas the exponent of the resting metabolic rate is interesting on its own, our model suggests that, when comparing performance across body size, the exponent of the foraging rate is even more important. We assumed that foraging rate always increases with body size ($b_3 > 0$), but the increase can be concave or convex (fig. 1b). Concavity favors smaller individuals because it means that per unit mass, the efficiency in resource gathering increases with decreasing body size. The converse is also true that convexity benefits larger individuals (figures 2–5c). Unlike the exponent of resting metabolic rate, there is no clear value for the exponent for foraging rate (see section Model Description: Power law and parameter justifications). Some theoretical models adopted a single value of 0.75, similar to the exponent of resting metabolic rate, but the choice was not based on empirical data (Yodzis and Innes 1992; Brown et al. 1993). Recent studies and reviews have shown that the exponent b_3 is more variable than the resting metabolic rate exponent b_2, and that factors such as the spatial dimensionality

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of search (i.e., 2- vs. 3-dimensional), searching ability (e.g., visual acuity or maneuverability), and species interactions (e.g., competition) can all shape the exponent of foraging rate (Pawar et al. 2012; Kalinkat et al. 2015). We suggest that how resource acquisition scales with body mass is worth much further empirical investigation because of its potential to generate different qualitative patterns in performance curves.

A non-intuitive and interesting result is the role of resource quality when foraging time is limited. In general, we found that performance increases with body size, but for a certain range of resource quality and a highly concave foraging rate, performance peaks at intermediate body size. If resource quality is too low, not enough energy is acquired and individuals of all sizes have negative net energy gain. In contrast, if resource quality is high, individuals of all sizes have positive net energy gain, but the low mass-specific metabolic cost confers the advantage to large individuals. If resource quality is within an certain range (see Appendix), resource quality alone (and not quantity) can select for different body sizes. Optimal body size would then shift to lower values as resource quality decreases even if everything else remains constant. These dual conditions might look restrictive, but our analytical results also show that the range of resource quality allowing this outcome increases with temperature. There are no data to confirm this theoretical finding, but the fact that it is a possibility underscores the idea that one should look at the ecological context in determining species performance (Sears and Angilletta 2015).

Although we focus on individual performance, the results have larger-scale implications. For instance, Bergmann's rule is the macroecological pattern that animals tend to be larger in colder environments (Bergmann 1847; Blackburn et al. 1999). Several mechanisms have been proposed to generate the body size cline. From an energetic perspective, large individuals do better in cold environments than smaller ones because they are better at conserving heat (due to lower surface area-to-volume ratio or to lower conductance) or better at resisting starvation. Although our principal goal is not to explain Bergmann's rule, our model draws attention not only to energetic cost but also to energetic gain. Our results suggest that efficiency in foraging and resource availability have the potential not only to explain Bergmann's rule but also its inverse, which has been documented for insects (Cushman et al. 1993; Loder 1997; Blackburn et al. 1999).

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Future model investigations could explore the optimal body size for a given set of parameter values and thus propose the shape of its dependence on temperature.

In summary, we attempted to understand how body size and temperature shape performance by developing and analyzing a mathematical model. We found that there is no single theoretically-expected relationship of how thermal performance changes with body size. Niche breadth can increase, decrease, or shift depending on the parameters for metabolic rate, foraging rate, thermoregulation, and resource availability. We have illustrated here how the model can be used to verify verbal arguments such as the relationship between body size and warm-up behavior, and also to reveal patterns that arise beyond simple intuition such as the importance of resource quality and size-specific foraging rate in determining optimal body size. However, the major contribution of this model is the ability to extend feedback between theory and data. We hope this work is helpful in highlighting potentially important parameters to measure, and also by providing a clear theoretical relationship among the variables that will guide future empirical work.

Literature Cited

Amarasekare, P., and V. Savage. 2012. A framework for elucidating the temperature dependence of fitness. The American Naturalist 179:178–191.

Angilletta, M. J. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press.

Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology 27:249–268.

Bakken, G. S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. Journal of Theoretical Biology 60:337–384.

Barlow, C. A. 1962. The influence of temperature on the growth of experimental populations of *Myzus persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas) (Aphididae). Canadian Journal of Zoology 40:145–156.

Bartholomew, C. A., and T. M. Casey. 1977*a*. Endothermy during terrestrial activity in large beetles. Science 195:882–883.

Bartholomew, G., and T. Casey. 1977*b*. Body-temperature and oxygen-consumption during rest

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and activity in relation to body size in some tropical beetles. Journal of Thermal Biology 2:173–176.

Bartholomew, G. A., and B. Heinrich. 1978. Endothermy in African dung beetles during flight, ball making, and ball rolling. The Journal of Experimental Biology 73:65–83.

Bartholomew, G. A., J. R. B. Lighton, and G. N. Louw. 1985. Energetics of locomotion and patterns of respiration in tenebrionid beetles from the Namib desert. Journal of Comparative Physiology B 155:155–162.

Bartholomew, G. A., D. Vleck, and C. M. Vleck. 1981. Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturniid moths. Journal of Experimental Biology 90:17–32.

Bergmann, C. 1847. Uber die verhaltnisse der warmeokonomie der thiere zu ihrer grosse. Göttinger Studien 3:595–708.

Birch, L. C. 1953. Experimental background to the study of the distribution and abundance of insects: I. the influence of temperature, moisture and food on the innate capacity for increase of three grain beetles. Ecology 34:698–711.

Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and distributions 5:165–174.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. The American Naturalist 142:573–584.

Buckley, L. B. 2008. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. The American Naturalist 171:E1–E19.

Calder, W. A. 1984. Size, function, and life history. Courier Corporation.

Calosi, P., D. T. Bilton, and J. I. Spicer. 2008. Thermal tolerance, acclimatory capacity and vulnerability to global climate change. Biology Letters 4:99–102.

Campbell, G. S., and J. M. Norman. 2012. An introduction to environmental biophysics. Springer Science & Business Media.

Chown, S. L., and S. Nicolson. 2004. Insect physiological ecology: mechanisms and patterns. Oxford University Press.

Cushman, J. H., J. H. Lawton, and B. F. J. Manly. 1993. Latitudinal patterns in European ant

assemblages: variation in species richness and body size. Oecologia 95:30–37.

534 Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings
536 of the National Academy of Sciences 105:6668–6672.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and
538 temperature on metabolic rate. Science 293:2248–2251.

Hanski, I., and Y. Cambefort. 1991. Dung beetle ecology. Princeton University Press.

540 Heinrich, B. 1975. Thermoregulation in bumblebees 2. Energetics of warm-up and free flight. Journal of Comparative Physiology 96:155–166.

542 ———. 1979. Keeping a cool head: honeybee thermoregulation. Science 205:1269–1271.

Holling, C. S. 1966. The strategy of building models of complex ecological systems. Pages 195–214
544 *in* Systems Analysis in Ecology. Academic Press New York.

Huey, R. B., and D. Berrigan. 2001. Temperature, demography, and ectotherm fitness. The
546 American Naturalist 158:204–210.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms:
548 a discussion of approaches. American Zoologist 19:357–366.

Isaac, N. J. B., and C. Carbone. 2010. Why are metabolic scaling exponents so controversial?
550 Quantifying variance and testing hypotheses. Ecology Letters 13:728–735.

Kalinkat, G., M. Jochum, U. Brose, and A. I. Dell. 2015. Body size and the behavioral ecology
552 of insects: linking individuals to ecological communities. Current Opinion in Insect Science 9:24–30.

554 Kammer, A., and B. Heinrich. 1974. Metabolic rates related to muscle activity in bumble bees. Journal of Experimental Biology 61:219–227.

556 Kearney, M., R. Shine, and W. P. Porter. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proceedings of the National Academy
558 of Sciences 106:3835–3840.

Kingsolver, J. G. 2009. The well-temperatured biologist. The American Naturalist 174:755–768.

560 Kingsolver, J. G., H. A. Woods, L. B. Buckley, K. A. Potter, H. J. MacLean, and J. K. Higgins. 2011. Complex life cycles and the responses of insects to climate change. Integrative and
562 Comparative Biology 51:719–732.

Kleiber, M., et al. 1947. Body size and metabolic rate. Physiological Reviews 27:511–541.

564 Kooijman, S. A. L. M. 2009. Dynamic energy budget theory for metabolic organisation. Cambridge University Press.

566 Kozłowski, J. 1996. Energetic definition of fitness? Yes, but not that one. The American Naturalist pages 1087–1091.

568 Kozłowski, J., M. Czarnołęski, and M. Dańko. 2004. Can optimal resource allocation models explain why ectotherms grow larger in cold? Integrative and Comparative Biology 44:480–493.

570 Kozłowski, J., and J. Weiner. 1997. Interspecific allometries are by-products of body size optimization. The American Naturalist pages 352–380.

572 Loder, N. 1997. Insect species-body size distributions. Ph.D. thesis. University of Sheffield.

Maino, J. L., and M. R. Kearney. 2015. Ontogenetic and interspecific scaling of consumption in 574 insects. Oikos 124:1564–1570.

May, M. L. 1985. Thermoregulation. Comprehensive Insect Physiology, Biochemistry and Pharmacology 4:507–552.

Nervo, B., C. Tocco, E. Caprio, C. Palestrini, and A. Rolando. 2014. The effects of body mass on 578 dung removal efficiency in dung beetles. PloS One 9:e107699.

Niitepõld, K. 2010. Genotype by temperature interactions in the metabolic rate of the Glanville 580 fritillary butterfly. Journal of Experimental Biology 213:1042–1048.

Nisbet, R. M., E. B. Muller, K. Lika, and S. A. L. M. Kooijman. 2000. From molecules to ecosystems 582 through dynamic energy budget models. Journal of Animal Ecology 69:913–926.

Pawar, S., A. I. Dell, and V. M. Savage. 2012. Dimensionality of consumer search space drives 584 trophic interaction strengths. Nature 486:485–489.

Peters, R. H. 1986. The ecological implications of body size, vol. 2. Cambridge University Press.

586 Precht, H., J. Christophersen, H. Hensel, and W. Larcher. 1973. Temperature and life. Berlin: Springer-Verlag.

588 Ratkowsky, D. A., J. Olley, and T. Ross. 2005. Unifying temperature effects on the growth rate of bacteria and the stability of globular proteins. Journal of Theoretical Biology 233:351–362.

590 Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. The American Naturalist 163:429–441.

592 Schmidt-Nielsen, K. 1984. Scaling: why is animal size so important? Cambridge University Press.

594 Sears, M. W., and M. J. J. Angilletta. 2015. Costs and benefits of thermoregulation revisited: Both

the heterogeneity and spatial structure of temperature drive energetic costs. The American Naturalist 185:E94–E102.

Van der Have, T. M. 2002. A proximate model for thermal tolerance in ectotherms. Oikos 98:141–155.

Van der Have, T. M., and G. De Jong. 1996. Adult size in ectotherms: temperature effects on growth and differentiation. Journal of Theoretical Biology 183:329–340.

Van Voorhies, W. A. 1996. Bergmann size clines: a simple explanation for their occurrence in ectotherms. Evolution pages 1259–1264.

Verdú, J. R., J. Alba-Tercedor, and M. Jiménez-Manrique. 2012. Evidence of different thermoregulatory mechanisms between two sympatric *Scarabaeus* species using infrared thermography and micro-computer tomography. PloS One 7:e33914.

Verdú, J. R., L. Arellano, and C. Numa. 2006. Thermoregulation in endothermic dung beetles (Coleoptera: Scarabaeldae): Effect of body size and ecophysiological constraints in flight. Journal of Insect Physiology 52:854–860.

Viljanen, H. 2009. Dung beetle communities in Madagascar. Ph.D. thesis. Faculty of Biosciences, University of Helsinki.

West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science 276:122–126.

Wolfram Research, I. 2015. Mathematica, Version 10.1. Champain, Illinois.

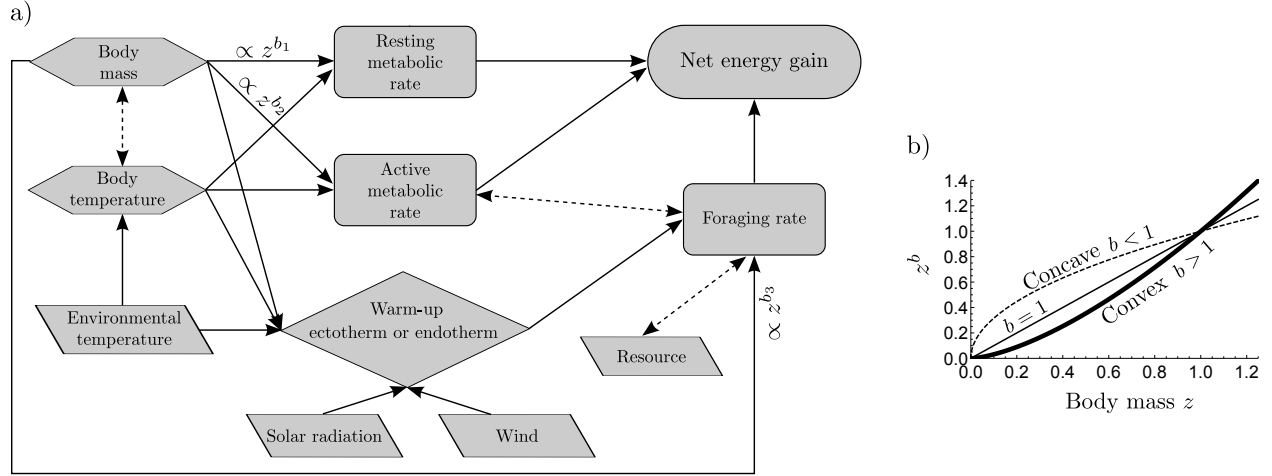Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. The American Naturalist pages 1151–1175.

Figure 1: Model components. (a) Unidirectional solid lines show one component affecting another. Bidirectional dashed lines show a correlation or indirect link between the two components. Input variables are denoted by hexagons for intrinsic variables and non-equilateral parallelograms for environmental variables. The main processes are denoted by rounded rectangles (metabolic and foraging rates) and rhombus (warm-up needs to be completed before foraging). (b) Power law functions of body mass, z, are used throughout the model for the relationship between body mass and metabolic and foraging rates in (a). The expression z^b is concave when $0 < b < 1$ and convex when $b > 1$.
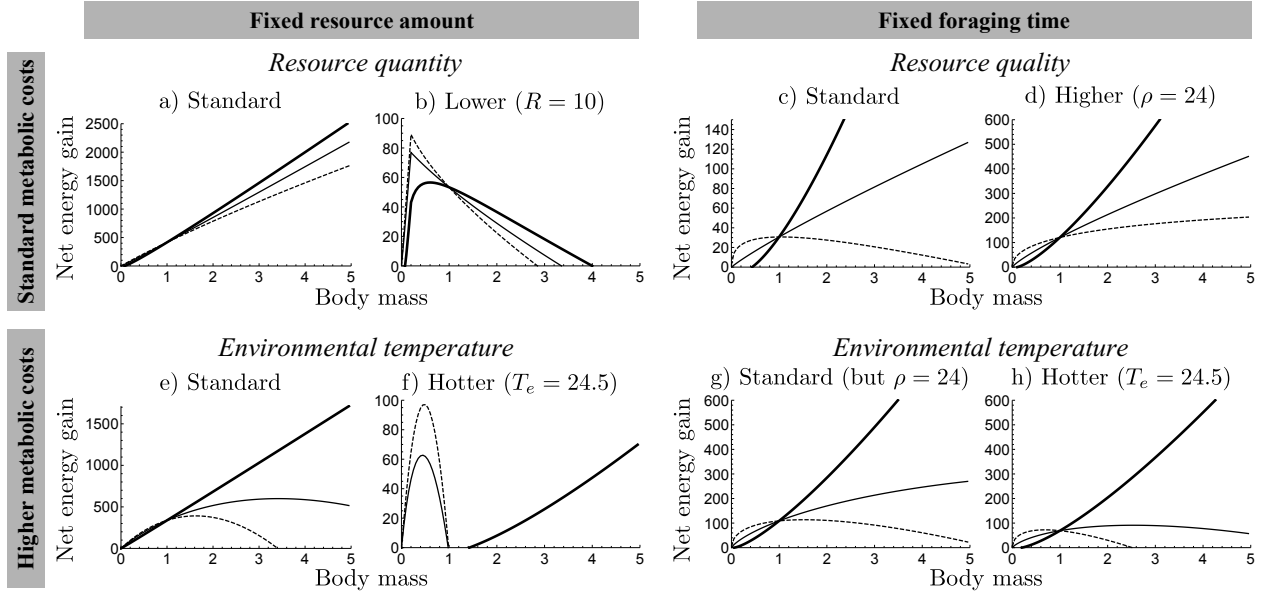
Figure 2: Scenarios whereby thermal performance does or does not peak at intermediate body mass. In each panel, dashed, thin, and thick lines depict different foraging rate exponents ($b_3 =$ 0.5, 0.8, and 1.25, respectively). "Standard" extrinsic parameter values are resource quantity $R = 500$ (defined only when the resource amount is fixed; panels a,b,e,f), resource quality $\rho = 12$, foraging time $\tau_f = 45$ min (defined only when foraging time is fixed; panels c,d,g,h), and environmental temperature $T_e = 15°C$. Intrinsic parameter values for active metabolic rate are $a_2 = 20a_1$ and $b_2 = 0.75$ for "standard" (panels a–d), and $a_2 = 30a_1$ and $b_2 = 1.25$ for "higher" (panels e–h). Additional parameter values and measurement units are provided in Table 1.
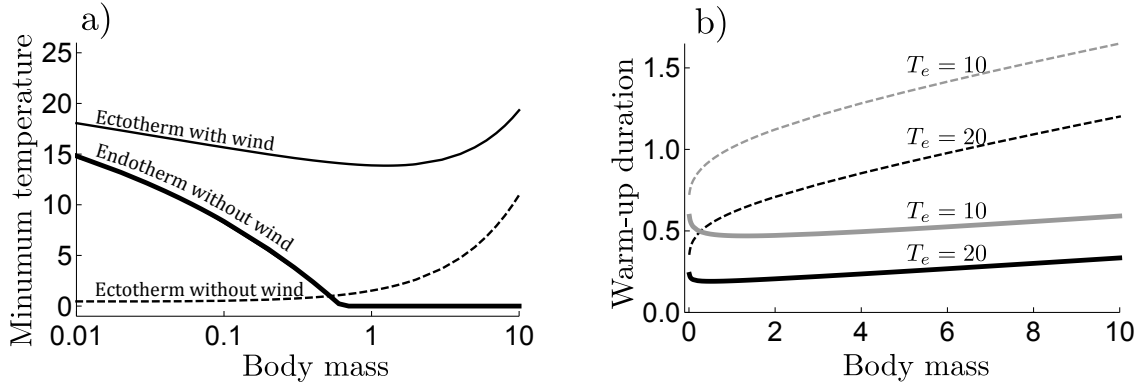
Figure 3: Warm-up for ectotherms and endotherms. a) Lowest temperature that allows the completion of warm-up, as a function of body mass. The individual is given a maximum of six hours to complete warm-up. Thick, thin, and dashed lines represent endotherms with laminar convection, ectotherms with laminar convection, and ectotherms with free convection, respectively. Solar radiation is 1/4 the value at 30° latitude during equinox, and the convection factor is $K_2 = 0.1$. b) Duration of warm-up for endotherms (thick lines) and ectotherms (dashed lines) as a function of body mass and temperature, for free convection. Solar radiation is halved and $K_2 = 1$. For a) and b), wind speed $u = 1$, contraction frequency constant $a_w = 1.25$, and other parameter values and units are in Table 1.
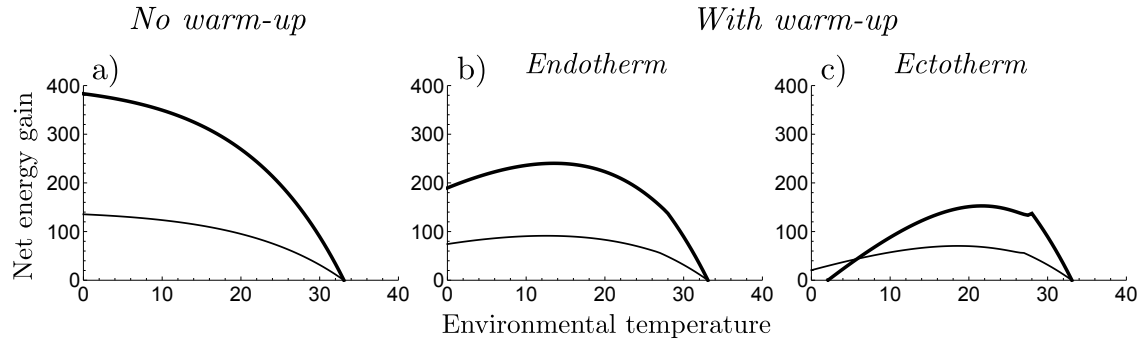
Figure 4: Effect of warm-up on thermal performance for small (thin lines, $z = 0.5$) and large (thick lines, $z = 2$) individuals under free convection. Warm-up starts half an hour after sunrise with a total foraging time $\tau_f = 1$. Parameter values are $\rho = 24$, $a_2 = 10$, $a_1 = 1$, $b_1 = b_2 = b_3 = 0.75$, and otherwise as in Table 1.
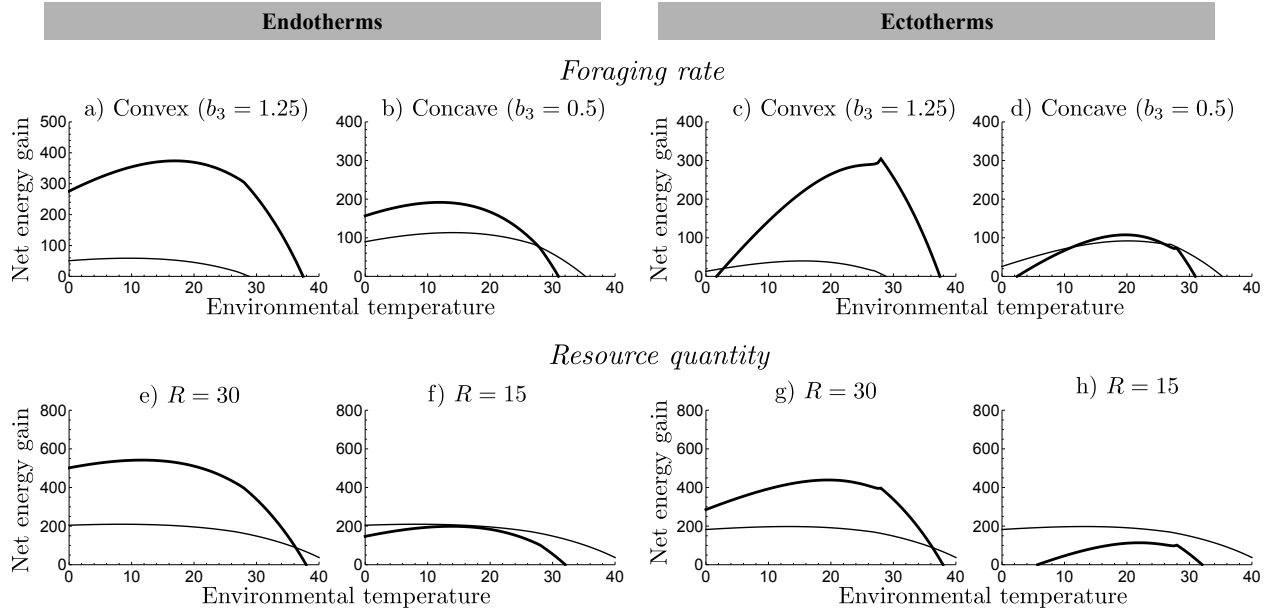
Figure 5: Foraging rate and resource quantity affect thermal performance curves. Results are shown for small (thin lines, $z = 0.5$ in a–d, $z = 0.2$ in e–h) and large (thick lines, $z = 2$) individuals. Other assumptions are free convection, warm-up starting half an hour after sunrise, $\rho = 24$, $a_2 = 10$, $a_1 = 1$, $b_1 = b_2 = 0.75$. For a–d, foraging time is $\tau_f = 1$. For e–h, $b_3 = 0.75$. Units and other parameter values are in Table 1.

Table 1: Values and ranges of parameters used

	Definition	Value or range	Units	Ref.
	Intrinsic body size scaling			
a_1	Coefficient for resting metabolic rate	$\propto 1$	$\mathrm{J\,s^{-1}}$	[1]
b_1	Exponent for resting metabolic rate	0.75		[2]
a_2	Coefficient for active metabolic rate	10-30 $\times a_1$	$\mathrm{J\,s^{-1}}$	[3]
b_2	Exponent for active metabolic rate	0.75-1.25		[1]
a_3	Coefficient for foraging rate	1	$\mathrm{g\,s^{-1}}$	
b_3	Exponent for foraging rate	0.5-1.25		[4]
c_0	Intercept for minimum temperature for activity	28	$^\circ$C	[5]
c_1	Slope for minimum temperature for activity	0.75	$\mathrm{g\,^\circ C^{-1}}$	[5]*
	Physical and thermodynamic constants			
δ	Mass density	0.15×10^6	$\mathrm{g\,m^{-3}}$	[6]
a_w	Frequency of contraction	0.25	$\mathrm{s^{-1}}$	[7]*
s	Specific heat capacity	3.3472	$\mathrm{J\,g^{-1}\,C^{-1}}$	[1]
e	Energy per contraction	0.04184	$\mathrm{J\,g^{-1}}$	[8]
K_1	Default conductance	$0.05\,c_p$	$\mathrm{J\,s^{-1}\,m^{-2}\,^\circ C}$	[9]
K_2	Default convection	1	$\mathrm{J\,s^{-1}\,m^{-2}\,^\circ C}$	[9]
	Extrinsic constants			
c_p	Molar specific heat of air	29.3	$\mathrm{J\,mol^{-1}\,C^{-1}}$	[9]
u	Wind speed	0.1	$\mathrm{m\,s^{-1}}$	
σ	Stefan-Boltzman constant	5.67×10^{-8}	$\mathrm{J\,m^{-2}\,s^{-1}\,K^{-4}}$	
ε	Emissivity of gray body	0.93		[9]
ρ	Energy density per gram of resource	10-100	$\mathrm{J\,g^{-1}}$	
r_3	Scale factor for solar radiation	0.5		

[1] Heinrich (1975)
[2] Kleiber et al. (1947); Peters (1986); Gillooly et al. (2001)
[3] Bartholomew et al. (1981); Niitepõld (2010)
[4] Pawar et al. (2012); Nervo et al. (2014); Maino and Kearney (2015)
[5] Bartholomew and Casey (1977b)
[6] THR unpub. data
[7] Bartholomew and Casey (1977a)
[8] Kammer and Heinrich (1974)
[9] Campbell and Norman (2012)

*means that the value is approximated.