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Short communication

Energy conservation in hibernating endotherms: Why “suboptimal” temperatures are optimal

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ABSTRACT

Many endotherms use facultative heterothermic responses of torpor or hibernation to conserve energy during periods of low energy availability. A common assumption when estimating winter energy budgets is that endotherms should hibernate at the ambient temperature (T_a) that minimizes torpid metabolic rate (TMR) and maximizes the duration of torpor bouts. However, previous studies of the energetic benefits of hibernation have assumed constant T_a within hibernacula. Here we use an individual-based energetic model to estimate overwinter energy expenditure of mammals hibernating at T_a s that vary temporally. We show that, in accordance with the principles of Jensen's inequality, hibernators can conserve energy by selecting microclimates warmer than the single T_a value that minimizes TMR (T_{min}). As temporal variation in T_a increases, endotherms should choose microclimates with mean T_a s progressively warmer than T_{min} . Further, as thermal conductance decreases, as it does with increasing body mass and use of social thermoregulation, the mean T_a that minimizes overwinter energy expenditure approaches, but never equals, T_{min} . We suggest that the commonly held assumption of stable microclimates in hibernacula has skewed the interpretation of the optimal expression of hibernation for energy conservation. Our results contradict much of the accepted understanding of hibernation energetics and add to a growing body of literature proposing that hibernating at a T_a warmer than T_{min} is optimal.

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1. Introduction

Many mammals use facultative heterothermic responses (torpor and/or hibernation) to reduce metabolic demands during periods of low energy availability. Because the primary benefit of facultative heterothermy is thought to be energy conservation, most studies have focused on quantifying the relationship between ambient temperature (T_a) and torpid metabolic rate (TMR) (e.g., Geiser, 2004; Willis et al., 2005; Dunbar and Tomasi, 2006). During torpor and hibernation, endotherms defend a reduced body temperature (T_b) setpoint that may be as much as 40 °C below normothermic levels, with fundamentally different T_a –TMR relationships above and below the T_a where TMR is minimized (T_{min}). At $T_a > T_{min}$, TMR decreases with T_a , typically with Q_{10} values of 2–3 (Geiser, 2004). At $T_a < T_{min}$, TMR increases linearly with decreasing T_a as animals increase metabolic thermogenesis in order to defend their T_b and avoid freezing if T_a falls below freezing (Buck and Barnes, 2000). Many researchers have argued that, in order to minimize TMR and maximize energy conservation, selection of microclimates in which $T_a \approx T_{min}$ is preferred and even optimal for

hibernating mammals (e.g., Körtner and Geiser, 1998; Dunbar and Tomasi, 2006). However, recent theoretical and experimental work suggests that the benefit of energy conservation is counteracted by physiological and ecological costs associated with maintaining a low T_b , and that the optimal cost-benefit ratios are in reality attained by hibernating at T_a s higher than T_{min} (Humphries et al., 2003; Boyles et al., 2007; Angilletta et al., forthcoming). Admittedly, this view is based largely on assumptions, rather than empirical evidence, because the costs have only relatively recently received attention from researchers (Angilletta et al., forthcoming).

Importantly, the prediction that hibernating mammals should choose microclimates warmer than T_{min} can be made on the basis of energetic considerations alone. In other words, it is not necessary to invoke non-energetic costs to argue that the “optimal” T_a for hibernation is actually “suboptimal” in terms of overall energy conservation. Instead, we can use the principles of Jensen's inequality, which is a mathematical proof that has important implications when analyzing non-linear relationships (Ruel and Ayres, 1999). When applied to biological systems it states, *inter alia*, that predicting optimal behavior cannot be done from mean values alone but also depends heavily on the variance and skewness of the relationships in question (Martin and Huey, 2008). Ruel and Ayres (1999) suggest that variance in T_b increases metabolic rate and Martin and Huey (2008) show that skewed performance curves in

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ectotherms combine with imperfect thermoregulation to result in the optimal expression of T_b being below the value that maximizes performance.

In theory, similar principles should hold for predicting “optimal” hibernating microclimates for energy conservation, because the relationship between T_a and TMR is also a skewed, non-linear relationship. Specifically, the fractional increment in TMR associated with a decrease in T_a of $X^\circ\text{C}$ below $T_{\min}$ is greater than the increment associated with an increase in T_a of $X^\circ\text{C}$ above $T_{\min}$. It would be easy to qualitatively extend the results of Ruel and Ayres (1999) and Martin and Huey (2008) to hibernating endotherms but the piecewise nature of the formulae relating T_a to TMR and torpor bout duration necessitates a more quantitative approach. Here, we report the results of an individual-based modeling exercise which shows that, for the purposes of energy conservation, variation in T_a in hibernacula leads to an optimal hibernating T_a above $T_{\min}$.

2. Materials and methods

We modified an energetic model used previously to estimate overwinter energy expenditure (Humphries et al., 2002; Boyles and Brack, 2009; Boyles and Willis, 2010). We applied the model to a typical hibernating species, the little brown bat (*Myotis lucifugus*), but we purposely generalized the model such that our results are not highly accurate representations of hibernation by little brown bats, but are instead a proof of point that can be conceptually applied to any hibernating species. With only minor exceptions (see below), we followed the modeling technique, including parameter values,¹ of Humphries et al. (2002). This basic model has been improved upon elsewhere (Boyles and Brack, 2009; Boyles and Willis, 2010), but these improvements are unnecessary to make the present point. Briefly, the model estimates energy expended each hour over the course of winter. During hibernation, fat is metabolized at a rate determined by TMR. Periodically, the animal arouses to euthermic T_b and fat is metabolized at resting metabolic rate for 3 h (Thomas et al., 1990; Humphries et al., 2002). Energy expenditure during the warming phase of arousal is calculated as the energy necessary to warm from torpid T_b to euthermic T_b and the cooling phase is calculated as 67% of the warming phase (Thomas et al., 1990). We conducted all simulations in Python 2.6.4. A complete description of the model and computer simulation techniques are available in Boyles and Brack (2009).

To simulate variation around the mean T_a (T_{mean}) we included two new variables in the model, namely temperature change per hour (ΔT_a ; $^\circ\text{C}/\text{h}$) and a range of values over which T_a can fluctuate (T_{breadth}). For each hour, the model randomly chooses a ΔT_a within the bounds of each simulation (± 0.01 , 0.1, 0.25, 0.5, or $1^\circ\text{C}/\text{h}$) and adds that value to the T_a from the previous hour, essentially creating a “random walk” bounded by T_{breadth} at one of three levels (± 1 , 5, or 10°C around T_{mean}). If the T_a chosen for a given hour is outside $T_{\text{mean}} \pm T_{\text{breadth}}$, then a new T_a is chosen. If this T_a is also outside $T_{\text{mean}} \pm T_{\text{breadth}}$, T_a is set at $T_{\text{mean}} \pm T_{\text{breadth}}$ for that hour. Because the pattern in T_a variation is random for each individual, T_{mean} is not controlled in the model and simulations can result in T_{mean} values that depart from a specific T_{mean} of interest. To ensure an adequate number of simulations for each T_{mean} value, we discarded any simulations that yielded T_{mean} values that differed by more than 0.25°C from the T_{mean} of interest, and repeated the simulations until we had modeled energy expenditure for 100

individuals at each T_{mean} value. The magnitudes of T_a variation we have modeled are representative of the range of microclimates experienced by hibernating endotherms in a variety of habitats (Supplementary materials), although the patterns of variation may not necessarily be representative of natural environments. In reality, the temporal variation in T_a experienced by many hibernating endotherms may be better described by functions other than a random walk, and different environments are likely to have different patterns of “noise” in T_a (Vasseur and Yodzis, 2004). While more realistic patterns of T_a variation should be considered in species/population-specific models of hibernation energetics, our goal in this paper is merely proof of concept, so we have chosen a straightforward modeling technique to describe patterns of T_a .

To demonstrate the effects of changing the relative slopes of the relationships between T_a and overwinter energy expenditure, we also modeled the effect of changing thermal conductance, which affects TMR when $T_a < T_{\min}$, but not when $T_a > T_{\min}$; under the latter conditions TMR is directly dependent on T_b rather than rates of heat loss, whereas when $T_a < T_{\min}$ a T_b setpoint is defended by means of metabolic thermogenesis (Heldmaier and Ruf, 1992). Specifically, increasing thermal conductance increases the cost of hibernating at T_a s cooler than $T_{\min}$ but not the cost of hibernating at T_a s warmer than $T_{\min}$. Changing thermal conductance can represent several important aspects of hibernation energetics. For example, thermal conductance scales allometrically, with larger species having lower thermal conductance (Geiser, 2004), and huddling during hibernation lowers effective thermal conductance (Boyles et al., 2008). We modeled thermal conductance at three levels (0.007, 0.07, and $0.7 \text{ ml O}_2/(\text{g h } ^\circ\text{C})$), which span the range of values found in hibernating mammals (Geiser, 2004).

We modified Humphries et al.'s (2002) model in two ways. First, we did not model mass-dependent effects, i.e., our model calculates mg of fat metabolized over the course of winter per g of body mass at the beginning of winter. This simplification changes the slopes of curves, but not the T_a associated with minimum energy expenditure, which was the variable of interest in our analyses. Second, because we modeled fluctuating T_a , the formulae used by Humphries et al. (2002) for calculating torpor bout durations are not applicable. Instead, we followed these authors in assuming torpor bout durations are determined by energy expenditure (as measured via oxygen consumption), and calculated oxygen consumed at minimum TMR ($0.03 \text{ ml O}_2/(\text{g h})$) over the course of a torpor bout of average length (792 h). Thus the model simulates an arousal each time 23.76 ml O_2 is consumed.

3. Results

As reported elsewhere (Humphries et al., 2002), hibernating at $T_a = T_{\min}$ minimizes overwinter energy expenditure in a constant thermal environment (Fig. 1). Fluctuating T_a has two effects on energy expenditure. First, energy expenditure increases when compared to constant T_a . Second, even small fluctuations in T_a over the course of winter make the optimal T_{mean} for energy conservation warmer than $T_{\min}$ (Fig. 1). Optimal T_{mean} increases as maximum ΔT_a increases, but the relationship is not linear because optimal T_{mean} reaches a plateau (Fig. 2). Generally speaking, the plateau occurs at a T_{mean} such that any temperatures below $T_{\min}$ are either excluded completely (e.g., when $T_{\text{breadth}} = 1$, optimal T_{mean} is $T_{\min} + 1^\circ\text{C}$) or at the extreme of possible T_a s as necessitated by T_{breadth} (e.g., when $T_{\text{breadth}} = 5$, optimal T_{mean} is $T_{\min} + 4^\circ\text{C}$). The requirement of the model that T_{mean} for the winter is within $\pm 0.25^\circ\text{C}$ of the desired mean T_a ensures that extreme temperatures would rarely be experienced anyway. Increasing thermal conductance leads an increase in the T_{mean} that minimizes overwin-

¹ Parameter values can be found in the supplementary materials of Humphries et al. (2002) at <http://www.nature.com/nature/journal/v418/n6895/supinfo/nature00828.html>.

Fig. 1. Body mass-independent energy expenditure over the course of a 193-day winter for a representative mammalian hibernator, *Myotis lucifugus*. This simulation represents an environment in which T_a can vary up to 5 °C above or below the mean T_a value. The lines correspond to the fat metabolized at various rates of change in T_a . Thermal conductance was set at 0.055 ml O₂/(g h °C) (Humphries et al., 2002).

ter energy expenditure with values increasing as maximum ΔT_a increases (Fig. 3).

4. Discussion

Using a well established modeling technique, we show that the mean T_a that minimizes energy expenditure over the course of hibernation is above T_{min} if there is any temporal variation in T_a . Since variation in T_a occurs in even the most stable hibernacula, including burrows (Buck and Barnes, 1999) and caves (Brack, 2007), we predict that energetically ideal hibernacula are those with microclimates generally warmer than T_{min} . This prediction arises from the energetic inequality of fluctuations in T_a above and below T_{min} reflecting the non-linear relationships involved (Ruel and Ayres, 1999). For example, assuming parameters used in the present model, hibernating in a thermally stable environment 2 °C above T_{min} increases overwinter energy expenditure by 35% whereas hibernating 2 °C below T_{min} increases overwinter energy expenditure by 428%.

Fig. 2. The T_{mean} which minimizes overwinter energy expenditure in a representative mammalian hibernator, *Myotis lucifugus*, at various rates of change in T_a , assuming three different bounds for variation in T_a . Thermal conductance was set at 0.055 ml O₂/(g h °C) (Humphries et al., 2002).

Fig. 3. The T_{mean} which minimizes overwinter energy expenditure in a representative mammalian hibernator as thermal conductance increases, assuming T_a can vary by as much as 10 °C around the mean T_a at five different rates of change.

Thermal conductance during hibernation is related to both body mass (M_b) and huddling. As thermal conductance increases, the slope relating TMR to T_a when $T_a < T_{min}$ becomes steeper and the relative energetic costs of hibernating above and below T_{min} change. The cost of hibernating in microclimates that occasionally drop below T_{min} will be relatively higher for individuals or species with higher thermal conductance, and thus the optimal temperature for energy conservation should approach, but never reach, T_{min} as M_b or cluster size increases. Importantly, the optimal temperature for energy conservation is always warmer than T_{min} , even though low thermal conductance and thermally stable microclimates lead to an estimate of optimal $T_{mean} = T_{min}$ in our model (Fig. 3). This occurs because we modeled T_a in 1 °C increments and so true values, which are slightly above T_{min} , round down to T_{min} . Regardless, over the course of winter, it is energetically beneficial for all species to hibernate at T_a s that are generally warmer than T_{min} unless the microclimate is perfectly stable thermally.

Although we did not model the energetic benefits of daily heterothermy, the principles of Jensen's inequality should also apply. In situations where $T_a \approx T_{min}$, the optimal selection of microclimates to conserve energy should be qualitatively the same as for hibernation; that is, animals should choose warmer microclimates. However, because microclimates experienced by daily heterotherms are often warm enough that T_a never falls below T_{min} (e.g., Willis et al., 2005; Willis and Brigham, 2007), daily heterotherms may experience the opposite situation and can conserve energy by choosing microclimates as cool as possible.

Our results directly contradict the notion that choosing microclimates where $T_a \approx T_{min}$ is the most energetically efficient expression of hibernation (Humphries et al., 2002; Dunbar and Tomasi, 2006), and add to a rapidly growing literature that takes an adaptive view of endothermic thermoregulation (Humphries et al., 2003; Boyles et al., 2007; Angilletta et al., forthcoming). These authors argue that a preference for microclimates warmer than T_{min} should be driven by non-energetic costs of hibernation. While the universality of the conclusions from these papers has been questioned recently (Stawski and Geiser, 2010), we show that even in the absence of non-energetic costs, endotherms hibernating anywhere that is not perfectly stable thermally should choose microclimates warmer than T_{min} to maximize energy conservation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2010.03.018](https://doi.org/10.1016/j.ecolmodel.2010.03.018).

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