



Baby in the bathwater: Should we abandon the use of body temperature thresholds to quantify expression of torpor?

R.M. Brigham^{a,*}, C.K.R. Willis^b, F. Geiser^c, N. Mzilikazi^d

^a Department of Biology, University of Regina, Regina Sask., Canada S4S 0A2

^b Department of Biology, University of Winnipeg, Winnipeg, Man., Canada R3T 2N2

^c Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, 2351 NSW, Australia

^d Department of Zoology, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth 6031, South Africa

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ABSTRACT

Boyles et al. (this issue) argue against the use of body temperature (T_b) thresholds to quantify the expression of torpor in endotherms and our purpose is to provide a counterpoint argument. We contend that T_b thresholds provide valuable information about ecological factors influencing the evolution of thermoregulation. We also point out shortcomings of the so-called heterothermy index proposed as an alternative. However, to be clear, we do agree with Boyles et al. (this issue) that the use of torpor thresholds can limit some aspects of the study of thermoregulation and applaud the more widespread incorporation of theoretical underpinnings proposed by Boyles et al. (this issue) and others.

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1. Introduction

Boyles et al. (this issue) argue against the method of distinguishing between torpid and non-torpid states in endotherms based on body temperature (T_b) thresholds. They argue that T_b thresholds eliminate the potential for ecophysiologicals to place thermoregulation by endotherms in an adaptive context because they exclude endotherms traditionally classified as homeotherms and encourage a “stamp collecting” mentality, where the expression (or not) of torpor is simply cataloged in species after species without considering its adaptive significance. We wholeheartedly agree with Boyles et al. (this issue) that the evolutionary physiology literature on hibernation and daily torpor (see e.g., Geiser and Ruf, 1995) will benefit from stronger theoretical underpinning based on evolutionary biology and we applaud their efforts, and those of others, to further develop this framework (Angilletta et al., 2010; Boyles et al., 2011). We also agree that our understanding of thermoregulation by endotherms would benefit from greater inclusion of homeotherms in comparative analyses and that use of arbitrary T_b thresholds (e.g., 30 °C) may limit the inference to be gained from inter-specific comparisons. However, we argue that Boyles et al. (this issue) dismissal of T_b thresholds amounts to throwing out the baby with the thermal biology bathwater. While acknowledging the beneficial aspects of their

proposed approach, our purpose is to play devil's advocate and highlight both theoretical and practical objections.

2. What is torpor?

First, it is critical to define what we actually mean when we use the word torpor. Boyles et al. (this issue) refer to T_b thresholds for torpor as being inconsistent with IUPS (2003), which defines torpor on the basis of “behavioral responsiveness to stimuli”. However, in our view and as pointed out elsewhere (Willis, 2007), this definition is misleading and outdated, has led to considerable confusion in the literature and, in practice, is not what the vast majority of ecophysiologicals mean when they talk about torpor. For our purposes we and in practice most studies employ a much less arbitrary definition (which we urge the IUPS Thermal Commission to adopt), which is something like: torpor is a physiological state associated with controlled reductions of metabolism and T_b [i.e., the setpoint for T_b] resulting in energy savings compared to defense of normothermic T_b (Geiser, 2004). As pointed out by Boyles et al., this issue and others, many endotherms in deep torpor can readily respond to stimuli. There are numerous published examples of activity, including foraging and even flight, by endotherms at low energy-saving T_b (Willis and Brigham, 2003; Willis, 2007). Most ecophysiologicals would agree that these T_b reflect “torpor” (references in Boyles et al. (this issue); Willis and Brigham, 2003), with the most extreme example observed in torpid Planigales moving to basking sites at a T_b of 13.8 °C (Warnecke and Geiser, 2009). Interestingly,

* Corresponding author. Tel.: +1 306 585 4255; fax: +1 306 337 2410.

E-mail addresses: mark.brigham@uregina.ca (R.M. Brigham), c.willis@uwinnipeg.ca (C.K.R. Willis), fgeiser@une.edu.au (F. Geiser), nomakwezi.mzilikazi@nmmu.ac.za (N. Mzilikazi).

Boyles et al. (this issue) provide a clear example of the confusion caused by the behavioral definition when they concede the potential benefits of using metabolic rate (MR) to quantify heterothermy instead of a T_b threshold. We agree with the use of MR (see below), but this is just as inconsistent with the IUPS definition as the use of a T_b threshold. When ecophysiologicalists discuss torpor, what they are really referring to is an energy-saving reduction in the setpoint for core T_b . This is an on versus off type of response, which we argue is reflected in a threshold.

3. Do torpor and homeothermy represent distinct physiological states?

Boyles et al. (this issue) suggest there is little evidence to conclude that heterothermic and homeothermic endotherms are representative of distinct physiological states and that T_b flexibility is better represented as a continuum from perfect homeothermy to pronounced heterothermy. On the contrary, we argue that there is evidence to support a non-arbitrary distinction between species based on their ability to adjust the T_b setpoint as a behavioral or physiological response to energy availability. This can occur spontaneously under natural conditions or in the lab, even in the presence of *ad lib* food (Djungarian hamster (*Phodopus sungorus*): Ruf and Heldmaier, 1992; European hamster (*Cricetus cricetus*): Wollnik and Schmidt, 1995; stripe-faced dunart (*Sminthopsis macroura*): Song and Geiser, 1997; edible dormouse (*Glis glis*): Wilz and Heldmaier, 2000). It also occurs with food restriction (Elephant shrews (*Elephantulus* spp): Lovegrove et al., 2001; pouched mice (*Saccostomus campestris*): Mzilikazi and Lovegrove, 2002). A combination of environmental costs and benefits appear to have led to selection pressure favoring the ability to dramatically alter the T_b setpoint in some endotherms, but not others. Thus, there appears to be a phenotypic and mechanistic dichotomy (i.e., neural mechanisms likely in the hypothalamus and potentially other cellular mechanisms, which serve to protect tissues from thermal damage) that differentiates heterothermic from homeothermic species. Thinking only in terms of a continuum and throwing out a discreet distinction between heterothermic and homeothermic endotherms may be misleading in its own right because it fails to account for what appear to be functionally distinct phenotypes. The use of T_b thresholds also allows quantification of both the depth and the duration of heterothermic responses, which is critical to determining their energy and adaptive value, albeit we need to be conservative when for example T_b falls just a degree or two below or above the threshold.

4. Do T_b thresholds dismiss homeothermy as “ecologically and evolutionarily inconsequential”?

Boyles et al. (this issue) suggest that little can be learned about the adaptive significance of thermoregulatory strategies based on T_b thresholds in part because studies dependent on T_b thresholds treat homeotherms as “ecologically and energetically inconsequential” and implicitly assume that homeotherms do not maximize fitness. Boyles et al. (this issue) seem to misunderstand what most studies of torpor in endotherms aim to do: understand ecological, behavioral and/or physiological factors influencing the expression of adjustments in the setpoint for T_b . These studies certainly do not assume that species or individuals that do not express torpor during certain circumstances are acting in a way that does not reflect fitness costs and benefits. On the contrary a large body of literature, all reliant on T_b thresholds, has revealed an enormous amount about the selective pressures that influence

how endotherms thermoregulate in the wild. For example, use of thresholds has told us about the influence of life history stage (Hallam and Mzilikazi, 2011), weather, food availability (Wilson et al., 2010), photoperiod (Genin and Perret, 2003), phylogenetic history (Körtner and Geiser, 2011), roosting or nesting conditions (Merola-Zwartjes and Ligon, 2000) and other ecological variables on patterns of thermoregulation in captive and free-living animals of many species. This is not to say that we cannot learn new things by following Boyles et al. (this issue) advice to incorporate data on homeotherms in comparative analyses within a more rigorous theoretical framework. The theoretical approach advocated by Angilletta et al. (2010) and Boyles et al. (2011) might lead to exciting advances in our understanding of the evolution of heterothermy versus homeothermy. However, to suggest that T_b thresholds necessarily fail to help us understand selection pressures influencing thermoregulation by endotherms is an unnecessarily strong overstatement in our view.

5. Are we just “stamp collecting”?

Boyles et al. (this issue) also appear dismissive of collecting measurements of similar variables from multiple species (i.e., what they term “stamp collecting”) when it comes to depth and duration of torpor. We argue (and expect Boyles et al. (this issue) would agree) that, in general, this kind of study repetition is actually critical to the comparative method, which forms the basis of evolutionary physiology. For example hundreds of studies have “stamp collected” measurements of basal or resting metabolic rates of endotherms, enabling an exciting and important comparative literature (e.g., Lovegrove, 2000; McKechnie and Wolf, 2004). Certainly results of studies on individual species should be placed in the appropriate ecological and evolutionary context but we argue that most studies of heterothermy, in fact, do this. Indeed, the “surprise” that Boyles et al. (this issue) refer to when a given species does not express torpor in the field or lab (e.g., Wilson et al., 2010) is simply a reflection that is based on the ecology of a study animal; the authors of a given study have made a prediction that was not satisfied. Figuring out why a given species violates or satisfies our predictions (i.e., does it express an adjustment of the T_b setpoint and reduction of T_b below some, hopefully standardized, threshold) is critical if we are to place heterothermy in an adaptive context. Studies based on T_b thresholds can clearly aid in this effort, as long as editors and reviewers are just as likely to accept papers reporting the absence of torpor as those reporting its occurrence. This is not simple “stamp collecting” and it can help understand selection pressures favoring the evolution of flexibility in the setpoint for T_b .

6. Heterothermy index: an alternative?

Although we differ on the points above, we agree with much of Boyles et al. (this issue) nicely explained rationale for not using arbitrary T_b thresholds. Inconsistency among threshold values for different species can limit the inference to be drawn from comparative studies and the concern that many analyses might omit energetically and ecologically important shallow torpor bouts is a legitimate one. While the absolute value for a T_b threshold may appear arbitrary, it is often picked in relation to the normothermic T_b and thus apparent inconsistencies in fact reflect differences in normothermic T_b and not how much T_b has to be reduced to reach the setpoint. Geiser and Mzilikazi (2011) show that defining a precise threshold value does not really matter because of the clear bimodal distribution of T_b . Any T_b

selected as a threshold around 30 °C will result in the same outcome for other torpor variables, i.e. T_b thresholds are robust.

In our view, T_b thresholds based on changes in MR at the onset and completion of torpor bouts will best capture the energy implications of adjustment in the T_b setpoint; this approach is supported by one comparative study (Willis, 2007). However, relatively few data were available for Willis, (2007) and we need more studies that aim to determine the T_b and/or skin temperature (T_{sk}) at which energy savings occur due to setpoint adjustments. T_{sk} is commonly used as an estimate for T_b in studies of small free-ranging animals (e.g., Willis and Brigham, 2003). Another approach is to define the T_b or T_{sk} threshold as some value below the normothermic or perhaps modal T_b or T_{sk} for a given species or individual (e.g., McKechnie et al., 2007). This approach is more systematic than selecting an arbitrary T_b threshold or relying on behavior to define the threshold. However, in the absence of data confirming that these values correspond with the onset of metabolic savings as a result of an adjustment in T_b setpoint, this approach relies on untested assumptions.

Boyles et al. (2011) proposed the heterothermy index (HI) as an alternative to T_b thresholds altogether and, presumably, this is the metric Boyles et al. (this issue) would advocate. The HI identifies even small heterothermic responses on a continuous scale in much the same way that standard deviation quantifies variation in a given sample of data for any continuous variable. A clear benefit of HI is that it allows homeotherms to be analyzed alongside heterotherms but so could, for example, average T_b . Homeotherms maintaining stable T_b will exhibit low values of the HI while hibernators that express large fluctuations in T_b will exhibit large values. We are convinced HI provides a useful comparative index that has the potential to help improve the understanding of adaptive thermoregulation in endotherms. However, we argue that HI quantifies something quite different from values provided by T_b thresholds and cannot be considered a “replacement”. The most serious limitation is that, like the concept of “degree minutes” (number of minutes multiplied by number of degrees spent below a threshold temperature; Barclay et al., 2001), the HI fails to account for the substantial difference in energy (and likely adaptive) value of shallow, long-duration torpor bouts compared to deep, short-duration bouts. HI values for a species using short deep torpor could be nearly equivalent to those for a species using long, shallow torpor even though the energy and likely fitness consequences of these two patterns would be enormously different. On the other hand the careful use of a non-arbitrary threshold T_b (e.g., one based on the decline in MR resulting from a T_b setpoint adjustment) can allow for calculation of both depth and the duration, both of which are needed to capture the true adaptive value of torpor. The HI, in its current form, does not differentiate between these two important aspects of heterothermy.

A second limitation of HI is that it hinges on knowing or assuming the “optimal T_b for performance”. Presumably this would have to mean the optimal T_b for “behavioral performance”, which links HI to the problematic IUPS definition for torpor discussed above. However, in the absence of data on “optimal T_b ” for the vast majority of endotherms, Boyles et al. (2011) suggest using the upper modal value of T_b recorded during a study as a proxy optimal T_b for that individual or species. This may be an acceptable compromise but, to our knowledge, the assumption that heterothermic endotherms “perform optimally” at their upper modal T_b (i.e., the T_b they most commonly experience while active in the wild) is untested and there are reasons to assume that the upper modal T_b may not actually reflect the most optimal T_b for performance (Willis, 2007).

Thirdly, there are also issues with putting HI into practice. The first problem with it is that the values it generates have no

inherent meaning. How does one think about a species with an index value of 40 versus 2? Is it possible for a single value to adequately describe the inherent complexities of temporal variation in T_b in relation to ambient variables expressed by a species or individual? HI also does not appear to have any ecological, physiological or behavioral predictive value. For example what kinds of animals are expected to have low/high HI? Alternatively, under what conditions would a low/high HI be predominant? How does a low/high HI translate to fitness?

A fourth disadvantage of HI relates to the reduction of MR during torpor. If HI is to serve as a proxy for MR during torpor, it cannot simply assume that T_b reflects MR during torpor in all species and in all physiological states in the same way. It is well known that even at the same T_b the MR of daily heterotherms and hibernators differ substantially, likely because the two groups differ in the extent to which they employ metabolic inhibition. Hibernators are able to reduce MR during torpor at high T_b by about 50% or more with only a small change of T_b (Song et al., 1997; Tøien et al., 2011), whereas daily heterotherms appear unable to do this as effectively. Further, MR during torpor at the same T_b will differ substantially between a thermoconforming or thermoregulating torpid animal and the same HI therefore may reflect entirely different energy expenditures.

HI requires virtually continuous 24 h/day recordings of individuals to be most effective. While data logging receivers will help in this regard, many of the species under study will not always use the same sites during each inactive period and often leave the vicinity (and thus signal range for radio-transmitters) during the active period. In this sense, HI lends itself better to studies employing surgically implanted or externally affixed data loggers that record T_b or T_{sk} continuously but the requirement to recapture individuals to collect the data will prove enormously challenging for many species. This returns us to one of Boyles et al. (this issue) criticisms of T_b thresholds—that results of studies on different species may not be comparable. It is just as likely that not all species will be equally amenable to the type of data collection needed to make use of HI, which may limit its value as a comparative metric. Like T_b , HI is also a proxy for and the integration of MR of the animal under study. The technological ability to indirectly but reliably quantify MR in free-ranging animals may not be far off (via, for example, heart rate, Signer et al., 2011) and methods that better reflect the metabolic status of individuals in real-time need to be pursued. In the interim, the question arises: Why employ yet another indirect metric that is little more than a proxy for metabolic heat production: the real currency of interest for studies of heterothermy in endotherms?

In spite of these issues it is our view that a metric such as the HI is a step forward for research about the nature of heterothermic responses and can serve as a useful comparative complement to measures of torpor depth and duration, depending on the objectives of a given study. However we feel it is unwise to rely solely on the use of such a metric, particularly until it can be modified to better capture the distinction between depth and duration of torpor. The metric that suits a study best will depend on the questions being asked and whether there are enough good data to generate HI.

Precisely what torpor is and where it starts and ends is ultimately less important than why it evolved, why it appears to be used differently between species, when it is used and the cues animals use to “decide” whether or not to use it. By identifying its use with the aid of a T_b threshold these questions can be (and have been) addressed and we disagree with Boyles et al. (this issue) that we have just been “stamp collecting”. Adding HI index or some derivative of it to our toolbox of methods will likely enhance our understanding of the evolution of thermoregulation by endotherms, as will the better incorporation of homeotherms

into comparative analyses. However, we must also be careful not to dispose of 'our best' and a highly practical method for quantifying torpor with the methodological bathwater.

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