

## A New Comparative Metric for Estimating Heterothermy in Endotherms

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Accepted 8/13/2010; Electronically Published 10/27/2010

### ABSTRACT

A major focus in the study of endothermic thermoregulation has been the description of thermoregulatory patterns used by various species and/or populations. Compared with ectotherms, relatively few attempts have been made to study the thermoregulation of endotherms in an adaptive framework. We believe that one of the main factors limiting this area of research has been the lack of an appropriate metric to directly compare body temperature ( $T_b$ ) variation across all endothermic species. Thus, we present a simple comparative metric, the heterothermy index (HI), to quantify the expression of heterothermy by endotherms during a given time frame. Key advantages of HI are that (1) it represents a new analytical technique that has different strengths than the metrics commonly used to describe variation in  $T_b$ , (2) it allows for evaluation of nonenergetic costs and benefits that affect the expression of heterothermy, and (3) it has the potential to unify research on homeotherms and heterotherms through quantitative comparative analyses that examine the entire continuum of thermoregulatory patterns. In short, we suggest that our metric provides a means to overcome one of the hurdles presently slowing the advancement of research on endothermic thermoregulation beyond the simple description of thermoregulatory patterns.

### Introduction

Thermoregulation has been a topic of intense research and has been recognized as a powerful theme for the study of adaptation

to environments (Kingsolver 2009). However, most of the research taking advantage of responses to environmental cues as a means to explicitly study thermoregulatory adaptation and evolution has been conducted on ectotherms (see reviews and discussion in Angilletta et al. 2002; Angilletta 2009; Kingsolver 2009); there have been far fewer attempts to study adaptive thermoregulation in endotherms. For many reasons, including large variances in body temperature ( $T_b$ ), ectotherms lend themselves to these studies. In contrast, endotherms may have been overlooked in this regard (Angilletta et al. 2010) because the fact that many species exhibit heterothermy was initially overlooked by physiological ecologists (e.g., Scholander et al. 1950). More recently, however, a proliferation of articles reporting temporal variation in  $T_b$  has led some authors to conclude that among endotherms, heterothermy is the rule rather than the exception (e.g., Arnold et al. 2004). Nevertheless, to date, very few attempts have been made to examine the adaptive significance of this variation (but see Humphries et al. 2003; Angilletta et al. 2010).

The explicit study of adaptive thermoregulation in ectotherms is at least three decades old (e.g., Huey and Slatkin 1976), but the advent of thermal indices to quantify thermoregulation in ectotherms (Hertz et al. 1993) has been identified as a significant advance in the field (Angilletta 2009). Here, we argue that one key hurdle in the study of thermoregulation in endotherms is the lack of an appropriate index to compare variation in  $T_b$  among species and/or populations. Several metrics have been suggested to quantify  $T_b$  variation, but each has significant limitations. The most common method, found in nearly all articles on the heterothermic responses of torpor and hibernation, involves quantifying the time spent below an arbitrary torpor cutoff  $T_b$ . Variations of this method have been proposed (Barclay et al. 2001; Willis 2007), but as with the original method, they are only applicable to species that use torpor. Besides the methods based on cutoff values, several other approaches have been suggested. One recently proposed metric estimates the instability in  $T_b$  by summing the absolute change in  $T_b$  from sampling period to sampling period (Gordon 2009). One possible limitation of this metric, depending on the goals of the analysis, is that it is probably not appropriate for hibernating species because they may maintain a relatively stable but very low  $T_b$  for extended periods, which would lead to underestimates of heterothermy. Yang and Gordon (1996) quantified the stability of  $T_b$  in normothermic rats exposed to a range of air temperatures as the percent change in core  $T_b$  per unit change in air temperature, but this approach is not suitable for comparing patterns of heterothermy. Finally, a mul-

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titude of computational techniques are commonly used by researchers studying circadian rhythms in  $T_b$ , but these metrics generally focus on finding evidence of rhythmicity, not assessing the relative use of heterothermy (Refinetti et al. 2007).

The main argument against using a simple metric for quantifying variation in  $T_b$  is that it does not necessarily represent the energetic benefit associated with a given reduction in  $T_b$  (Willis and Brigham 2003). While the relationship between energy and  $T_b$  variation has received the most attention, this probably reflects the fact that most work on heterothermy has been conducted by physiological ecologists whose primary interest has been the consequences of variation in  $T_b$  for energy and occasionally for water balance. However, a multitude of nonenergetic costs and benefits of thermoregulation should also be considered, and several recent modeling and theoretical articles have discussed a diverse suite of factors, including many completely unstudied ecological variables that should affect the expression of  $T_b$  (Pravosudov and Lucas 2000; Humphries et al. 2003; Angilletta et al. 2010). We are not implying that it is impossible to study these nonenergetic factors by using other descriptors of variation in  $T_b$ . Instead, we are suggesting that the use of a single metric of heterothermy should allow for better evaluation of the ratio of the overall costs to the overall benefits without implicitly focusing on energetic aspects. Through clever experimental design, the researcher should be able to determine which specific costs and benefits are most important in driving the expression of heterothermy in a given situation.

Here we outline a new metric for describing variation in  $T_b$  that can be applied to any endothermic species exhibiting any thermoregulatory pattern, improving the ability of researchers to address many questions about the evolution of thermoregulatory patterns in endotherms. Our main goal is to provide a metric that allows for the unification of research on thermoregulation in homeotherms and heterotherms, which have largely been studied separately in the past.

### The Heterothermy Index

We propose a new metric, called simply the heterothermy index (HI), to describe temporal variation in  $T_b$  of an individual during a given sampling period. We recognize that this metric may not be particularly useful in descriptive studies of a single population or species, and we stress that HI is intended for comparative purposes between or among many treatment groups or species. HI is calculated using the sort of  $T_b$  data already being collected.

HI can be calculated as

$$HI = \sqrt{\frac{\sum (T_{b-opt} - T_{b,i})^2}{n - 1}},$$

where  $T_{b-opt}$  is the optimal  $T_b$  for performance,  $T_{b,i}$  is the  $T_b$  measurement at time  $i$ , and  $n$  is the number of times  $T_b$  is sampled. In essence, the metric calculates the magnitude of a heterothermic response in relation to the  $T_{b-opt}$  an animal dis-

plays during a given time frame. Notice the equation for HI is a modified version of standard deviation. We follow definitions more similar to those used by ectotherm physiologists and theorists (e.g., see Angilletta 2009; Angilletta et al. 2010) than those used by endotherm physiologists because they have a longer history and tend to be better defined for building theory. Therefore, we define  $T_{b-opt}$  as the  $T_b$  that maximizes fitness in a hypothetically ideal environment (essentially a cost-free environment). This usage of the term “optimal” differs from that commonly employed by researchers studying torpor or hibernation, where it is often implied that the  $T_b$  an animal is maintaining under a given set of environmental conditions is optimal (e.g., Borgmann and Moon 1976; Kokurewicz 2004). Notice that in the latter sense,  $T_{b-opt}$  is exactly the same as observed  $T_b$ , and therefore nothing is gained by distinguishing the two terms. Further, our metric assumes that thermoregulatory accuracy (i.e., the difference between mean  $T_b$  expressed and  $T_{b-opt}$ ) is important (Angilletta et al. 2010). One could argue that deep hibernators thermoregulate accurately at very low  $T_b$ 's, but these  $T_b$  values are far below  $T_{b-opt}$  as presently defined, so their HI values would be high.

### HI in Practice

Theoretically, calculating HI values should be simple, but in practice it may be complicated by uncertainties associated with measuring performance curves, and therefore  $T_{b-opt}$ , in endotherms. To our knowledge, no study has quantified  $T_{b-opt}$  in an endotherm in a manner conducive to calculating HI. Even in the ectotherm literature, where the concept of  $T_{b-opt}$  is well known and widely used, no single measurement of  $T_{b-opt}$  is used to the exclusion of all others (Angilletta 2009). In fact, it is likely that the appropriate measure of  $T_{b-opt}$  (e.g., muscle tone, immune function, or running speed) will be both question and species specific. Therefore, we base our formulation of the metric on the best (and probably most general) method to estimate  $T_{b-opt}$  in endotherms that is presently available while recognizing that interpretations may need to be refined as our understanding of endotherm thermal physiology advances. In fact, we encourage researchers to address this topic and alter the formula for HI accordingly. We could assume that  $T_b$  is adaptive, and thus  $T_{b-opt}$  should equal the most commonly experienced  $T_b$  during the period of activity (Angilletta et al. 2010). Unfortunately, determination of this value requires behavioral observations that might not be available, so we suggest using a simple proxy to estimate the most commonly experienced  $T_b$ : the modal  $T_b$ . In practice, the modal  $T_b$  ( $T_{b-mod}$ ) can be calculated as the mode of all temperatures recorded if the distribution is unimodal and the mode of the peak at the highest  $T_b$  value if the distribution is bi- or multimodal (McKechnie et al. 2007; Smit and McKechnie 2010). Therefore, HI can be rewritten as

$$HI = \sqrt{\frac{\sum (T_{b-mod} - T_{b,i})^2}{n - 1}}.$$

While we can use theoretical arguments to predict that  $T_{b-mod}$  should be close to  $T_{b-opt}$  in most scenarios because endotherms should maintain an active  $T_b$  close to  $T_{b-opt}$  whenever possible, an important avenue for future research is to test the validity of using  $T_{b-mod}$  as a proxy of  $T_{b-opt}$ . Such studies will undoubtedly prove fruitful for reasons extending well beyond the definition of the present metric. While these studies may lead to better proxies of  $T_{b-opt}$ , they will not change the conceptual value of having a single comparative metric of heterothermy.

HI has several characteristics that should prove useful for analyses. First, it combines both magnitude of the deviation from normothermic  $T_b$  and time spent away from that temperature into one continuous variable. Heterothermy is usually described by  $T_b$  minima or maxima and, separately, by time spent beyond the  $T_b$  cutoff value. Using these values as a metric of heterothermy can lead to conflicting interpretations of the level of heterothermy expressed. Second, HI has an absolute bound of 0 on one end, which describes an individual maintaining perfect homeothermy during the sampling period and a sliding bound of approximately  $|T_{b-opt} - \bar{T}_e|$ , where  $\bar{T}_e$  is operative temperature of the environment on the other end, which describes an individual maintaining perfect poikilothermy. In practice, the upper bound will be biologically constrained at a value of  $\sim 40$ . For example, if a 24-h time frame was chosen for a mammal hibernating with a constant  $T_b$  of  $2^\circ\text{C}$  over the entire period but for which modal  $T_b$  is  $37^\circ\text{C}$ , the HI value

would be  $35.8^\circ\text{C}$ . Third, HI takes into account all data collected, whereas analyses using the  $T_b$  cutoff method often disregard variation in  $T_b$  that does not exceed the cutoff value. Likewise, describing heterothermy by simple minimum or maximum  $T_b$  values disregards most of the data and relies on what are necessarily extreme values in  $T_b$  distributions, which is analogous to using an outlier to describe a normal statistical distribution. Fourth, HI values have a temporal component (unlike minimum  $T_b$ ) and can be calculated for any time frame with multiple samples assuming either (a)  $T_{b-opt}$  is known beforehand (which may be necessary in telemetric studies if gaps exist in the data set caused by animals foraging) or (b) the sampling period includes a normothermic active period. Finally, and most importantly, HI values can theoretically be calculated for any individual of any species, providing a single value for each individual that can then be assessed statistically.

Like any method, the proposed metric has weaknesses. First, it does not completely eliminate the possibility of two individuals with different thermoregulatory patterns yielding the same value. This situation is much more likely when using simpler descriptors, such as time spent torpid or minimum  $T_b$ . For example, instances of two animals decreasing  $T_b$  to the same temperature, but for vastly different lengths of time, will be common. While the nature of HI ensures that biologically realistic examples of this happening will be rarer than using other methods of estimating heterothermy, it nevertheless can occur.

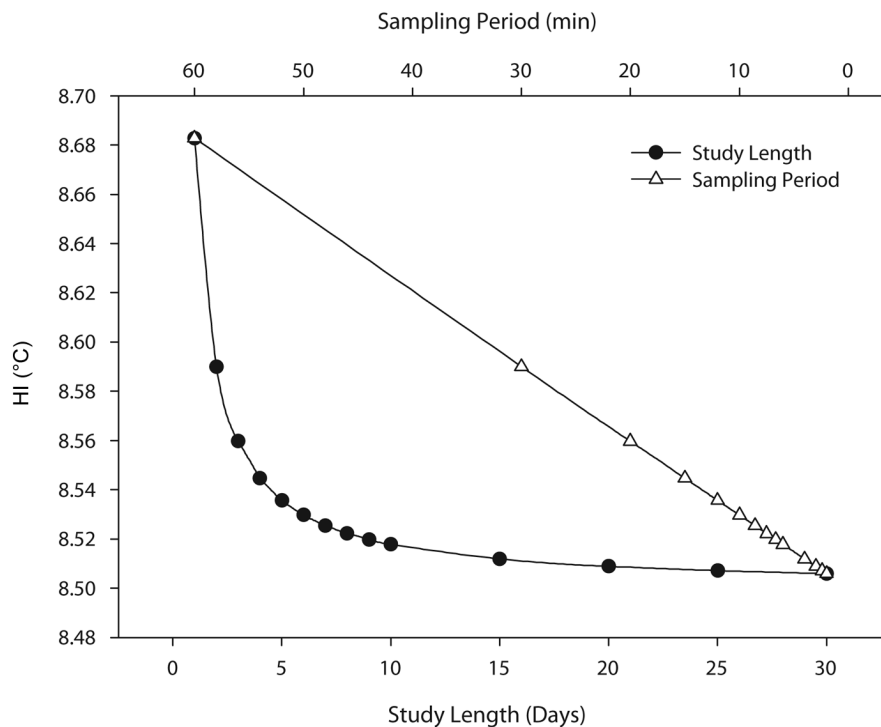


Figure 1. Example of bias in heterothermy index (HI) values at small samples assuming an endotherm that maintains  $T_{b-opt} = 37^\circ\text{C}$  for 18 h/d and goes into torpor at  $T_b = 20^\circ\text{C}$  for 6 h/d. Increasing the study length (circles) or decreasing the sampling period (triangles) both lead to a decrease in sampling bias. In this example, the bias is small ( $<0.2^\circ\text{C}$ ), even with the smallest data set (although it can be proportionally larger in some data sets, especially if the HI value is small).

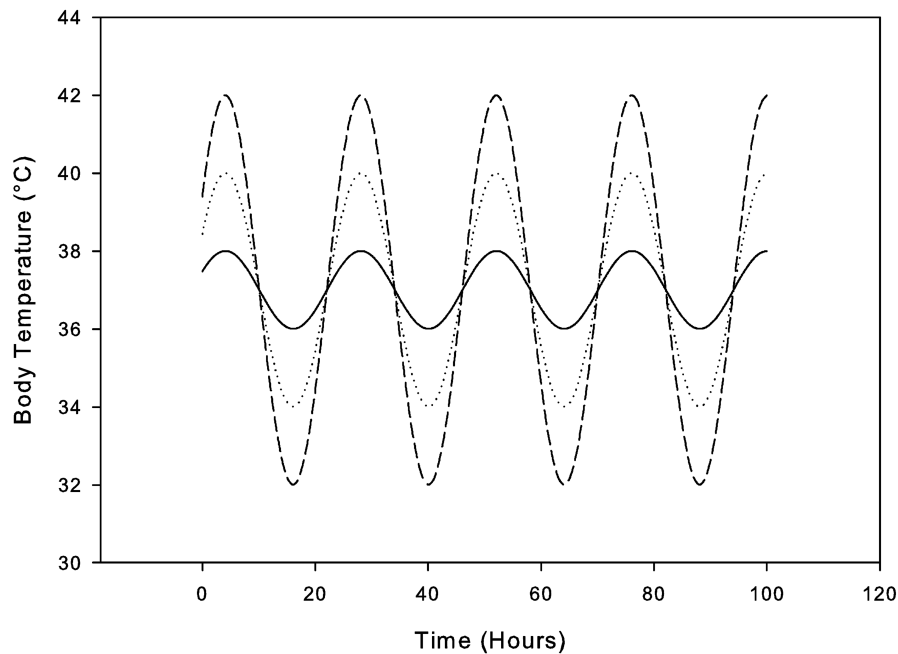


Figure 2. Hypothetical  $T_b$  curves represented by sine waves with identical means but different amplitudes. These curves lead to HI values of 0.86°, 2.58°, and 4.30°C over the 100-h sampling period.

For example, two animals with  $T_{b-opt} = 37^\circ\text{C}$ , one of which lowers its  $T_b$  to  $20^\circ\text{C}$  for 4 h/d and the other of which lowers its  $T_b$  to  $28^\circ\text{C}$  for 14 h/d, will both generate HI values of approximately 7, but the second animal probably realizes greater energetic benefits because of the nonlinear relationship between  $T_b$  and metabolic rate. Although HI values do not distinguish between the two patterns, the identical values nevertheless suggest that costs other than energy expenditure associated with homeothermy are driving the expression of heterothermy in the first animal. Second, like the equation for standard deviation on which it is based, HI is sensitive to sample size in very small samples. The sample size at which HI values asymptote will change based on the sampling scheme and should ideally be taken into account during experimental design. The bias will decrease proportionally as the length of the study increases or as the sampling interval decreases (assuming the  $T_b$  pattern is the same each day throughout the study). For example, in the case of a hypothetical organism represented in Figure 1, increasing the sample period to 2 d has the same effect on bias as halving the sampling interval. Therefore, decreasing the sampling interval may be the most appropriate way to limit bias in some studies (e.g., during spring or autumn, when the ambient temperature is changing daily), whereas increasing study length may be more appropriate in others (e.g., long-term laboratory studies under constant environmental conditions). Third, HI values will require periodic  $T_b$  sampling that does not disturb the study animal, so studies using colonic or rectal  $T_b$  measurements will likely be inappropriate. Finally, while HI makes no distinction between variation above and

below  $T_{b-mod}$ , a direction can be qualitatively determined by examination of a histogram of  $T_b$ .

### Circadian Rhythms of $T_b$

Some researchers may object to including normothermic variation in  $T_b$  associated with diel fluctuations in calculations of HI values (Lovegrove and Smith 2003), but these fluctuations nonetheless represent a departure, and probably an adaptive one, from perfect thermoregulation at the optimal  $T_b$  (Angilletta et al. 2010), and they are quantifiable as such. Further, there is increasing evidence that many species, particularly tropical and subtropical species, do not maintain precisely regulated circadian  $T_b$  rhythms considered part of “classic” endothermic thermoregulation (sensu Aschoff 1982). Many of these species exhibit labile normothermic  $T_b$  without defense of a single  $T_b$  set point, clouding the distinction between “normothermy” and “heterothermy” (e.g., Merola-Zwartjes and Ligon 2000; McKechnie and Lovegrove 2001; Wooden and Walsberg 2002). In our opinion, these examples justify the use of HI values to quantify any variation in endotherm  $T_b$  whether or not it reflects classically defined circadian rhythms.

If  $T_b$  variation within a species is related only to a normothermic circadian rhythm, the  $T_b$  distribution should usually be bimodal, with  $T_{b-mod}$  represented by the modal temperature of the upper peak. For example, consider the circadian rhythms of three individuals following hypothetical  $T_b$  curves represented by sine curves with the same mean  $T_b$  and frequency of daily cycles but with varying amplitudes (Fig. 2). Using a cutoff

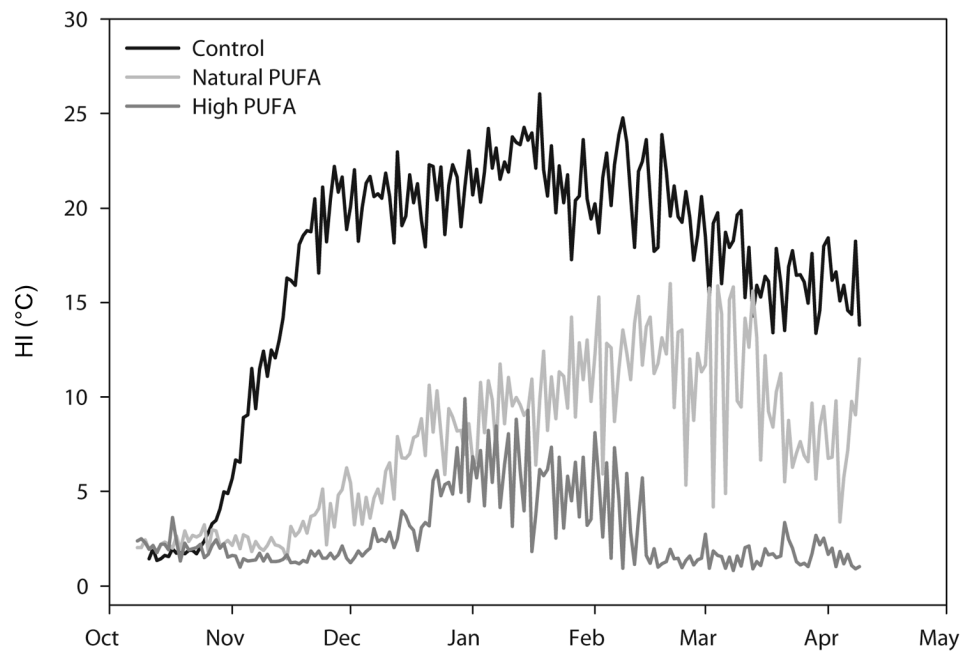


Figure 3. Daily heterothermy indices (HI) averaged for eastern chipmunks *Tamias striatus* on three different diets: a natural control diet, a supplemented diet with approximately natural polyunsaturated fatty acid (PUFA) content, and a supplemented diet of both increased food and increased PUFA content. Using HI allows for analyses at a much higher temporal resolution than using the torpor cutoff method. Data from Munro et al. (2005).

value of below 32°C would lead to the conclusion that none of these individuals use torpor, and these fluctuations would be ignored in most articles on facultative heterothermy. While it may be true that none of the patterns meet a classical definition of torpor, it is difficult to argue that individuals exhibiting the three  $T_b$  patterns in Figure 2 are using the same thermoregulatory pattern (Lovegrove and Heldmaier 1994). HI, on the other hand, treats this variation in  $T_b$  on the same conceptual scale as variation associated with torpor or hibernation. In this case, the three individuals have HI values of 0.86°, 2.58°, and 4.30°C.

### Comparing Intraspecific Patterns of Thermoregulation

HI will also provide values for heterothermy that may be more conducive to statistical analyses than metrics used at present. For example, Munro et al. (2005) compared torpor patterns of eastern chipmunks (*Tamias striatus*) under varying levels of food availability and dietary polyunsaturated fatty acids (PUFA). These authors quantified mean length of torpor bouts, total time spent torpid, and percentage of time in various states, among other parameters. Their results showed that increasing the amount of available energy and PUFAs led to a decrease in average torpor bout length and overall percentage of time spent torpid (although these results may contradict other work by these authors [Munro and Thomas 2004], the interpretation is not particularly important in the context of this article). Essentially, the same conclusions can be drawn from analyzing HI values for each treatment group. However, use of the  $T_b$

cutoff method limits temporal resolution to periods long enough to calculate descriptive statistics on torpor bouts, which is often several months (e.g., Landry-Cuerrier et al. 2008) or an entire season (e.g., Munro et al. 2005). Calculating HI values for the same data set (Fig. 3) allows for the identification of patterns that would be difficult to detect using the torpor cutoff method. For instance, use of HI makes it possible to quantify variation in heterothermy expression down to the shortest time frame used in calculations; it is therefore possible to determine on which (if any) days the expression of heterothermy varied significantly among the three treatment groups. Further, because the torpor cutoff method implicitly assumes that any variation in  $T_b$  that does not reach the cutoff value is equal to 0 variation, statistical comparisons of heterothermy on days when no torpor is recorded in one or more groups or populations would be questionable if based on any method other than categorically based analyses (i.e., torpor or no torpor). Higher temporal resolutions also allow for the calculation of correlations between the relative level of heterothermy and environmental variables. These are just a few of the interesting questions regarding temporal variation in heterothermy that cannot be adequately addressed using the cutoff method.

HI also represents a convenient method for comparing heterothermy between different treatment groups for which the torpor cutoff method is not applicable, for instance, between adult and juvenile muskoxen (*Ovibos moschatus*) during winter feeding bouts (Munn et al. 2009). This species exhibits  $T_b$  fluctuations much too small to be considered torpor, so the only

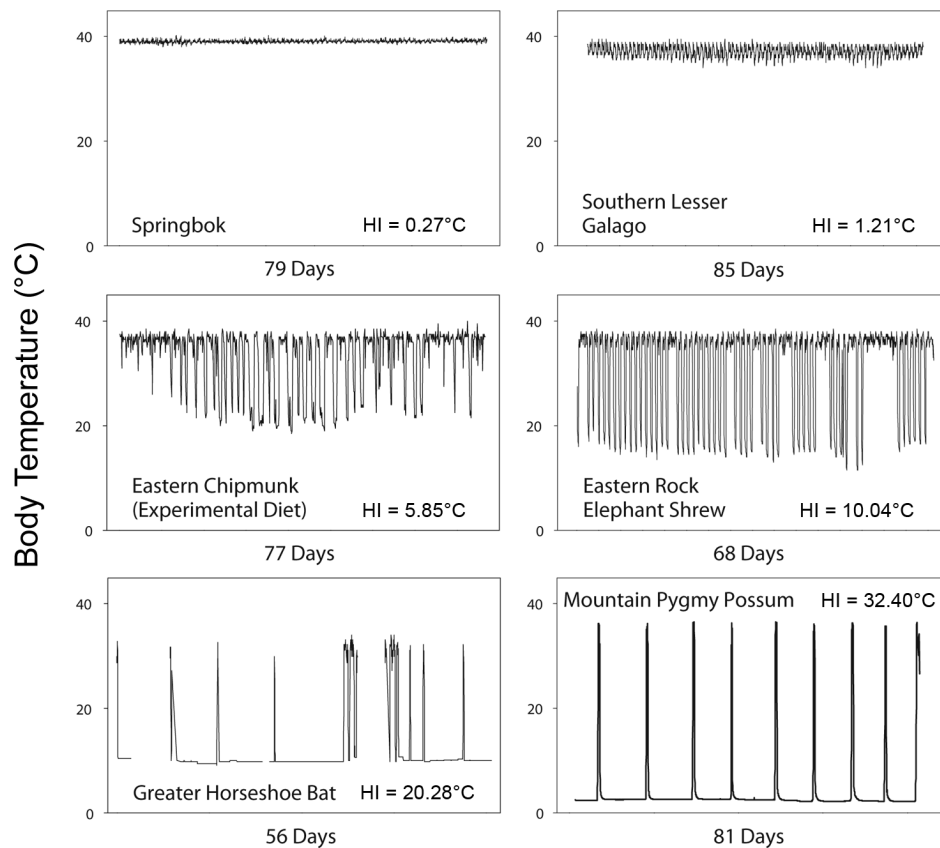


Figure 4. Representative traces of a variety of thermoregulatory patterns and their average daily heterothermy index (HI). The HI for each tracing was calculated as the average HI for each 24-h period. The title of the X-axis represents the length of the entire tracing; in some cases, daily averages were calculated from fewer days because of missing data. To emphasize the flexibility of the HI approach, we made no attempt to standardize the period analyzed. Data are from Kortner and Geiser (1998), Park et al. (2000), Mzilikazi and Lovegrove (2004), Munro et al. (2005), Mzilikazi et al. (2006), and Hetem et al. (2009).

possible way to compare heterothermy between adults and juveniles is with the minimum  $T_b$ . However, this may miss important temporal patterns, such as the time spent below  $T_{b-opt}$ .

### Comparing Interspecific Patterns of Thermoregulation

While HI is valuable in comparing treatment groups within a study, we believe that its most useful attribute is that it allows for any species, regardless of thermoregulatory pattern, to be included in a single analysis, thereby unifying research on homeotherms and heterotherms. As simple examples, we calculated average daily HI values for mammals representing a range of thermoregulatory patterns. Figure 4 shows  $T_b$  traces for “representative” individuals of six mammal species for which complete or nearly complete winter tracings are available. Qualitative observations agree well with calculated daily HI values. Individuals that exhibit lower minimum  $T_b$  values and longer, more frequent torpor bouts have higher HI values.

Several advantages of using a single continuous metric to describe the thermoregulatory pattern of any species will become clear when reanalyzing previously described relationships across species, and more importantly, questions arise that would

be difficult to answer when heterothermy is defined via a torpor cutoff value. For example, several articles have reported a strong interspecific relationship between torpor characteristics and body mass (Geiser and Ruf 1995; Geiser 2004; Willis 2007). An important step in the study of endothermic thermal physiology would be to extend these analyses to determine whether variation in  $T_b$  is related to body mass across all species. More likely, the wide range of body masses of species showing little variation in  $T_b$  would lead to a triangle-shaped pattern (i.e., large residuals at low body masses and small residuals at high body masses), but a phylogenetically independent analysis (Garland et al. 1992, 1993; Blomberg et al. 2003) would likely also be needed (and would be possible using HI).

The use of a single metric also allows for more complete analyses of relationships between metabolic variables and thermoregulatory patterns. Geiser and colleagues (Geiser and Ruf 1995; Geiser 2004) have argued extensively and convincingly for a physiological distinction between species that exhibit only daily heterothermy and those capable of hibernation, based on variables describing energy expenditure (e.g., metabolic rates, thermal conductance, and  $Q_{10}$  values) and torpor patterns (e.g.,

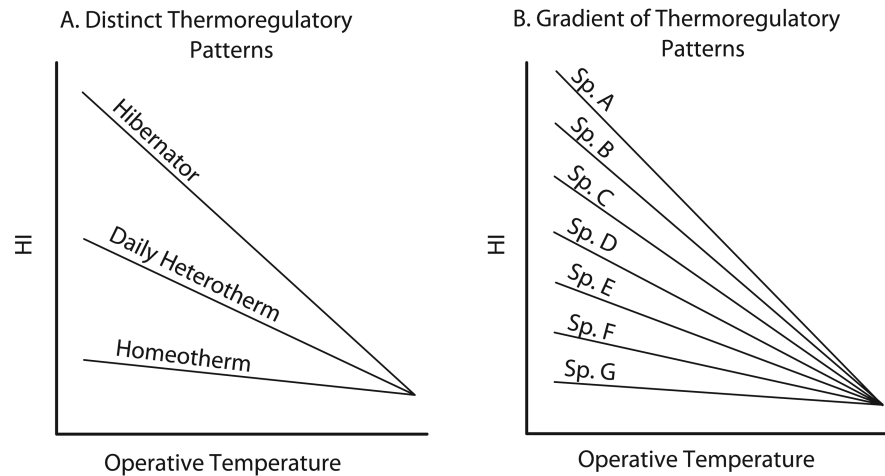


Figure 5. Previously unanswerable questions can be addressed using a single metric of heterothermy. For example, it is possible to determine if three distinct thermoregulatory patterns exist among endotherms representing homeotherms, daily heterotherms, and hibernators (A) or if a gradient of patterns exists between the two extremes with each species best described alone (B).

maximum torpor bout length and minimum  $T_b$ ). HI provides a robust method to determine whether this distinction extends to thermoregulatory patterns employed by all species or whether species can more adequately be described as falling along a gradient of thermoregulatory patterns (sensu Angilletta et al. 2010). Unlike previous analyses (Geiser and Ruf 1995; Geiser 2004), species that exhibit no torpor can be included. If three distinct thermoregulatory patterns exist in endotherms (i.e., homeothermy, daily heterothermy, and hibernation), we would predict the relationship between  $T_e$  and HI values of any species could be best described by one of three lines (Fig. 5A). If a gradient of thermoregulatory patterns exists, a model including a separate relationship for each species will fit the data better (Fig. 5B).

Finally, HI will be convenient in many comparative analyses. For instance, it will be possible to address questions about heterothermy in relation to phylogenetic age (e.g., are more basal taxa more heterothermic?), taxonomy (e.g., are mammals more heterothermic than birds?), or ecological factors (e.g., are desert species more heterothermic than mesic species?) using HI. The inclusion of all endothermic species on one scale, as is possible with HI, allows for more powerful analyses, both conventional and phylogenetically independent, than using the categorical distinctions of torpor versus no torpor that are frequently used.

## Conclusions

We propose a new comparative metric to quantify variation in  $T_b$  over any time frame in endotherms and provide several examples of where it can be employed. Advantageously, our metric is simple to calculate from  $T_b$  data that are routinely collected, so reanalysis of nearly any data set is possible. Because so many data sets already exist, we can begin addressing questions that require comparison of individuals during different

seasons, populations inhabiting different regions, or species that have evolved entirely different ecologies, physiologies, and life histories.

While HI may be most immediately useful to biologists studying torpor and hibernation, it has applications well beyond that subdiscipline, the most important being the study of adaptive thermoregulation, which to date has focused heavily on ectotherms (Huey and Slatkin 1976; Angilletta et al. 2002; Kingsolver 2009). A hurdle in the study of adaptive thermoregulation in endotherms has, in our opinion, been the lack of an appropriate index to estimate variation in  $T_b$  across all endotherms. By placing thermoregulatory strategies of all endothermic species on one scale, we can begin looking at ecological and evolutionary forces that drive optimal expression of  $T_b$ . Further, we can widen the focus of comparative studies from species that display fluctuations large enough to meet a torpor cutoff value to all species across the entire continuum of endothermic thermoregulatory patterns. In general, variation in  $T_b$  has been studied in three contexts essentially independently of each other: (1) documenting occurrence of facultative responses of torpor and hibernation and to a much lesser extent the adaptive reasons for these responses (e.g., Geiser 2004), (2) documenting and describing circadian rhythms (e.g., Refinetti and Menaker 1992), and (3) determining the significance of regional and temporal hyperthermia in hot climates (e.g., Mitchell et al. 2002). Use of a single comparative metric means we can incorporate research done by labs in each of these three research foci to increase our understanding of larger patterns in endothermic thermoregulation.

We suggest that important early steps in the application of this metric should be to determine (1) the relationships between variation in  $T_b$  and other commonly measured characteristics such as body mass and (2) whether physiological distinctions between homeotherms, daily heterotherms, and hibernators

translate into distinct differences in thermoregulatory patterns or whether a gradient of patterns exist. Ultimately, however, the goal should be to ask questions about the adaptive significance of the thermoregulatory patterns and answer those questions with manipulative experiments and comparative analyses (Angilletta et al. 2010) made easier by use of a single metric of heterothermy.

### Acknowledgments

Special thanks to Dr. Craig Willis and Dr. Mark Brigham, who disagree with many of our assertions herein but nonetheless made the article stronger by providing their usual brilliant comments. D. Munro, M. Humphries, and D. Thomas kindly provided the entire data set from one of their studies for our reanalysis. M. Brigham, F. Geiser, R. Hetem, G. Kortner, A.-M. Mustonen, N. Mzilikazi, K. Park, G. Rathbun, and S. Zervanos provided body temperature data—some presented herein, some not—for the figures. We thank three anonymous reviewers for their constructive comments on an earlier version of the manuscript.

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