In recent years, there has been a proliferation of papers reporting temporal variation of body temperature ($T_b$) in endotherms. For several reasons, not least the importance of facultative hypothermic responses in the evolution of endothermy (e.g., Grigg et al., 2004; Malan, 1996), the majority of these papers have focused on describing patterns of torpor and hibernation (hereafter, collectively referred to as “torpor”). Generally speaking, the authors of these papers rely on threshold $T_b$ values (referred to the “cut-off method” herein) to distinguish between homeothermic and heterothermic species. In practice, the cut-off method categorizes each $T_b$ datum as either torpor or normothermy based on whether the $T_b$ is above or below the cut-off value. The method is logistically simple and therefore an attractive method to analyze $T_b$ data. However, it has several inherent problems and implications, some recognized but others not, and we believe that authors should be aware of the limitations of the technique.

Theoretically, using a consistent threshold to define periods of torpor makes comparing torpor patterns (e.g., the number and length of torpor bouts) between individuals, populations, and species logistically feasible. In practice, however, the cut-off method suffers from several problems that make comparative analyses based on this technique questionable. As widely recognized and often pointed out by other authors (Barclay et al., 2001; Willis, 2007), this method relies on the largely arbitrary determination of appropriate $T_b$ cut-off values and leads to considerable variation in application of the method from study to study. For example, Barclay et al.’s (2001) survey of recent literature shows that torpor cut-off values range from 26°C to 36°C with no consistency, even among studies on related taxa. Even after recognizing that different species can be physiologically defined as entering torpor at different temperatures (Merola-Zwartjes and Ligon, 2000), the often arbitrary nature of $T_b$ values used makes direct comparisons between studies statistically difficult at best.

Several attempts have been made to impose empirical validity on the definition of torpor cut-off values (McKechnie et al., 2007; Smit and McKechnie, 2010; Willis, 2007), but these methods have not yet been widely employed.

One key issue is whether cut-off values correspond with transitions between different physiological states. Very few data are available in this regard, but in at least some species the $T_b$ ranges of different physiological states have been shown to overlap. Merola-Zwartjes and Ligon (2000) showed that the upper $T_b$ limits for torpor (defined as the loss of the capacity for flight and responses to external stimuli) in Puerto Rican Todies (Todus mexicanus) was 29.3°C, but the lower limit for non-torpid individuals was 27.9°C. Likewise, the capacity for flight at $T_b < 30$°C (a value often used as a cut-off) has been demonstrated in several bat species (Choi et al., 1998; Genoud, 1993; Hirshfield and O’Farrell, 1976; Studier and O’Farrell, 1972) and one bird species (Austin and Bradley, 1969). The notion that an endotherm capable of coordinated locomotion should be considered torpid, purely on account of a reduced $T_b$, is inconsistent with the IUPS definition of torpor (IUPS Thermal Commission, 2003). Although reduced responsiveness to external stimuli (or lethargy) associated with a low $T_b$ would impose an ecological cost on a torpid endotherm, very few studies have investigated how locomotor performance correlates with $T_b$ in endotherms. Therefore, unless torpor cut-off values can be shown to correspond to an actual physiological state, the use of this method will remain arbitrary.

Besides the arbitrary nature of $T_b$ cut-off values (Barclay et al., 2001; Willis, 2007), several other problems may be associated with definitions of torpor based on specific $T_b$ values. First, because most studies focus on determining when an animal is torpid, any period where the animal’s $T_b$ does not reach the cut-off is implicitly disregarded as ecologically and energetically inconsequential, despite the fact that shallow bouts are likely important to the animal in terms of energy balance (Willis and Brigham, 2003). It is difficult to argue that a bout in which minimum $T_b$ is 1°C above the cut-off value is ecologically less important to the animal than a bout...
in which minimum $T_b$ is 1 °C below it. In theory, this problem can be alleviated (but not completely avoided) using metabolic rates to define torpor instead of $T_b$ (Willis, 2007), but again, this approach has rarely been employed.

Second, the cut-off method leads to a dichotomous categorization of species—either a species’ $T_b$ varies enough to cross the cut-off established by the authors and is therefore a “heterotherm”, or does not and is therefore a “homeotherm”. While these distinctions should obviously be considered qualitative and not quantitative, they have had three unfortunate and, in our opinion, largely unrecognized effects on the study of thermoregulation in endotherms. First, the use of these qualitative categories has encouraged “stamp-collecting” studies where the goal is often to simply determine if a species can be considered a heterotherm, with seemingly less attention paid to ecological or evolutionary drivers behind variation in $T_b$. Because the primary research question in such cases is simply whether a species uses torpor, most studies that involve recording $T_b$ involve species that researchers expect to exhibit torpor and it is often discussed as unexpected if those animals remain homeothermic (e.g., see Wilson et al., 2010). This trend undoubtedly biases our understanding of the distribution of heterothermy across the mammalian and avian phylogenies. Second, grouping species into categories makes comparisons of $T_b$ variation across all species nearly impossible. This puts an unnecessary constraint on how we view the evolutionary and ecological importance of variation in $T_b$ in endotherms (Angilletta et al., 2010) because analyses do not give equal weight to species that use torpor and those that do not. Third, one of the consequences of the widespread use of arbitrary cut-off values has been that the study of heterothermy has often taken a somewhat phenomenological direction, with an emphasis on identifying patterns rather than broad-scale processes.

Finally, using a $T_b$ cut-off implicitly assumes that species considered homeotherms do not attempt to maximize fitness in an adaptive way. The logic follows as such: in a hypothetical environment with no costs, energy availability (Gilchrist, 1995) and maintaining a wide thermal breadth is costly (Gabriel and Lynch, 1992). In reality, costs inherent to perfect thermoregulation mean that every species displays some degree of variation in $T_b$ (Angilletta et al., 2010). Therefore, variation in $T_b$ can be viewed as an indicator of the relative strengths of costs and benefits of precise thermoregulation (i.e., maintaining perfectly constant, high $T_b$; sensu Angilletta et al., 2010) for an organism. In other words, as the cost/benefit ratio of maintaining a high, constant $T_b$ increases, variation in $T_b$ should increase as well. Assuming this logic is reversible and it is possible to quantify variation in $T_b$, we should be able to estimate relative costs and benefits of perfect thermoregulation for a given individual (or population or species) for a given set of environmental conditions. In some instances, using the torpor cut-off approach to estimate heterothermy necessarily assumes a cost/benefit ratio of essentially zero (i.e., very low costs and very high benefits to perfect thermoregulation) for all species whose $T_b$ does not fluctuate enough to reach the arbitrarily defined cut-off value. For example, using the standard measure of time spent torpid, any species that does not reach the cut-off value would have a value of zero, regardless of whether their $T_b$ fluctuates by 1 °C or 5 °C (Fig. 1B). Thus, the implication is that species with both 1 °C and 5 °C have the same cost/benefit ratio of thermoregulation (although not necessarily the exact same costs and benefits). However, if the cost/benefit ratio truly was equal for all organisms that do not make the cut-off value, we should never record any $T_b$ in a species considered a homeotherm that is above the cut-off line but different than the optimal $T_b$ for fitness (i.e., $T_b$ variation should be zero for all homeothermic species). One could argue that these small fluctuations are simply the result of some biophysical constraint on perfect homeothermy, but it has been argued elsewhere that small fluctuations must be adaptive or endotherms would all maintain constant $T_b$’s at the lowest temperature that does not sacrifice performance (Angilletta et al., 2010). Obviously this is a theoretical, not logistical issue and may not be vital when comparing the time two individuals spend in torpor. However, the use of torpor cut-off values involves the implicit assumption that small fluctuations in $T_b$ are non-adaptive, and is a characteristic of which authors using the torpor cut-off approach should be aware.

We argue that overemphasis on use of the torpor cut-off has stifled creativity in the study of $T_b$ patterns in endotherms. Unfortunately, because the weaknesses of the cut-off method have rarely been discussed, few alternate techniques are presently available to analyze $T_b$ patterns in studies of homeothermy and heterothermy (Boyles et al., 2011; Gordon, 2009). Each of the available techniques has different strengths and weaknesses (Boyles et al., 2011), but we argue the weaknesses of the cut-off method are substantial. Thus, we suggest that analytical methods other than (or occasionally in conjunction with) the torpor cut-off method are likely to lead to more efficient acquisition of knowledge regarding heterothermy in endotherms. We suggest that major advances in this field will come more quickly if, in addition to clever experiments, researchers actively attempt to determine new methods to analyze $T_b$ patterns.

Fig. 1. (A) A trade-off exists between performing at a high level or across a wide temperature range (Gilchrist, 1995). In a hypothetical environment with no costs, a thermal specialist that maintains a constant body temperature ($T_b$) should have higher performance, and therefore higher fitness than a thermal generalist that exhibits wide fluctuations in $T_b$ (adapted from Angilletta et al., 2010). (B) Use of a torpor cut-off value to define heterothermy necessitates that all species that exhibit fluctuations in $T_b$ too small to make the arbitrary torpor cut-off set by the authors receive the same heterothermy value (in this example, measured as time in torpor) and therefore experience the same cost/benefit ratio of thermoregulation. Every species that falls into this category should maintain a perfectly constant $T_b$ (i.e., no variation in $T_b$) because the cost/benefit ratio is the same as maintaining any level of variation up to the torpor cut-off, while the performance is maximized.

References


