

# Embracing heterothermic diversity: non-stationary waveform analysis of temperature variation in endotherms

Danielle L. Levesque<sup>1</sup> · Allyson K. Menzies<sup>2</sup> · Manuelle Landry-Cuerrier<sup>2</sup> · Guillaume Larocque<sup>3</sup> · Murray M. Humphries<sup>2</sup>

Received: 1 September 2016 / Revised: 3 December 2016 / Accepted: 26 February 2017 / Published online: 28 March 2017  
© Springer-Verlag Berlin Heidelberg 2017

**Abstract** Recent research is revealing incredible diversity in the thermoregulatory patterns of wild and captive endotherms. As a result of these findings, classic thermoregulatory categories of ‘homeothermy’, ‘daily heterothermy’, and ‘hibernation’ are becoming harder to delineate, impeding our understanding of the physiological and evolutionary significance of variation within and around these categories. However, we lack a generalized analytical approach for evaluating and comparing the complex and diversified nature of the full breadth of heterothermy expressed by individuals, populations, and species. Here we propose a new approach that decomposes body temperature time series into three inherent properties—waveform, amplitude, and period—using a non-stationary technique that accommodates the temporal variability of body temperature patterns. This approach quantifies circadian and seasonal variation in thermoregulatory patterns, and uses the distribution of observed thermoregulatory patterns as a

basis for intra- and inter-specific comparisons. We analyse body temperature time series from multiple species, including classical hibernators, tropical heterotherms, and homeotherms, to highlight the approach’s general usefulness and the major axes of thermoregulatory variation that it reveals.

**Keywords** Heterothermy · Homeothermy · Endothermy · Thermoregulation · Torpor · Hibernation · Body temperature · Additive quantile regression

## Introduction

“Heterothermy: The pattern of temperature regulation in a tachymetabolic species in which the variation in core temperature, either nychthemorally or seasonally, exceeds that which defines homeothermy (Gk. hetero—different; therme—heat).”—(IUPS Thermal Commission 2003).

Endotherms are not strict homeotherms and show a large degree of variation in the precision of their body temperature ( $T_b$ ) regulation.  $T_b$  variability includes daily changes between active and rest phase as well as more extreme differences, with accompanying decreases in metabolic rates, in the form of daily torpor or hibernation (Boyles et al. 2013; Ruf and Geiser 2015). Yet, when compared with the comprehensive literature on the evolution and adaptive significance of  $T_b$  variability in ectotherms, our understanding of homeothermy and heterothermy in endotherms is lacking (Angilletta et al. 2010; Boyles et al. 2013). This is in large part due to a historical focus on a torpor versus homeothermy dichotomy that largely ignored non-torpid variability in  $T_b$  (Boyles et al. 2013), a northern temperate research bias (Dausmann et al. 2009; Canale et al. 2012) and, perhaps most importantly, a lack of consensus on basic definitions of the various thermoregulatory states (Dausmann

Communicated by F. van Breukelen.

This manuscript is part of the special issue Hibernation—Guest Editors: Frank van Breukelen and Jenifer C. Utz.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00360-017-1074-9) contains supplementary material, which is available to authorized users.

✉ Danielle L. Levesque  
danielle.l.levesque@maine.edu

<sup>1</sup> School of Biology and Ecology, University of Maine, Orono, ME 04469, USA

<sup>2</sup> Natural Resource Sciences, McGill University, Macdonald Campus, Sainte-Anne-de-Bellevue, QC H9X 3V9, Canada

<sup>3</sup> Quebec Centre for Biodiversity Science, McGill University, Montreal, QC H3A 1B1, Canada

et al. 2009; Boyles et al. 2011b; Canale et al. 2012; Ruf and Geiser 2015). Increasingly, as we gather more data from species from around the globe, and especially those from lower latitudes, where climate and resource availability are less predictable, the lines between the classic definitions of a ‘homeotherm’ (little to no  $T_b$  variability), ‘daily heterotherm’ (short shallow torpor bouts) and ‘hibernator’ (multi-day torpor) are becoming increasingly blurred (Dausmann et al. 2009; McKechnie and Mzilikazi 2011; Canale et al. 2012; Boyles et al. 2013). Although it might be possible to classify a species in one of the categories based on its physiological potential (Ruf and Geiser 2015), such strict categories are often not reflective of what happens at an individual or population level in the field, where heterothermy can be highly variable and dependent on a number of physiological and environmental factors (Lehmer et al. 2006; Landry-Cuerrier et al. 2008; Canale et al. 2012).

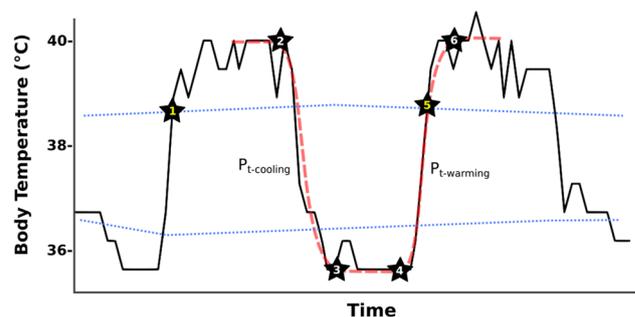
Metrics or standardizable methods of defining torpor have received recent attention (Willis 2007; Boyles et al. 2011b; Muñoz-Garcia et al. 2013), yet an often arbitrary cut-off temperature is still one of the more common methods for determining torpor use (Boyles et al. 2011a). Attempts have been made to include a less arbitrary characterization of  $T_b$  variability by also including simultaneous measures of metabolism (Muñoz-Garcia et al. 2013); however, this is not yet feasible under most free-ranging conditions and therefore is not practical in most research contexts. The most commonly employed metric to date has been the heterothermy index (HI, Boyles et al. 2011b). The HI gives an index of the variability of  $T_b$ , with the advantage of including variability both above or below ‘normothermic’  $T_b$ . However, the HI has a number of drawbacks. The first is that the HI is a single descriptor, too often averaged over time. Therefore, unless specified by the user, it does not discriminate for example, between short, deep torpor bouts and long, shallow torpor bouts; two types of torpor expression that are often different at a physiological level (Geiser 2004; Ruf and Geiser 2015). The HI also relies on identifying a fixed ‘normothermic’ value, which is not possible for many highly heterothermic species (Eisen-traut 1960; Stephenson and Racey 1994; Levesque et al. 2014).

A pre-requisite for understanding the physiological, ecological, and evolutionary implications of endotherm heterothermy is a generalized analytical approach for evaluating and comparing the diversified nature and full breadth of heterothermy expressed by individuals, populations, and species. In this paper, we introduce a new analytical method that expresses  $T_b$  variation as individual waveforms, which maximizes generality and standardization while avoiding thresholds and many a priori assumptions. When applied to a wide range of species with differing levels of  $T_b$  variability, we hope to characterize the major axes

of thermoregulatory variation and provide a consistent, repeatable means of classifying  $T_b$  patterns.

## Materials and methods

We characterize  $T_b$  variation as a series of waveforms, each with a characteristic shape, period, and amplitude. The code needed to run the analytical method we propose is provided in Supplementary Materials in the R language (R Core Team 2016). Because patterns of variation in  $T_b$  can change over time, we use a non-stationary technique, additive quantile regression analysis (Koenker et al. 1994; Koenker 2016) that segments the time series into a series of clips, each comprising warm to cold to warm variation, then fit a separate waveform to each clip. We avoid a threshold-based definition of variation of interest (e.g.  $T_b < 30^\circ\text{C} = \text{torpor}$ , or  $T_b \text{ range} > 5^\circ\text{C} = \text{heterothermy}$ ) by calculating 25th and 75th percentile additive quantile regression envelopes and then extracting clips in which  $T_b$  goes above the 75th percentile, then below the 25th percentile, then back above the 75th percentile envelopes (Fig. 1). This prioritizes the dominant amplitude waveform present in any given segment. For example, if a time series begins with small amplitude variation between 35 and 37°C for several days, then transitions to larger amplitude variation between 20 and 36°C, the clip algorithm would identify and analyse 1–2°C amplitude waves at the start of the time series and the 8–16°C amplitude waves later in the time series. This approach does not preclude examination of finer amplitude oscillations present within larger amplitude



**Fig. 1** A sample trace illustrating 75 and 25% quantile regression lines (lower and upper dotted blue lines, respectively). The full waveform starts 1 when body temperature rises above the 75% line (dotted green line), continues until it has dipped below the 25% (dotted blue) line and ends when it reaches the 75% line once more (5). The red dashed line represents the fitted logit curves. The temperature difference between the predicted estimates from the logit curves at points 3 and 2 is the cooling amplitude, while the difference between points 6 and 4 is the warming amplitude. The full period (times at 5–1) can be decomposed into a warm (2–1), cooling (3–2), cool (4–3) and warming (6–4) phases. The cooling and warming rates represent the steepness of decrease and increase of the associated logit curves

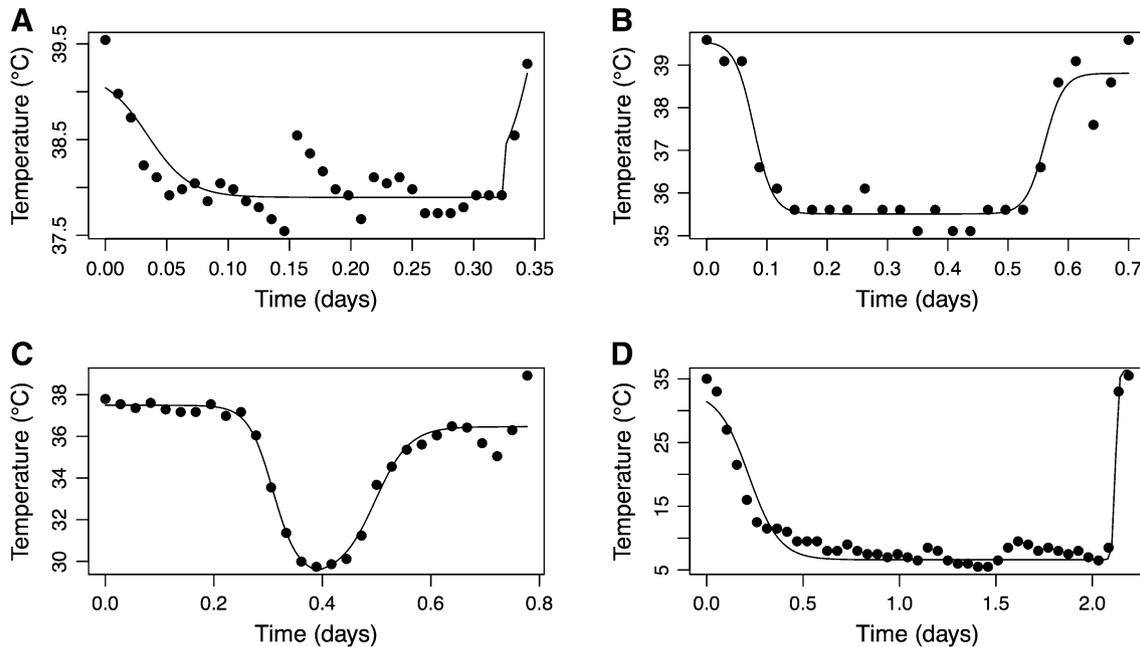
waves, which can be analysed as the residuals of the dominant amplitude waveform (see “Discussion”).

Body temperature variation differs from a simple sine wave and most other symmetrical waveforms, because cooling tends to take longer than warming and there is often (but not always) an extended period of thermal stasis at the bottom and/or the top of the waveform. Nevertheless, we have found fitting two logit curves—one for the warm to cool phase and one for the cool to warm phase, with the second logit constrained to begin at the same  $T_b$  where the first logit ended—to be a robust and flexible waveform that provides an excellent goodness of fit to diverse forms of  $T_b$  variation (Fig. 1). These two logit curves are fitted through a nonlinear optimization function to the temperature readings in each clip.

Once a waveform is fit to a clip, we extract six properties of the clip and waveform; amplitude, period (calculated from the clip), cooling rate, warming rate, warm  $T_b$  and cool  $T_b$ . Amplitude, in units of temperature (typically °C), reflects the extent of  $T_b$  variation from the top of the waveform to the bottom of the waveform. Period, in units of time (min, h, or days), reflects the duration (return time) of dominant amplitude temperature variation. Period can be broken down into four phase durations—warm, cooling, cool, warming—that together sum to the full cycle period. Cooling rate is calculated as the scaling factor of the logit curve during the cooling phase and expressed in °C/min. Similarly, warming rate is calculated as the scaling factor of the logit curve

during the warming phase and is also expressed in °C/min. Two additional properties, related to amplitude, but focused on  $T_b$  values rather than the extent of  $T_b$  variation, are warm  $T_b$ , expressed in units of temperature and calculated as the average of all  $T_b$  measures comprising the warm phase, and cool  $T_b$ , in the same units, calculated as the average of  $T_b$  measures comprising the cold phase (Figs. 1, 2).

We suggest five diagnostics to identify and possibly filter out waveforms that are poorly supported by the data. The first diagnostic concerns the convergence of the optimisation routine. If, for a given clip, the optimisation did not converge, it usually implies that the fit of the model to the data is very poor or impossible. The second diagnostic is an  $r$ -squared goodness of fit measure, derived from model sums-of-squares divided by the total sum of squares. It varies between 0 and 1, with 1 reflective of a perfect fit between the fitted curve and  $T_b$  observations. The third diagnostic, amplitude:precision ( $A:P$ ), is the ratio of the fitted curve’s amplitude and the precision of the  $T_b$  recording device. The fourth diagnostic, period:frequency ( $P:F$ ), is the ratio of the fitted curve’s period and the frequency of  $T_b$  observations made by the recording device. The final diagnostic was based on the minimum number of observations required to fit a complete waveform (i.e. a minimum of six observations was required). In the analyses presented in the “Results” section, we have excluded any waveforms that (1) did not converge, (2) where  $r^2 < 0.5$ , (3)  $A:P < 2$ , (4)  $P:F < 4$ , and/or (5) where the number of observations is  $< 6$ .



**Fig. 2** Examples of waveforms and fitted curves from **a** a red squirrel with a period of <1 day, **b** a treeshrew with a period of 1 day, **c** a daily torpor bout from a mouse lemur, and **d** a multiday torpor bout from a hibernating chipmunk

The process of decomposing the time series into a series of clips, then fitting a waveform to each clip, then reporting the properties of the fitted waveforms yields a series of values describing the nature of  $T_b$  variation over time. The process started with a time series of  $T_b$  observations and progresses to a time series of waveform properties. This is indeed a progression, because the extracted waveform properties are of the correct type and in the right units to be of interest and to be directly interpretable by thermal biologists; amplitudes in units of temperature, periods in units of time (and decomposable into phases), cooling and warming rates in units of temperature per time, and absolute temperatures in temperature units. However, the analysis does not yield a single value for each of these variables of interest, nor does it automatically yield an average or a range. Instead it yields a series of values, reflective of the diversity of body temperature fluctuations expressed by individual animals and how these vary over time. We encourage investigators to employ methods of data analysis and data visualization that exhibit rather than conceal the extent of within and among individual variation in body temperature

fluctuations. In the “Results” section we highlight several analytical and visualization approaches, which we believe to be useful in this regard.

For the purpose of this paper we performed a preliminary set of analyses on five species representing classical homeotherms, daily heterotherms, and hibernators. To best tailor our analytical approach to the diversity of temperature profiles (Table 1), we analysed a temperate homeotherm (the red squirrel, *Tamiasciurus hudsonicus*, Order: Rodentia), a tropical homeotherm (the large treeshrew, *Tupaia tana*, Order: Scandentia), a daily heterotherm (the golden-brown mouse lemur, *Microcebus ravelobensis*, Order: Primates), a temperate hibernator (the eastern chipmunk, *Tamias striatus*), and a tropical hibernator (the greater hedgehog tenrec, *Setifer setosus*).

## Results

By employing a flexible, adjustable boundary, through additive quantile regression analysis, we were able to

**Table 1** Description of temperature profiles from one representative individual of five species, representing classical homeotherms, daily heterotherms, and hibernators used to best tailor our waveform analysis

Species	Location	Time of the year	Sampling frequency (min)	Number of clips	% clips remaining after running diagnostics
Red squirrel <i>Tamiasciurus hudsonicus</i> <sup>a</sup> $T_b$ $n=3$	Yukon, Canada (61°N, 138°W)	Jan–Mar (temperate winter)	15	94	47% (44 clips)
Chipmunk <i>Tamias striatus</i> <sup>b</sup> $T_{skin}$ $n=3$	Quebec, Canada (45°25'N, 71°40'W), Pennsylvania, USA (40°38'N, 76°00'W)	Nov–Apr (temperate winter)	30	104	62% (64 clips)
Mouse lemur <i>Microcebus ravelobensis</i> <sup>c</sup> $T_b$ $n=1$	Ankarafantsika NP (16°19'S, 46°48'E), Madagascar	May–Sep (Austral winter)	40	120	77% (92 clips)
Tenrec <i>Setifer setosus</i> <sup>c</sup> $T_b$ $n=1$	Ankarafantsika NP (16°19'S, 46°48'E), Madagascar	May–Nov (Austral winter)	42	80	64% (52 clips)
Treeshrew <i>Tupaia tana</i> <sup>d</sup> $T_b$ $n=3$	Kampung Barieng (1°30'N, 10°10'E), Sarawak Malaysia	Nov–May (monsoon season)	42	199	99% (197 clips)

Temperature profiles were “clipped” into multiple waveforms, each comprised of a warming and a cooling phase. The *number of clips* represents the total number of waveforms extracted from the initial temperature profile, whereas the *% clips remaining after diagnostics* represents those clipped waveforms that, after a filtering process, were considered supported by the data

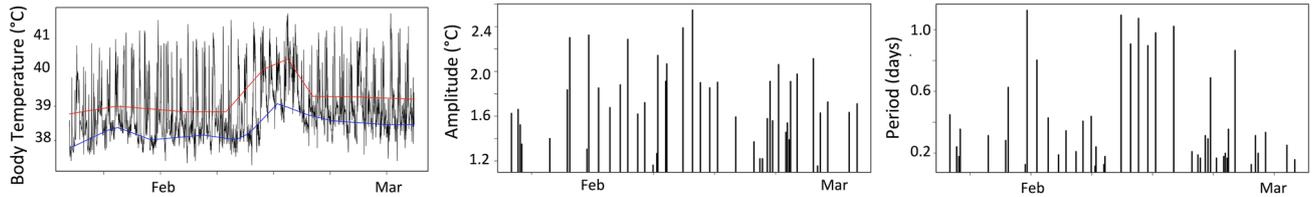
Data source: <sup>a</sup>S.B. Woods and MMH unpublished data, <sup>b</sup>Munro et al. (2005), <sup>c</sup>Lovegrove et al. (2014), <sup>d</sup>DLL, B.G. Lovegrove and A.A. Tuen unpublished data

determine the dominant amplitude waveforms for species with a wide range of  $T_b$  variability. Without discriminating between warming or cooling, our method is versatile enough to be able to characterize the seasonal variation in a temperate hibernator (eastern chipmunk, Figs. 3, 4) as well as the fine-scale facultative increases in  $T_b$  seen in a tropical homeotherm (large treeshrew, Fig. 3). Similarly, through the use of a standardized set of analyses, we are able to make meaningful between-species comparisons

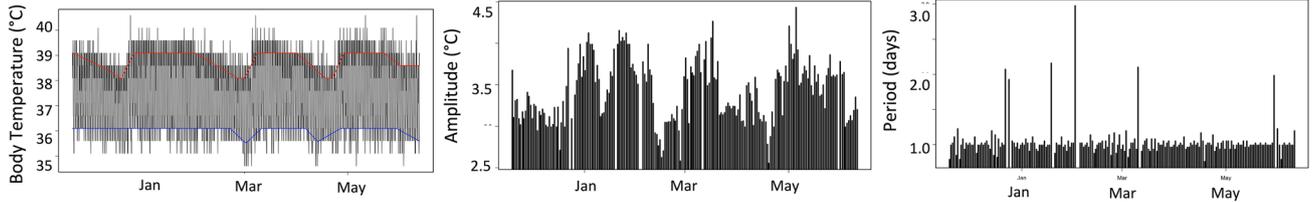
(Fig. 5) as well as account for both seasonal and individual variability.

For the five species we analyzed, our method was successful at tracking variation in the dominant pattern of  $T_b$  variation, and allowed us to repeatedly measure multiple waveform metrics over time (Figs. 3, 4, 5). In fact, intra-individual variation in  $T_b$  waveforms is well captured by our method at multiple timescales. Our approach clearly shows the larger scale seasonal pattern of temperate

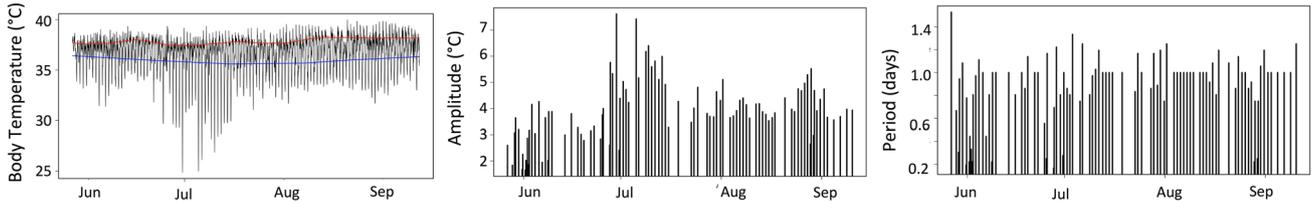
The North American red squirrel, *Tamiasciurus hudsonicus*



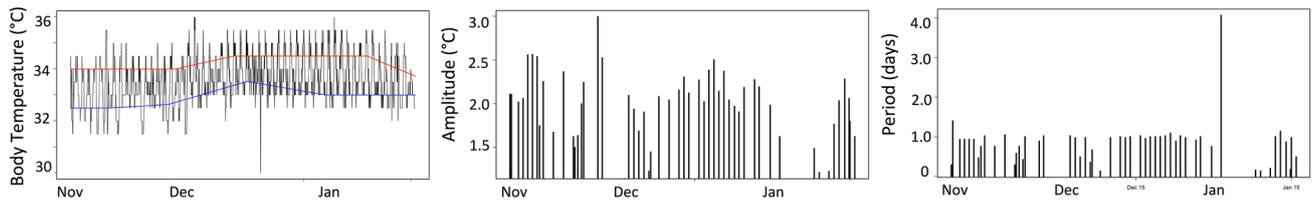
The large treeshrew, *Tupaia tana*



The golden-brown mouse lemur, *Microcebus ravelobensis*



The greater hedgehog tenrec, *Setifer setosus*



The eastern chipmunk, *Tamias striatus*



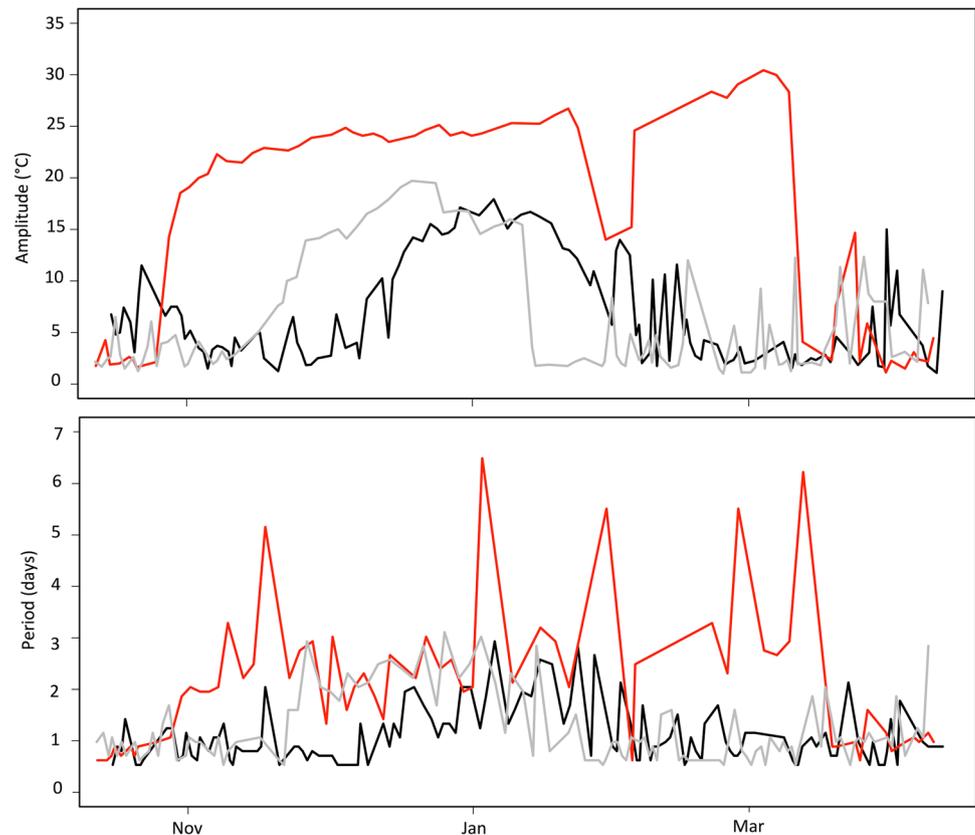
**A**

**B**

**C**

**Fig. 3** Full  $T_b$  traces (a) for the five species analysed showing the 75th and 25th quantile envelopes and dominant waveform amplitude (b) and period (c)

**Fig. 4** A within-species comparison of chipmunks fed diets differing in the level of poly-unsaturated fatty acid (see Munro et al. 2005, for details). The three individuals (representative of different treatments: control = *red*, natural PUFA = *grey*, high PUFA = *black*) show differences in amplitude and period of the dominant  $T_b$  waveforms throughout hibernation



hibernation (Fig. 3a), but also responds to the finer scale variation between reproductive states in a more homeothermic mammal (the large treeshrew Fig. 3b, where the changes in amplitude potentially correspond to the estrous cycle, DLL pers. obs.). Furthermore, inter-individual differences associated with experimental treatment or different environmental contexts can be clearly distinguished across time (Fig. 4).

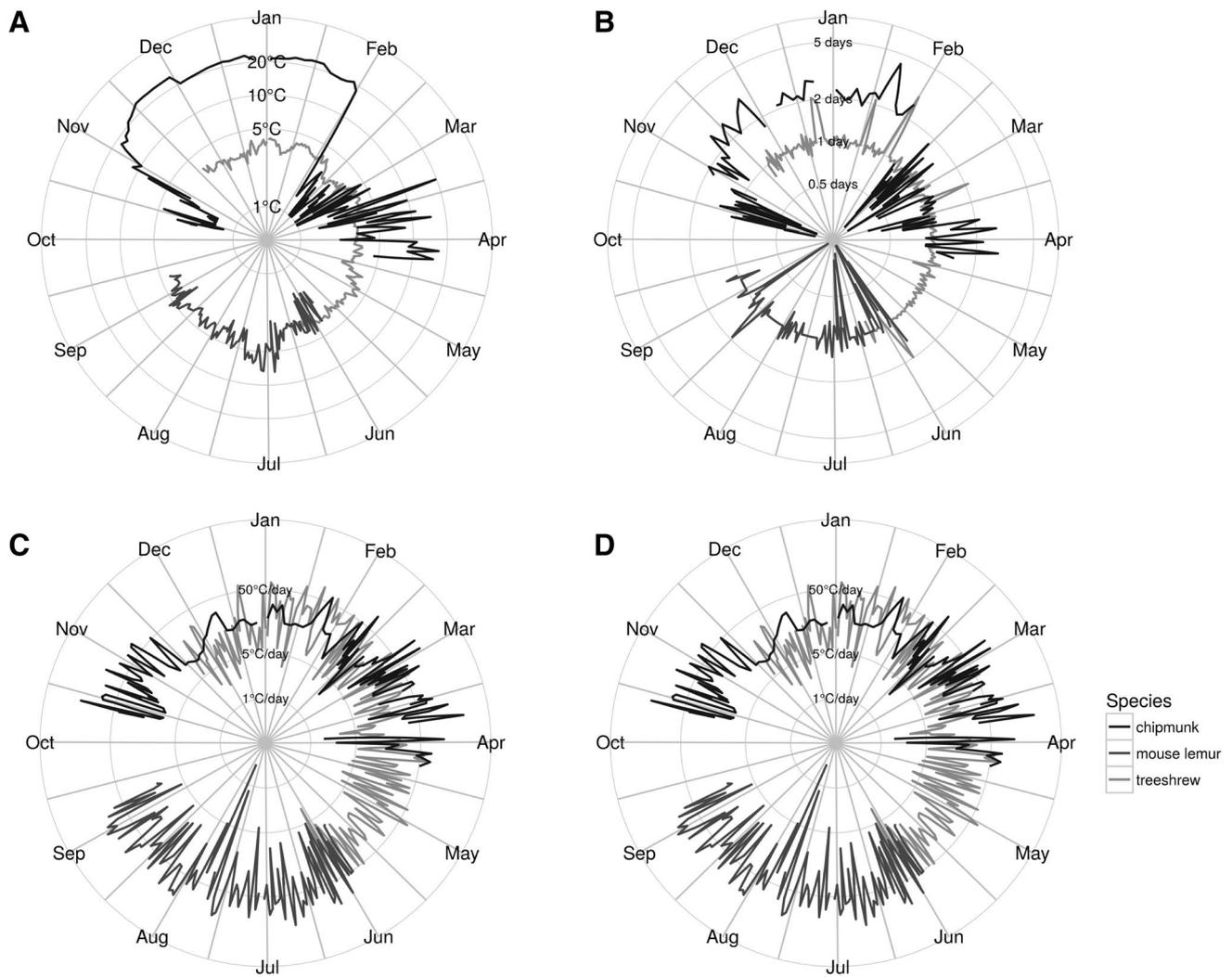
In addition to identifying what previous methods would have classified as torpor, our analysis was able to identify, and make available for comparison, diel patterns in  $T_b$ . For some species (such as the large treeshrew, Fig. 3) the dominant waveform occurred over a 24-h period covering a single active and resting period. However, for others (the red squirrel, and the chipmunk Figs. 2, 3) the dominant waveform often had a period of less than a day. This is not an error, but rather an indication that for some species the rest-phase decrease in  $T_b$  is less than the variability that occurs during the active phase.

We used a variety of diagnostics to assess fit or “goodness” of clips extracted from the raw data. None of the clips were excluded based on convergence values suggesting the logit–logit waveform is accurate, for the most part. Filtering by  $r^2$  values alone excluded the largest number of clips, with only a few being excluded by amplitude, precision or number of observations. Even though an average of 30% of

total clips identified were excluded after running diagnostics, most of these were small amplitude and short period waves and, the majority of clipped bouts could still be used to visualize dominant patterns in  $T_b$  variation (Table 1). Our current analyses focused primarily on the methods for determining and characterizing dominant waveforms and extract basic parameters for each waveform. Future refinements in the curve fitting approach could allow the detection of finer waveform characteristics, and the automated classification of waveform properties (e.g. passive versus active warming).

## Discussion

The study of endothermic thermoregulation has largely focused on homeothermy, torpor, and mean  $T_b$  (Clarke and Rothery 2008; Lovegrove 2012b; Ruf and Geiser 2015), as a result, a true understanding of the level and the degree of variability in endothermic  $T_b$  has eluded us. This, in turn, has hampered our ability to adequately test hypotheses on the evolution of endothermy. Our analysis provides a means of quantifying, and qualifying,  $T_b$  variability in a standardized manner that can be applied to both between- and within-species studies. By expressing  $T_b$  variation as a series of waveforms, we are able to calculate period,



**Fig. 5** Yearlong  $T_b$  from a chipmunk (hibernator), mouse lemur (daily heterotherm) and a homoeotherm (treeshrew) illustrating the major characteristics of each waveform **a** amplitude, **b** period, **c** cooling rates and **d** heating rates. The data are plotted on a log scale for visual clarity

amplitude, warm and cool  $T_b$ , and rates of warming and cooling from a number of contrasting  $T_b$  patterns using the same set of equations. We use non-discrete, data-informed parameters to define and describe heterothermy, as opposed to forcing discrete and arbitrary thresholds or categories on a widely variable trait. Although we set a user-defined envelope within the data (e.g. 75th and 25th quantiles), this boundary is defined by the range of  $T_b$  values in the dataset and, thus, flexibly responds over time to variations of  $T_b$ ; as the degree of heterothermy varies (i.e. over time or across species), so do the boundaries. This approach allows a thorough and systematic visualization of heterothermy both among and between species at various timescales and across ecological contexts.

When applied to multiple species, our method simplifies comparisons and facilitates visualization of inter-species variation. In fact, this approach reveals areas of overlap

between species commonly classified according to discrete heterothermy categories (Fig. 5). A further strength of our analyses is that the same methods are used in both within- and between-species analyses. Previous multi-species comparisons have had to rely on the physiological extremes experienced by a species, which can be considered to be their fundamental physiological niches, while our technique allows for more flexible analyses of realised niches (sensu Landry-Cuerrier et al. 2008). Not only will this be useful when comparing patterns of heterothermy under different environmental conditions, it is also the type of data that are needed for broader studies into the evolution of heterothermy and homeothermy in endotherms (Angilletta et al. 2010; Lovegrove 2012a). With the addition of a wider range species we hope to be able to assess the performance of fitting different waveforms, to refine our diagnostic process, and to better understand overall

variability of temperature regulation across a broad range of thermoregulatory patterns. Because our approach fits a separate waveform to each clip, it is possible to vary not only the amplitude and period but also the waveform shape over time. This latter possibility is attractive because it can help to differentiate bouts of  $T_b$  variation that are reflective of passive or active processes.

In the present approach, we have focused on the largest amplitude and longest waves present in the temperature time series. Nevertheless, shorter period and smaller amplitude variation may be present within larger waves. These waves within waves could be detected as residual variation around the fitted large wave, analogous to spectral or wavelet decomposition which has recently been applied to ambient temperature patterns (Dillon et al. 2016). Interestingly, the potential for non-stationarity in the largest waveforms also applies to any waves within waves that might be present. There is no reason, a priori, to expect these smaller waves to be constant through time. For example, there may be periodicity in  $T_b$  during a prolonged baseline torpor that is not present during entry into and arousal from torpor. The ability to search for smaller scale temperature variation in each clip, and each phase of each clip, without assuming the form of variation will persist over time, is another major advantage of the non-stationary clip-based approach we suggest.

## Conclusion

Using additive quantile regression analysis, we developed a new approach that decomposes  $T_b$  time series into three inherent properties—waveform, amplitude, and period—using a non-stationary technique that accommodates temporal variation in body temperature patterns. When applied to multiple species, our method enables comparisons and facilitates visualization of inter-species variation. In fact, this approach reveals a distinct overlap between species commonly classified according to discrete categories of heterothermy (Fig. 5). Using this technique to analyse the body temperature patterns of a wider range of species will allow for a broad phylogenetic and geographic analysis of endothermic  $T_b$  variability.

**Acknowledgements** We wish to thank the participants of the 14th International Hibernation Symposium in Las Vegas, August 2016, Brian McGill, Justin Boyles, and one anonymous reviewer for their helpful comments. We also thank all of our colleagues who provided us with raw data for analysis. AKM was funded by an NSERC (Canada) Vanier Graduate Scholarship. DLL was supported by the USDA National Institute of Food and Agriculture, Hatch project number 21623 through the Maine Agricultural & Forest Experiment Station. Maine Agricultural and Forest Experiment Station Publication Number 3524.

## References

- Angilletta MJ Jr, Cooper BS, Schuler MS, Boyles JG (2010) The evolution of thermal physiology in endotherms. *Front Biosci* 2:861–881
- Boyles JG, Smit B, McKechnie AE (2011a) Does use of the torpor cut-off method to analyze variation in body temperature cause more problems than it solves? *J Therm Biol* 36:373–375. doi:10.1016/j.jtherbio.2011.07.007
- Boyles JG, Smit B, McKechnie AE (2011b) A new comparative metric for estimating heterothermy in endotherms. *Physiol Biochem Zool* 84(1):115–123. doi:10.1086/656724
- Boyles JG, Thompson AB, McKechnie AE, Malan E, Humphries MM, Careau V (2013) A global heterothermic continuum in mammals. *Glob Ecol Biogeogr* 22(9):1029–1039. doi:10.1111/geb.12077
- Canale CI, Levesque DL, Lovegrove BG (2012) Tropical heterothermy: does the exception prove the rule or force a re-definition? In: Ruf T, Bieber C, Arnold W, Millesi E (eds) *Living in a seasonal world: thermoregulatory and metabolic adaptations*. Springer, Heidelberg, pp 29–40. doi:10.1007/978-3-642-28678-0\_3
- Clarke A, Rothery P (2008) Scaling of body temperature in mammals and birds. *Funct Ecol* 22:58–67. doi:10.1111/j.1365-2435.2007.01341.x
- Dausmann KH, Glos J, Heldmaier G (2009) Energetics of tropical hibernation. *J Comp Physiol B* 179:345–357
- Dillon ME, Woods HA, Wang G, Fey SB, Vasseur DA, Telemeco RS, Marshall K, Pincebourde S (2016) Life in the frequency domain: the biological impacts of changes in climate variability at multiple time scales. *Integr Comp Biol* 56 (1):14–30. doi:10.1093/icb/icw024
- Eisentraut M (1960) Heat regulation in primitive mammals and in tropical species. *Bull Mus Comp Zool* 124:31–43
- Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu Rev Physiol* 66:239–274
- IUPS Thermal Commission (2003) Glossary of terms for thermal physiology—Third edition (Reprinted from the Japanese Journal of Physiology). *J Therm Biol* 28(1):75–106
- Koenker R (2016) quantreg: Quantile regression. R package version 5.24.
- Koenker R, Ng P, Portnoy S (1994) Quantile smoothing splines. *Biometrika* 81(4):673–680
- Landry-Cuerrier M, Munro D, Thomas DW, Humphries MM (2008) Climate and resource determinants of fundamental and realized metabolic niches of hibernating chipmunks. *Ecology* 89(12):3306–3316
- Lehmer EM, Savage LT, Antolin MF, Biggins DE (2006) Extreme plasticity in thermoregulatory behaviors of free-ranging black-tailed prairie dogs. *Physiol Biochem Zool* 79(3):454–467
- Levesque DL, Lobban KD, Lovegrove BG (2014) Effects of reproductive status and high ambient temperatures on the body temperature of a free-ranging basoendotherm. *J Comp Physiol B* 184:1041–1053. doi:10.1007/s00360-014-0858-4
- Lovegrove BG (2012a) The evolution of endothermy in Cenozoic mammals: a plesiomorphic–apomorphic continuum. *Biol Rev* 87:128–162. doi:10.1111/j.1469-185X.2011.00188.x
- Lovegrove BG (2012b) The evolution of mammalian body temperature: the Cenozoic supraendothermic pulses. *J Comp Physiol B* 182(4):579–589. doi:10.1007/s00360-011-0642-7
- Lovegrove BG, Canale CI, Levesque DL, Fluch G, Řeháková-Petrů M, Ruf T (2014) Are tropical small mammals physiologically vulnerable to Arrhenius effects and climate change? *Physiol Biochem Zool* 87(1):30–45. doi:10.1086/673313

- McKechnie AE, Mzilikazi N (2011) Heterothermy in afrotropical mammals and birds: a review. *Integr Comp Biol* 51 (3):349–363. doi:[10.1093/icb/ucr035](https://doi.org/10.1093/icb/ucr035)
- Muñoz-García A, Ben-Hamo M, Korine C, Pinshow B, Williams JB (2013) A new thermoregulatory index for heterothermy. *Methods Ecol Evol* 5:141–145. doi:[10.1111/2041-210X.12131](https://doi.org/10.1111/2041-210X.12131)
- Munro D, Thomas DW, Humphries MM (2005) Torpor patterns of hibernating eastern chipmunks *Tamias striatus* vary in response to the size and fatty acid composition of food hoards. *J Anim Ecol* 74:692–700
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ruf T, Geiser F (2015) Daily torpor and hibernation in birds and mammals. *Biol Rev* 90(3):891–926. doi:[10.1111/brv.12137](https://doi.org/10.1111/brv.12137)
- Stephenson PJ, Racey PA (1994) Seasonal variation in resting metabolic rate and body temperature of streaked tenrecs, *Hemicentetes nigriceps* and *H. semispinosus* (Insectivora: Tenrecidae). *J Zool* 232(2):285–294
- Willis CKR (2007) An energy-based body temperature threshold between torpor and normothermia for small mammals. *Physiol Biochem Zool* 80 (6):643–651