Flickering body temperature anticipates criticality in hibernation dynamics

Daniel Oro[1] and Lidia Freixas[2]

[1]IMEDEA (CSIC-UIB)
[2]Granollers Natural Sciences Museum

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Abstract

Hibernation has been selected for increasing survival in harsh climatic environments. Seasonal variability in temperature may push the body temperatures of hibernating animals across boundaries of alternative states between euthermic temperature and torpor temperature, typical of either hibernation or summer dormancy. Nowadays, wearable electronics present a promising avenue to assess the occurrence of criticality in physiological systems, such as body temperature fluctuating between attractors of activity and hibernation. For this purpose, we deployed temperature loggers on two hibernating edible dormice for an entire year and under severe Mediterranean climate conditions. Highly stochastic body temperatures with sudden switches over time allowed us to assess the reliability of statistical leading indicators to anticipate tipping points when approaching a critical transition. Hibernation dynamics showed flickering, a phenomenon occurring when a system rapidly moves back and forth between two alternative attractors preceding the upcoming major shift. Flickering of body temperature increased when the system approached bifurcations, which were also anticipated by several metric- and model-based indicators. Gradual changes in air temperature drove long transient behavior (since flickering began long before bifurcations) and hysteresis. For hibernating animals, hysteresis may increase resilience when ending hibernation earlier than the optimal time, which may occur in regions where temperatures are sharply rising, especially during winter. Temporal changes in early indicators of critical transitions in hibernation dynamics may help to understand the effects of climate on evolutionary life histories and the plasticity of hibernating organisms to cope with shortened hibernation due to global warming.

Keywords

Critical transitions, resilience, climate, hibernation, small mammal, hysteresis, tipping point

INTRODUCTION

Evolution has selected to endorse resilience for buffering environmental impacts, protecting biological systems from failure. Complex responses to these impacts occur at all organizational levels, from cells and organs to populations and ecosystems. At the individual level, physiological responses are at the basis of resilience to enhance survival and reproduction. One particular life history strategy that has evolved to cope with environmental stress is dormancy or torpor. Dormancy is a physiological adaptation in some plants and animals, that can remain torpid for weeks, months and even years (Nowack *et al.*2017; Withers & Cooper 2019). In some mammals inhabiting seasonal ecosystems, dormancy during winter, also called hibernation, reduces the impacts of climatic stress. Hibernating species may reduce their metabolic rate for long periods, which results in higher survival and lower fecundity than close phylogenetic species that do not hibernate (Withers & Cooper 2019). The advantages of hibernating may explain the evolutionary success of ancestral mammals that survived the mass extinction at the Cretaceous–Palaeogene boundary following an unprecedented environmental perturbation (Lovegrove *et al.* 2014). A much higher than expected rate of recent extinctions in mammals has been recorded for homeothermic species, whereas hibernating species

seem to cope better with environmental impacts due to anthropogenic global change (Geiser & Turbill 2009). Some theoretical models show that in harsh environments, hibernation may be all that allows population persistence (Tuljapurkar & Istock 1993).

The understanding of the physiological dynamics by which air temperature influences the seasonality of life histories is crucial to assess the resilience of hibernating species to global warming (Caro *et al.*2013). In recent times, wearable electronic loggers have allowed researchers to analyze the dynamics of physiological systems, such as body temperature fluctuating between activity and hibernation states (Chmura *et al.* 2018; Scheffer *et al.* 2018). A straightforward pattern emerges when examining these studies: body temperature in hibernating mammals such as squirrels, marmots, tenrecs, echidnas, dormice and hamsters, changes abruptly between these states (Hut *et al.* 2002; e.g. Talaei *et al.* 2011; Williams*et al.* 2011; Hoelzl *et al.* 2015; Iwabuchi *et al.*2016). However, this highly stochastic physiological system has never been explored to assess whether these sudden switches correspond to tipping points between alternative basins of attraction through critical transitions. Critical transitions are non-linear, abrupt responses of some biological systems subjected to some type of environmental stress. These transitions occur when a threshold value for resilience has been crossed due to the cumulative stress, and beyond this tipping point, there is a sudden shift of state (Scheffer *et al.* 2001; Scheffer 2009). Hibernation has either been studied from the perspective of resilience, which is the property that mediates transition between alternative stable states. Hibernation dynamics also appear as a promising candidate for assessing our capacity for anticipating transitions between states. The anticipation of responses to stress, especially when responses are non-linear (e.g. critical transitions) remains a challenge for most biological systems (Scheffer *et al.*2009; Ghadami *et al.* 2018).

For hibernating dynamics, critical transitions would be a particular type of transition in which a gradual change in air temperature, once past a threshold value, would trigger an overwhelming shift of body temperature between the contrasting states of hibernation and activity (Scheffer 2009). Other physiological systems, such as functional heterogeneity of some progenitor blood cells, show critical transitions through bifurcation thresholds (Mojtahedi *et al.* 2016). Here, we deployed body temperature loggers to a small mammal, the edible dormouse (*Glis glis*), to assess the occurrence of criticality in hibernation dynamics and to deepen our understanding of resilience of hibernating animals to cope with environmental stress. We also assessed the performance of statistical leading indicators for anticipating a critical transition between stable states of activity in summer and hibernation in winter. Interestingly, the studied dormice are from a habitat at the edge of the distribution range, where patches of cold-temperate forests, their preferred habitat, are regressing due to rising temperatures in recent decades (Peñuelas & Boada 2003).

METHODS

Study animals and procedures

We kept one male and one female dormouse in outdoor captivity near the area where they were born, in the southernmost zone of the Iberian population of the species (Montnegre range). Adult dormice here have a weight of 150-200grs. The climate in this area is Mediterranean, with average temperatures of 15.85 °C (S.E. = 0.14, range: 0.47 °C - 34.11 oC) and 800-900mm rainfall. All individuals were 1y old when they entered the cage. Despite being sexually mature, they did not engage in reproduction during the study. The cage was ca. 6m^3 in size and it was set outdoors. Two nest boxes as those used in our field study (Freixas *et al.* 2012) were available for dormice, and food (mainly dry seeds of oak, chestnuts, hazelnuts and apple) was provided ad libitum. Dormice performed hibernation in a refuge underground specifically set for this purpose, as they mostly do in the wild. Data was collected automatically by a temperature data-logger (iButton$^{(r)}$ DS1922L-F5, accuracy: +- 0.5 degC, sampling frequency: 1/hour). Devices were surgically implanted intraperitoneally for an almost year-long period (341 days, 8192 temperature records for each individual). We recorded air temperature at the exact same time intervals also using an iButton device.

Statistical analysis

With the goal of determining which parts of the time series corresponded to the activity period or the

hibernation period, we ran an algorithm for calculating the Iterated Cumulative Sums of Squares (ICSS), which detects retrospective changes of variance for identifying breaking points.

We applied several metric-based and model-based approaches as leading indicators of early warning signals (EWS) of critical transitions for changes in body temperatures during hibernation (T_h) and estivation (euthermic temperature, T_e). We tested most indicators reviewed in (Dakos *et al.* 2012) to assess the limitations in their application and interpretation. First, we used the 'earlywarnings' package in R for calculating metric-based indicators: BDS tests, conditional heteroskedasticity (CH), nonparametric Drift-Diffusion-Jump (DDJ) models, and generic EWS (temporal autocorrelation at lag-1, standard deviation SD, and skewness) (details on how each indicator was applied are in Appendix S1, Table S1). We performed sensitivity analyses to assess the reliability of generic EWS depending on choices for data transformation, detrending and filtering (Dakos *et al.* 2012). Second, we ran model-based indicators on standardized data. We began by running a potential analysis for assessing the existence of both flickering and the occurrence of two stable states in the body temperature time series. We then fitted threshold AR(p) models to identify transitions between alternative states due to flickering in the time series. By using the Kalman filter and AIC values, we assessed which model with different orders ($p = 1, 2, 3$) best fit the data. The models also estimated the threshold value c and the variance of the process error and were as follows:

$$T(t) = \varnothing_0 + \sum_{i=1}^{p} \varnothing_i \left(T(t-i) - \varnothing_0 \right) + \varepsilon(t),$$

where $T(t)$ represents the changes of body temperature over time t; parameters $\varnothing_i$ had two sets of values depending on $T(t-1)$ being lower or higher than the threshold value c; $\epsilon(t)$ was a white noise process representing environmental variability. We also calculated the Kendall τ, which indicates the strength of the trend in the indicators for body temperatures. We also fitted time-varying AR(p) models and compared their fit to those obtained from threshold models to confirm than the latter better described the flickering features of the body temperature time series. All AR(p) models were fitted using the package 'setar' in R.

We also assessed the influence of air temperature on the dynamics of body temperature in our studied dormice. To simplify the analysis (i.e. avoiding including seasonality), we partitioned the time series between three periods: activity prior to hibernation, hibernation, and activity after hibernation, as indicated by the breaking point analysis (Appendix S1, Table S2). The models added the air temperature covariate (A) into the AR(p) models and were as follows:

$$T(t) = \beta A_i + \varnothing_0 + \sum_{i=1}^{p} \varnothing_i \left(T(t-i) - \varnothing_0 \right) + \varepsilon(t),$$

Here, we added the slope β of the effect of air temperature A_i on body temperature T. We then used AIC values of each model (with and without air temperature as explanatory variables) to select the best model. Fitting of models was carried out using the package 'TSA' in R.

RESULTS

The time series of the dormice's body temperature suggested flickering, rather than a critical slowing down (Fig. 1). The female entered the hibernation period 24 days earlier than the male (November 22 versus December 16, respectively), whereas the two dormice awoke from hibernation on the same day (May 29). During the activity period, T_e remained rather constant (with torpor bouts starting around mid-summer), with independence of the trends in air temperature, first increasing from the termination of hibernation to mid-summer and then decreasing to the onset of the next hibernation. On the contrary, during hibernation, T_h tracked air temperature very well, although several bouts to T_e occurred with increasing frequency as the transition to activity approached (Fig. 1). In the following sections, we show the results of hibernation dynamics by the use of indicators developed by Dakos *et al.* (2012).

Metric-based indicators

Results from BDS tests and their partial autocorrelation functions ACF show that we can reject the null hypothesis that the remaining time series residuals after detrending are independent and identically distributed, which is typical of a system approaching a critical transition (Appendix S1, Table S3 and Fig. S1).

ACF also showed that during the activity period, body temperature followed a circadian cyclicity, which was not apparent during hibernation. Conditional heteroskedasticity (CH) was erratic and did not clearly anticipate bifurcation between states (Appendix S1, Fig. S2). DDJ metrics were noisy when plotted against time, although they were suitable indicators of resilience for flickering data: resilience decreased as conditional variance, diffusion and jump intensity increased (Appendix S1, Fig. S3). Generic early warning signals (EWS) were also noisier for the transition to hibernation, likely because the time series started just before dormice began to show an increasing frequency of torpor bouts (Fig. 2). In general, there was an increase in the autocorrelation at lag-1 and in variance before the two transitions, whereas skewness decreased, likely due to the increase in excursions of body temperature to T_e over this period. Generic EWS showed similar performance for the time series encompassing the transitions and the whole time series (Appendix S1, Fig. S4 and S5, respectively). Sensitivities of all generic EWS tested in our study were low, i.e. results were robust regardless of different choices on bandwidth and size of the rolling window (Appendix S1, Fig. S6).

Model-based indicators

We fitted threshold AR(p) models (p [1,3]) and found that the best fitting model was AR(3) (Fig. 3). For female data, the models' fit were worse for $p = 1$ (ΔAIC $= 1242$) and $p = 2$ (ΔAIC $= 14$), similar to the male data ($p = 1$ (ΔAIC $= 2630$) and $p = 2$ (ΔAIC $= 15$)). The fit of the threshold AR(3) model was statistically better than that of a simple AR(3) model for the female ($\chi_3^2 + \chi_4^2 = 51.63$, $P < 0.001$) and the male ($\chi_4^2 + \chi_5^2 = 70.56$, $P < 0.001$). AR(p) models also showed that air temperature explained an important part of the deviance in body temperatures, especially during hibernation, when body temperature was highly synchronous with air temperature (Appendix S1, Table S4). The fitted model showed that there were alternative states between the activity and the hibernation states, separated by unstable saddle points that corresponded to flickering temperature causing a region of bistability (Fig. 4). The potential landscape confirmed the occurrence of flickering and of two minima (stable states) separated by a local maximum (unstable equilibrium) (Fig. 4). The potential was lower and more narrow (lower temperature range) for T_e during normal activity than for the hibernation temperature, and it showed a similar pattern for the two studied dormice. Switches between hibernation and activity occurred at different critical conditions of temperature, which was indicative of hysteresis. In late spring, dormice awoke at higher air temperatures than air temperature when they entered hibernation in late autumn (Fig. 5).

DISCUSSION

We show that criticality occurs in the hibernation dynamics of dormice. Around fold bifurcation points, a tiny change in ambient temperature pushes body temperature across boundaries of alternative states (from a euthermic temperature to a hibernation temperature) through large transitions. These critical transitions are characterized by flickering and punctuated changes in body temperature. Flickering is a type of complex dynamics that occur when a system rapidly moves back and forth to the vicinity of an alternative state preceding the upcoming critical transition (Scheffer *et al.* 2009; Dakos *et al.* 2013). In our study, flickering of body temperature started far from bifurcation points and it increased when the system approached these points. Thus, flickering anticipated critical transitions in hibernating dormice, as it likely does for dormice from the core of the range distribution and for other hibernating mammals, when looking at the dynamics of body temperatures (Hut *et al.* 2002; e.g. Talaei *et al.* 2011; Hoelzl *et al.* 2015). In humans, flickering may also anticipate physiological responses, such as epileptic seizures and narcolepsy (Scheffer 2009; Yang *et al.* 2016). Together with flickering, other indicators of EWS anticipated the approaching of critical transitions in hibernation dynamics. Previous studies suggest that, contrary to critical slowing down, flickering is associated with an increase in both variance and lag-1 autocorrelation, as we found in our study (Wang *et al.* 2012; Dakos *et al.* 2013). Nevertheless, the rest of indicators were less informative and even erratic: for instance, CH did not anticipate bifurcation, while DDJ metrics were very noisy. As Dakos et al. (2012) pointed out when developing the indicators, the performance of any indicator, as well as the interpretations based on them, is likely depending on the features and dynamics of the biological system studied.

Hibernation dynamics of dormice also have hysteresis, which shows the tendency of body temperature to remain on the same attractor until attaining a critical threshold value of air temperature, with the particularity

that bifurcations occurred at different air temperatures for each of the two cyclic transitions. These cyclic transitions resemble the dynamics of wake-sleep and microsleeps occurring for circadian cycles in mammals (Yang *et al.* 2016). Since hibernation is driven by seasonal climate, its dynamics follow cycles that are locked into phase (Scheffer 2009). This type of complex cyclic dynamics occur between coupled oscillators and commonly occurs in nature (e.g. heart beating, reproductive events, and predator-prey fluctuations). Epileptic seizures mentioned above occur by the phase locking of firing in neural cells (Scheffer *et al.* 2009). In our study, locking of forced hibernation by forcing winter occurs with 1:1 rhythm, which means that little climate forcing is enough for locking (Scheffer 2009). Phase locking occurs for global climatic indexes such as NAO and ENSO, which are known to be coupled with a number of local seasonal ecological processes.

Statistical indicators of EWS quantify critical transitions and resilience for very different ecological systems (Scheffer *et al.*2015), and we show that these generic indicators can be also applied to other dynamical systems sharing their fundamental properties, such as physiological hibernation. Other physiologically critical transitions during hibernation dynamics may occur and may be anticipated, such as lipid structure and enzyme function of mitochondrial membranes from liver, kidney, brown fat, and heart tissues. High-dimensional physiological systems, such as blood cells with functional heterogeneity or neurons involved in sleep-wake cycles, also show critical transitions that can be predicted before bifurcation (Mojtahedi *et al.* 2016). The same dynamics occur for homeostatic changes in hormone regulation, immune responses, gene expression and asthma incidence (Krotov *et al.* 2014; Trefois *et al.* 2015). Our capacity to anticipate pathological changes and loss of resilience, e.g. due to opposite physiological commitment to that intended in normal conditions, is crucial for human health (Scheffer *et al.* 2018). Interestingly, hibernation dynamics and human health converge due to the increased scientific interest in the benefits of dormancy for humans in coping with different stresses, e.g. the potential of a hibernating state in astronauts for deep space travel (Lovegrove *et al.* 2014). Similarly, EWS can be used to detect changes in the non-linear dynamics of body temperature and the resilience of hibernating mammals due to increasing climatic stress. Physiological variables can perform better to anticipate non-linear dynamics than noisier ecological variables (Perretti & Munch 2012; Benedetti-Cecchi *et al.* 2015), and the former may be a good bio-indicator of ecological changes and temporal variability in resilience. Given the potential consequences that hibernation dynamics may have on population fluctuations and extinction, there is a growing concern about the impacts of climate warming on hibernating species (Inouye *et al.* 2000).

The influence of climate may be greater for species such as edible dormice in our Mediterranean study area. Here, heat and drought waves are associated and their frequency is increasing (Diffenbaugh *et al.* 2007; Vautard *et al.* 2007), which is affecting cold-temperate forests, the preferred habitat of dormice (Peñuelas & Boada 2003). The potential impact on hibernating mammals in many regions is likely related to a loss of suitable habitat, mediated by climate variability, and not to a direct impact on hibernation dynamics. This is because hibernation is a very effective resilient physiological mechanism to cope with climatic stress (Lebl *et al.* 2011; Boutin & Lane 2014; Mitchell *et al.* 2018). Animals can adjust hibernation to maximize fitness, because it influences life-history traits such as recruitment by age and the onset of reproduction (Bieber *et al.* 2018). The evolution of hibernation has selected for a very plastic trait. The duration of hibernation may change with seasonal climate variability and with the availability of resources. For instance, rising temperatures cause earlier emergence from hibernation in the yellow-bellied marmot (*Marmota flaviventris*), which has led to a longer growing season and larger body masses before entering hibernation (Ozgul *et al.* 2010). The demographic consequences included higher adult survival and a sharp increase in population growth rate. Hibernation in dormice shows large differences between populations depending on local climate, and harsher and longer winter means longer hibernation times, e.g. up to 11 months (Hoelzl *et al.* 2015). Interestingly, life history strategies of dormice are very plastic depending on those local climatic conditions, since as long as the duration of hibernation increases, adult survival is higher and fertility is lower (Pilastro *et al.* 2003; Ruf *et al.* 2006; Lebl *et al.* 2011). Hysteresis, such as that shown by the studied Mediterranean edible dormice, may also increase resilience by avoiding the termination of hibernation earlier than the optimal time, which may occur in regions where temperatures are sharply rising, especially during winter (Mitchell *et al.* 2018). Experimental studies looking at how environmental stress affects hibernation dynamics (e.g. Siutz

et al. 2018) are promising to assess the changes in leading indicators of critical transitions. Exploring how criticality and tipping points appear in different hibernating animals with different evolutionary life histories and with varying ecological features may also shed light on how resilience of physiological systems cope with environmental stress.

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AUTHORSHIP

DO and LF conceived the study; LF performed the experimental work; DO carried out the statistical analysis and the writing

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Figure 1 Body and air temperature recorded during the study covering an entire year (data recording began in early autumn) for the female and male dormouse. Vertical dashed lines show the two extreme breaking points (using ICSS methods) that separate the hibernation period (central part) and the activity period (external parts). Limits for each season are also shown.
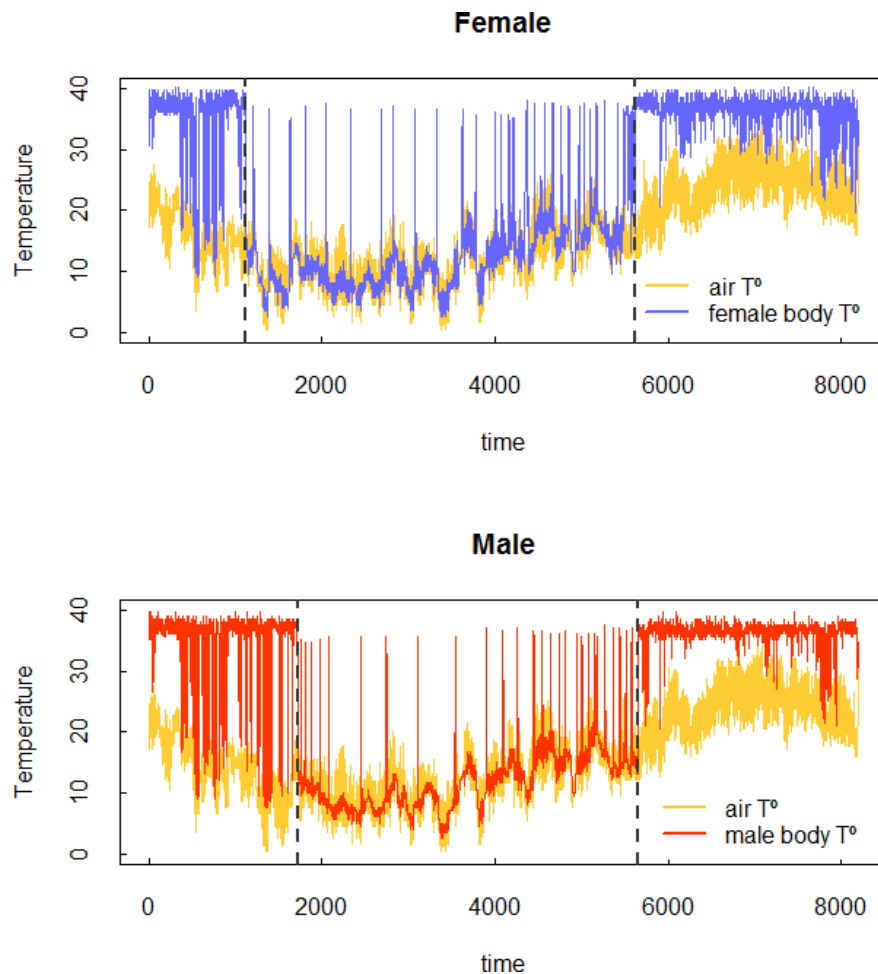
Female

Male

Female

Male
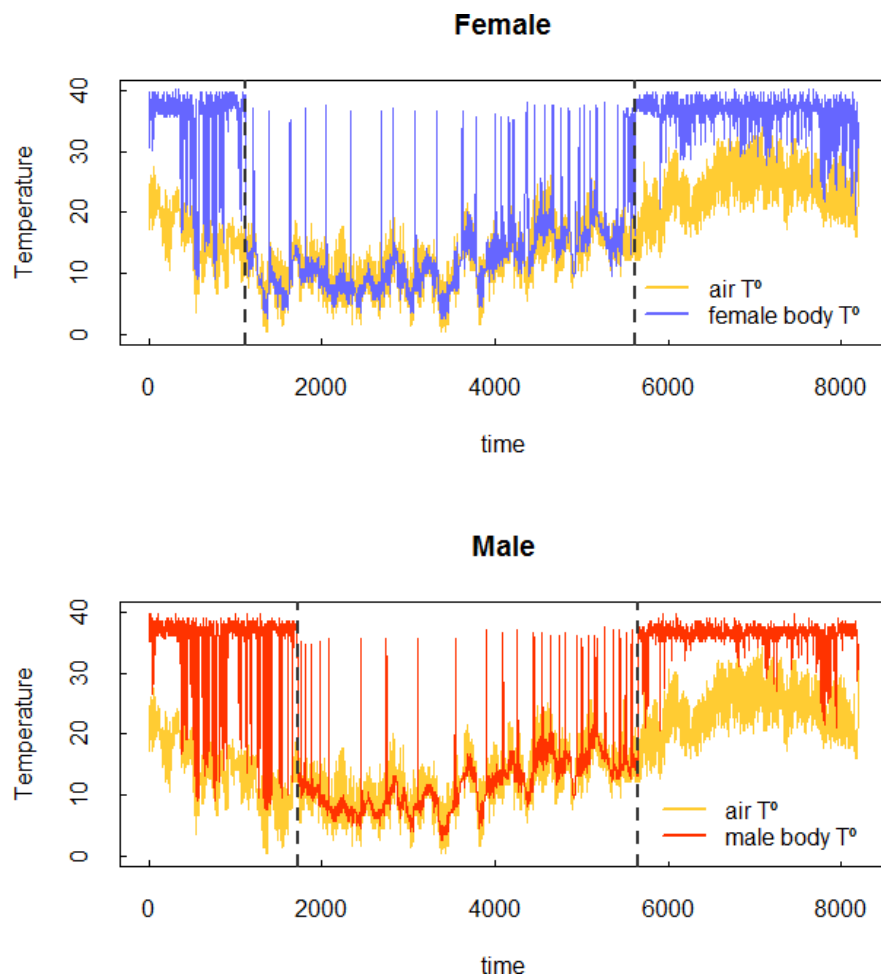
Figure 2 Metric-based rolling window indicators estimated for dormice body temperature (black lines) and air temperature (yellow lines) separated for each alternative state (activity and hibernation). (a and b) activity state and hibernation state for the female; (c and d) activity state and hibernation state for the male. Red lines show the Gaussian filtering of the time series. Panels 1, 2 and 3 show autocorrelation at lag-1 (AR(1)), standard deviation and skewness respectively, estimated within sliding windows of 20% the size of the time series. Yellow lines show the indicators for air temperature. The Kendall τ indicates the strength of the trend in the indicators for body temperatures.

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Figure 3 Fit of a threshold AR(3) model to body temperature (standardized data) for the female and the male dormice (a and b respectively). Blue and green points result from the fitted AR(3) model (for female and male respectively) and black lines show the real data. The yellow lines show the threshold value that separates the two AR(3) processes (which equal 31ºC for the two sexes). The inner panels show a zoom of

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an arbitrary chosen subset of the original data set shown by the shaded area.

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Figure 4 Equilibrium and hysteresis curves of dormice's body temperature as a function of air temperature variability (a and b for female and male, respectively). Dashed lines between the two bifurcation points $F_{1,2}$, show the bistability region separating the basins of attraction of the two stable branches, i.e. the hibernation state (green lines) and the activity state (black lines); a1 and b1 show the potential for body temperature for female and male dormouse respectively. The entire time series was used here.

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Figure 5 Hysteresis occurring between hibernation and activity states for the studied dormice (a and b correspond to female and male, respectively). Orange lines and points show the transition to hibernation (body temperature drop when air temperature decreased below a critical point) and red lines and points show the transition to an euthermic, activity state (body temperature increase when air temperature crossed a critical point). Each point represents the median value of body temperatures for each air temperature.