Climate Change and Thermoregulatory Consequences of Activity Time in Mammals

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ABSTRACT: Activity times structure the thermal environments experienced by organisms. In mammals, species shift from being nocturnal to diurnal and vice versa, but the thermal consequences of variable activity patterns remain largely unexplored. Here we used theoretical thermoregulatory polygons bounded by estimates of basal metabolic rates (BMR), maximum metabolic rates (MMR), and thermal conductance (C) in small mammals to explore the metabolic consequences of exposure to global-scale daytime and nighttime temperatures. Model predictions indicated higher metabolic scope for activity for nocturnal species at low latitudes and that reduced minimum C and larger body size increased the geographic range in which nocturnality was advantageous. Consistent with predictions, within rodents nocturnal species have low C. However, nocturnal mammals tend to be smaller than diurnal species, likely reflecting the importance of additional factors driving body size. Projections of warming impacts on small mammals suggest that diurnal species could lose habitable space globally. Conversely, warming could lift cool temperature constraints on nocturnal species and increase habitable space, suggesting that a shift toward nocturnal niches might be favored in a warming world. Taken together, these findings demonstrate the importance of energetic considerations for endotherms in managing global change impacts on nocturnal and diurnal species.

Keywords: biogeography, climate, endotherm, global change, metabolism, thermal biology.

Introduction

Mammals exhibit a great deal of variation with respect to activity patterns over diel time periods; ~70% of extant mammal species are nocturnal and 20% diurnal (Bennie et al. 2014). In fact, the origin of mammals in the Mesozoic was rooted in nocturnality (Gerkema et al. 2013). And while diurnality appears to have been present in the Paleocene-

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Eocene thermal maximum, there was also a likely an extirpation of diurnal mammals in the global cooling of the Eocene-Oligocene transition that followed (Wu et al. 2017). In vertebrates generally, there are important evolutionary consequences of diurnality and nocturnality as speciation is generally higher for diurnal species (Anderson and Wiens 2017). Ambient temperature (T_a; and associated variation in solar radiation) then appears to be an important factor in speciation and diversification patterns within mammals and vertebrates.

In small mammals in particular, activity patterns are especially plastic and sensitive to environmental conditions. Cold (and hunger) can induce diurnality in nocturnal mice with the accompanied increased energy demands and metabolic challenges (van der Vinne et al. 2014). In mice from temperate environments with relatively low T_a and food availability, diurnality is especially beneficial, as it reduces energy expenditure significantly (van der Vinne et al. 2015). Heat, on the other hand, can also have costly consequences and may have pushed bats, for example, to evolve nocturnal flight to reduce metabolic costs of flight and heat dissipation during the day (Voigt and Lewanzik 2011). Rodents are also known reduce activity significantly in response to heat or solar exposure (Bacigalupe et al. 2003). Nonetheless, the potential impact of elevated temperatures due to global warming on daily activity patterns, foraging efficiency, and, ultimately, population viability, has not been studied in detail in mammals as in lizards (Bozinovic and Vasquez 1999; Huey et al. 2010; Sinervo et al. 2010; Levy et al. 2019).

Within mammalian energetics, the issue of nocturnality versus diurnality remains largely untested across species, despite the clear importance for climate change vulnerability (Levesque et al. 2016). Furthermore, there is a tendency for mammals (large mammals in particular) to increase in nocturnality to avoid human disturbance effects (Gaynor et al. 2018). Changes in diel activity within mammals to avoid globally dominant human activities will have energetic consequences that could be exacerbated by climate

change (Gaynor et al. 2018). Similarly, mammals may respond to warming impacts by shifting diel patterns—McCain and King (2014), for example, found that species that are obligate nocturnal or diurnal are twice as likely to have responded to climate change in some way (e.g., extirpation or range shift) than species that can shift activity times. Therefore, addressing the metabolic consequences of diel variation in activity for mammals could provide key insights into both the evolution of mammals broadly as well as their vulnerability to climate change.

Here we examine the metabolic consequences and thermal adaptation implications of nocturnality and diurnality in small mammals using multiple lines of theoretical and empirical evidence. First, using the framework of Rezende and Bacigalupe (2015), we constructed general endothermic thermoregulatory polygons based on published measurements of basal metabolic rate (BMR), maximum metabolic rate (MMR), and thermal conductance (C). These polygons allow for predictions of metabolic scope for activity as a function of T_a and, therefore, based on nocturnal and diurnal thermal variation. Furthermore, we varied C and body mass (m_b) in the model to predict whether nocturnal or diurnal small mammals would be more likely to exhibit these traits to maximize metabolic scope for activity. Next, we used data sets on small mammal/rodent physiological traits by Naya et al. (2013), mammal body size by Jones et al. (2009), and diel activity patterns by Bennie et al. (2014) to test predictions made by the polygon approach. Finally, we applied a series of warming scenarios for variable activity times and traits to examine broad patterns of climate change implications. The results altogether highlight the divergent and variable environments experienced by diurnal and nocturnal mammals. Furthermore, through this approach we present a general thermoregulatory framework for determining the vulnerability associated with traits of endothermic species to increasing temperatures under climate change.

Methods

Model and Approach

We focused on small mammals (between 10 and 150 g) because they are speciose and data on thermal traits (BMR, MMR, and C) are readily available (Naya et al. 2013, 2018). To make predictions as to how nocturnal species might vary traits to maximize metabolic scope, we implemented the thermoregulatory polygon approach of Rezende and Bacigalupe (2015). Briefly, polygons are based on the basic principles of heat regulation and Newton's law of cooling as outlined by Scholander et al. (1950):

$$MR = C(T_b - T_a).$$

In this case, metabolic rate (MR) is a function of thermal conductance, body temperature (T_b) and air temperature (T_a). The thermoregulatory polygon is therefore bounded by BMR (bottom), MMR (top; see Rosenmann and Morrison 1974), as well as minimum and maximum C (respectively, C_{min} on left side and C_{max} or right side of the polygon). For a constant T_b, maximum and minimum metabolic rates can then be estimated for any given T_a using the polygon (fig. 1). Metabolic scope can then be calculated as the difference between the maximum metabolic rate and the minimum, that is, the ceiling and the floor of the thermoregulatory polygon observed at different T_a, which does not always correspond to the difference between MMR and BMR (Rezende and Bacigalupe 2015).

The model and all analyses detailed below were constructed and analyzed in R (R Core Team 2017). The full script for analyses is provided in a zip file (available online).[1]

Thermal Trait Parameters and Model/Polygon Construction

Thermal trait data were available from data sets in Rezende and Bacigalupe (2015) and Naya et al. (2013). We searched for congeners shared between the two data sets, and for those species ($n = 15$) we took the average body mass and C_{min} values from Rezende and Bacigalupe (2015). To calculate MMR and BMR, we used the allometric (based on body mass) scaling equations in Rezende and Bacigalupe (2015). Using these four metrics, we constructed a thermoregulatory polygon for mean trait values for small mammals that is partially independent of the empirical data of Naya et al. (2013) but also relevant to the results given the congener inclusion criteria (see below for more).

We also constructed additional polygons to test the effects of C_{min} and body mass (m_b) variation on metabolic scope. Using the congener data set, in addition to average body mass and C_{min}, we also took the maximum and minimum C_{min} and m_b values and constructed polygons while the other variables were held constant. For minimum and maximum C_{min}, we constrained the polygons and used the simplistic assumption that C_{max} would remain constant (relative to the average rodent) as would BMR and MMR, both of which are determined by body mass (see above). For minimum and maximum m_b, BMR and MMR were free to vary based on the allometric scaling and the model formulation. However, C_{min} and C_{max} were held constant and scaled on the basis of the m_b of an average rodent. In reality, C_{max} and C_{min} correlate with one another (Rezende and Bacigalupe 2015) as do C_{min} and BMR (Naya et al. 2013). Using this formulation of the model, we can better determine

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1. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.
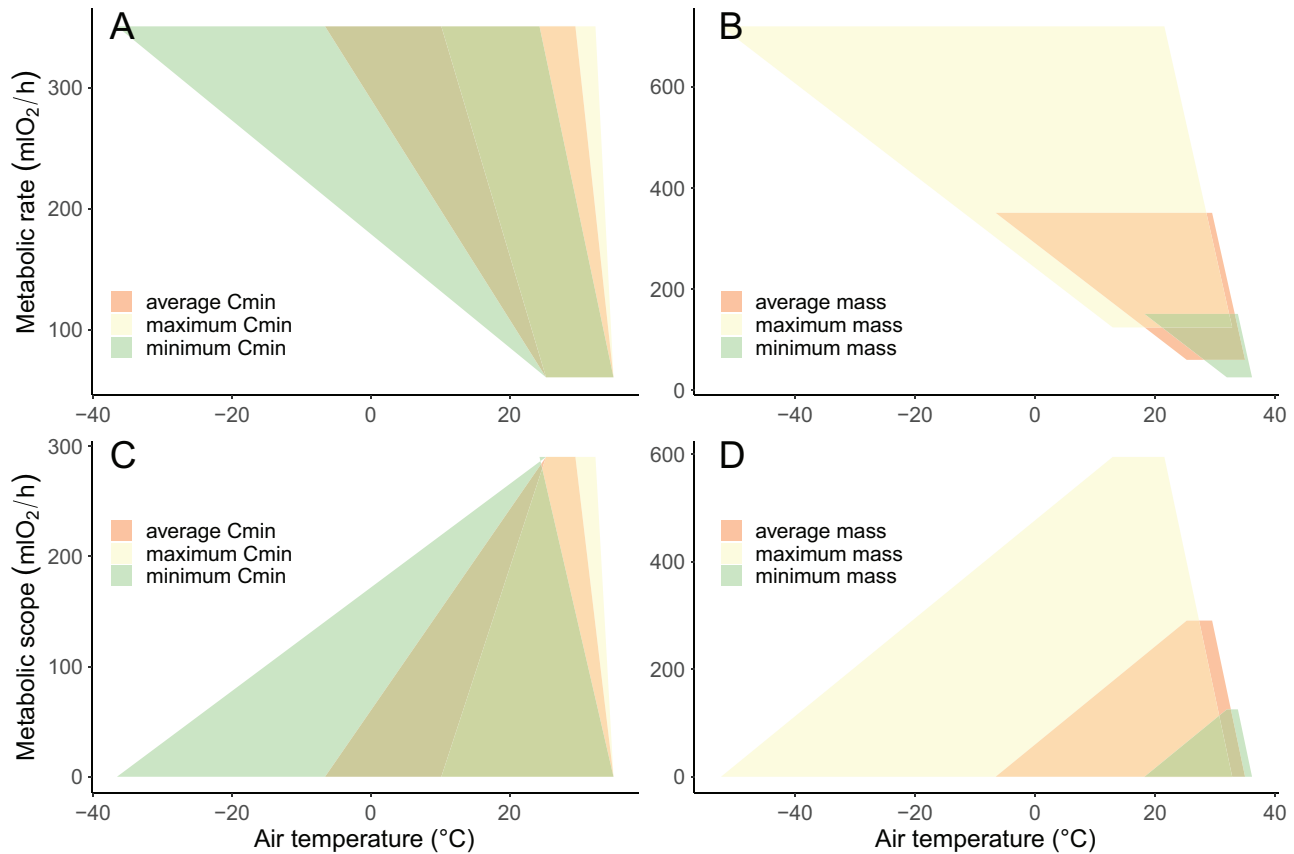
Figure 1: Thermoregulatory polygons calculated based on mean trait values for small mammals (orange), as calculated by parameters in Rezende and Bacigalupe (2015). Four additional polygons were formed by taking the minimum C_{min} (green, *A*), maximum C_{min} (yellow, *A*), minimum body mass (green, *B*), and maximum body mass (yellow, *B*) values. For scale, the average polygon (orange) for both models is identical. Metabolic scope for all polygons is shown in *C* and *D*.

how individual factors themselves affect thermoregulation (more on model assumptions below).

Climate Data and Calculation of Metabolic Scope

We obtained a spatial mapping of daytime and nighttime temperature data at a 2.5-degree resolution from Worldclim 1.4 (Hijmans et al. 2004) and analyzed how these data would affect metabolic scope for activity as a function of T_a employing the polygons described above. Daytime temperatures were taken as annual mean temperature plus the diurnal temperature range (DTR/2, following Harris et al. 2014). Night temperatures were the annual mean temperature minus DTR/2. Delta metabolic scope was then calculated as night scope minus day scope. We also identified areas where average night or day temperatures exceeded polygons, that is, areas where nocturnality or diurnality, respectively, were not possible. We calculated metabolic scope globally for all scenarios by running polygons through the spatially gridded Worldclim data.

Worldclim data are based on monthly averages across decadal time periods. The averaging across long time periods could mask important small-scale thermal variation. Importantly, at this resolution it is not possible to evaluate daily exposure to temperatures outside of thermoregulatory limits (daily extremes are averaged out). We therefore used the averaged daily minimum (night) and maximum (day) temperature data set from the Climate Prediction Center at National Atmospheric and Oceanic Sciences (https://www.esrl.noaa.gov/psd/data/gridded/data.cpc.globaltemp.html). This is a 0.5° by 0.5° gridded data set averaged from 1981 to 2010. We then passed polygons through the time series (daily averages) of selected grid points—we chose a resolution of 3.59° latitude by 7.19° longitude to optimize computational capacity and spatial resolution. As in the case of the spatial analysis described above, for each time series (365 days per grid) we first evaluated whether any nonzero values were estimated from the polygon function. If so, as above, we calculated the mean metabolic scope for every annual time series for every selected point in the

grid. We also calculated the number of days that temperatures exceeded (above or below) the metabolic capacity of the theoretical organism for day (maximum temperatures) and night (minimum temperatures).

Model Assumptions

Results based on the polygon approach must be understood in the correct context. With respect to the question of nocturnality versus diurnality, a diurnal animal will of course experience, in some way, nocturnal thermal conditions and vice versa. So for this application of the model, we assume that nocturnal species find refuge (e.g., underground) during the day and diurnal species find refuge during the night, such that they are less exposed to the thermal variation during their inactive periods—a reasonable assumption in that many rodent and small mammal burrows are buffered from high thermal variation of surface temperatures (Jackson et al. 2002; Williams et al. 2015). Similarly, the model does not take into account any seasonal variation in activity, a critical component of mammalian energetics (Kenagy et al. 2002; Humphries et al. 2004; Bronson 2009; Levy et al. 2019). The reality of thermal variation in the environment experienced by mammals is therefore clearly more complex than the model used here, where diurnal species only experience daytime temperatures and nocturnal species only experience nighttime temperatures. However, the model provides a heuristic perspective to exploring challenges to and patterns within diurnal and nocturnal thermal environments for species (and not a metabolic prediction per se).

The structure of the polygons and the parameters input into them provide additional sources of uncertainty. Body size is a primary factor determining metabolic patterns and thermoregulatory polygons (Rezende and Bacigalupe 2015)—we have restricted this analysis to small mammals (less than 150 g). Results from this application of the model are not likely generalizable to larger mammals. Metabolic scope is itself dependent upon temporal resolution and tends to be wider at finer scales (e.g., minutes) than coarser scales (e.g., weeks) as species can perform bursts of activity or reproduction at high or low temperatures for short periods of time (Rezende and Bacigalupe, 2015). Some small mammals can severely reduce energy expenditure but maintain high metabolic scope in extreme cold temperatures (Humphries et al. 2005). Species can also change activity times (within active periods) or otherwise behaviorally respond (use of microhabitats, change in posture, and more) to minute or hourly thermal variation (Beever et al. 2017); mammal distributions are sensitive to such local temperatures (Beaudrot et al. 2019). The extent to which mammals are capable of these responses then will ultimately determine their ability to persist in a given thermal regime.

This model also does not capture key components of the environment that will influence endotherm energetics and thermoregulation. For example, small mammals in hot arid environments can significantly reduce body temperatures and thermal stress through evaporative cooling (Zhu et al. 2008; Mitchell et al. 2018). Wind can alter thermal conductance and complicate the applicability of Newton's law of cooling in endotherm energetics (Tracy 1972). Finally, solar radiation and traits that alter reflectance (e.g., color) have primary roles in endotherm thermal biology (Medina et al. 2018). The generality and taxa-independent quality of the approach taken here means that many of these important thermoregulatory mechanisms are not adequately accommodated. However, as the aim of this analysis is to characterize patterns of metabolic challenges for diurnal and nocturnal species broadly, incorporation of additional thermoregulatory adaptations or responses are unlikely to significantly affect the results qualitatively. Furthermore, when observed patterns deviate from model expectations, the results are still informative in that such biophysical processes (not included in the model) may then be investigated for their part in determining broadscale distribution patterns of nocturnal and diurnal mammals.

Empirical Analysis of Thermal Traits and Model Testing

Using the full data set from Naya et al. (2013), we classified each species as "diurnal," "nocturnal," "cathemeral" (active during day and night), "crepuscular," or "unknown" based on Bennie et al. (2014). Following the approach of Naya et al. (2013), we took the residuals of m_b and C_{min} and tested whether there was an effect of activity time on thermal conductance. We used a Bonferroni correction for pairwise comparison between nocturnal and diurnal species.

We also did a phylogenetic generalized least squares (PGLS) analysis on m_b and C_{min}. For m_b data, we used the PanTHERIA data set (Jones et al. 2009) and extracted values for 2,460 mammals. We used the strict-consensus tree for 1,000 mammal phylogenies from Faurby and Svenning (2015) and assigned branch lengths arbitrarily according to Grafen (1989). We estimated λ using restricted maximum likelihood with the phytools package (Revell 2012). We did the regression of C_{min} ($\log_{10}$ transformed) against activity time and m_b ($\log_{10}$ transformed). For the m_b analysis, with the larger sample size, we also included latitude (also from PanTHERIA) and did a PGLS with activity, latitude, and their interaction.

Nocturnality across Latitude

We used the PanTHERIA data set (Jones et al. 2009) to identify minimum and maximum latitudinal ranges of 2,015 rodent species. For each of those species, we classified them

as nocturnal, diurnal, cathemeral, or unknown following Bennie et al. (2014) and recorded its presence within latitudinal bands of the same resolution as the day of analysis described above (of 3.59° latitude by 7.19° longitude). We then calculated nocturnality as the number of nocturnal species as a proportion of all species within that latitudinal band.

Modeled Climate Change Impacts Based on Thermoregulatory Polygons

To explore possible climate change impacts based on the thermoregulatory polygon model, we applied climate projection data to see how activity time and traits affected habitable space (where nocturnality or diurnality are possible) as defined by positive metabolic scope. The amount of space that is lost or gained relative to the baseline (as described in "Climate Data and Calculation of Metabolic Scope") represents the extremes for how warming might affect activity times or climatic suitability. As a first approximation, however, the test can distinguish how traits and climate change are differentially affected by variable mammal activity times.

We used the mean trait value estimates for small mammals from the Worldclim current climate data as the baseline. We then ran models for 2050 at the 4.5 representative concentration pathway, an emissions stabilization scenario, using five general circulation models (GCMs): CCSM4, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM, and MPI-ESM-LR. We chose these scenarios following Zurell et al. (2018), as they represent a variable range of global climate change scenarios. Data were downloaded at the 2.5° resolution from Worldclim 1.4 (Hijmans et al. 2004). For each GCM scenario and each scenario with variable traits (50% increase and decrease of both C_{min} and m_b), we calculated the amount of habitable space for mammals active during the day (diurnal) or night (nocturnal). For all scenarios, we then examined the change in habitable space from baseline (current climate and mean trait values).

Results

Modeled metabolic scope for nocturnal mammals tend to be much higher than scope for diurnal mammals in the tropics, while, conversely, metabolic scope tends to be higher for diurnal activity in the extratropics (fig. 2, which displays small mammal mean trait values). A few places globally exhibit regions where the average daytime temperature exceeds thermoregulatory limits of the theoretical average rodent (35.0°C based on the polygon derived from mean trait values) for diurnal species but not nocturnal species (~3% of global area, e.g., in the Sahara) and where mean nighttime temperatures exceed limits for nocturnal species (less than −6.5°C) but not diurnal species (~17% of global area, e.g., high-altitude sites such as the Tibetan

Plateau, the Rockies, and the Andes; fig. 2). We also ran this model using mean temperature from the warmest and coldest quarters and not only found similar results qualitatively but also that nocturnality was globally suitable during the warmest quarter (fig. S1; figs. S1–S4 are available online) and that diurnality was globally suitable during the coldest quarter (fig. S2). Within the parameter space of the small mammals examined, large m_b and low C_{min} led to an increase in area globally where metabolic scope was higher for nocturnal species (fig. 3).

Using the higher temporal resolution daily data set, consistent with the average temperature results, we found that modeled mean metabolic scope tends to be higher for nocturnal species in the tropics but lower for nocturnal species at higher latitudes (fig. 4A). The number of days where the daily temperature exceeded thermoregulatory limits peaked at midlatitude areas in both southern and northern hemispheres for diurnal species, while nocturnal species rarely experienced days where temperatures exceeded limits (fig. 4B).

Empirically, the proportion of nocturnal rodent species across latitude is highest (between 60% and 80%) at low latitudes, between roughly 30°S and 30°N (fig. 4C). Body mass is lower for nocturnal species than diurnal species and also varies across latitude (fig. 5; PGLS: $\lambda = 0.92$; latitude: $P = .004$; activity: $P < .001$; latitude × activity: $P = .01$). Nocturnal small mammal species also tend to have a lower C_{min} than diurnal species (fig. 5C; $P = .03$), which holds with the phylogenetic regression (PGLS: $\lambda = 0.71$, $P = .04$).

Projected warming impacts showed consistent loss of habitable space for diurnal mammals (fig. S3) and trait-dependent gains and losses for nocturnal mammals (fig. 6). Larger diurnal mammals are projected to lose more habitable space relative to smaller mammals (although diurnal metabolic scope increases markedly in high-latitude regions; fig. S4), while nocturnal mammals are projected to gain nearly all previously uninhabitable space under warming for larger body sizes and lower C_{min} (fig. 6).

Discussion

We have shown here that low thermal conductance (or high insulation) is associated with and metabolically favors nocturnality in small mammals; this trait (and others) as well as activity time will have important implications for how mammals respond to warming. Bennie et al. (2014) illustrated the high diversity of nocturnal mammal species in the tropics and their lower relative diversity in high-altitude regions such as the Tibetan Plateau and the Andes (in fig. 5 of Bennie et al. 2014; see also fig. 4 of this article)—the model results here demonstrate a clear physiological basis for these and other patterns in mammal distributions. In addition to this, we also show that functional traits such
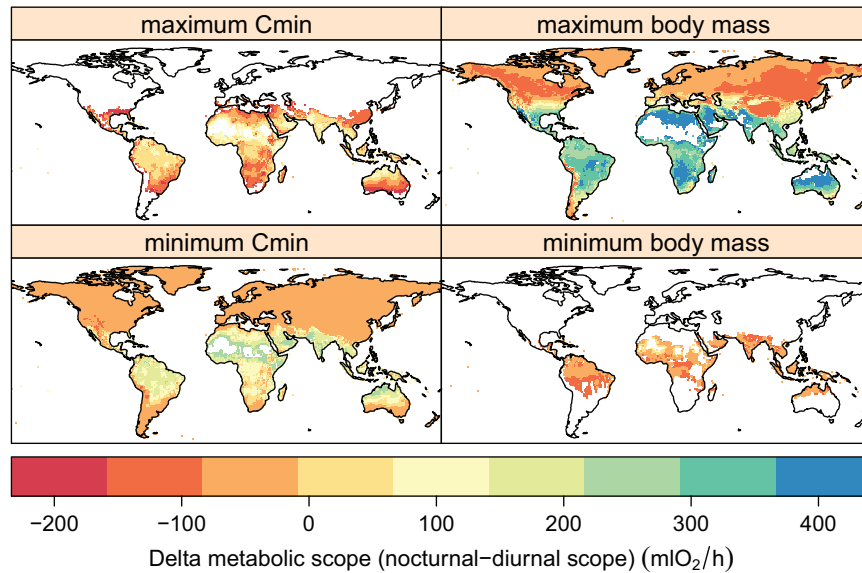
Delta metabolic scope (nocturnal−diurnal scope) (mlO$_2$/h)
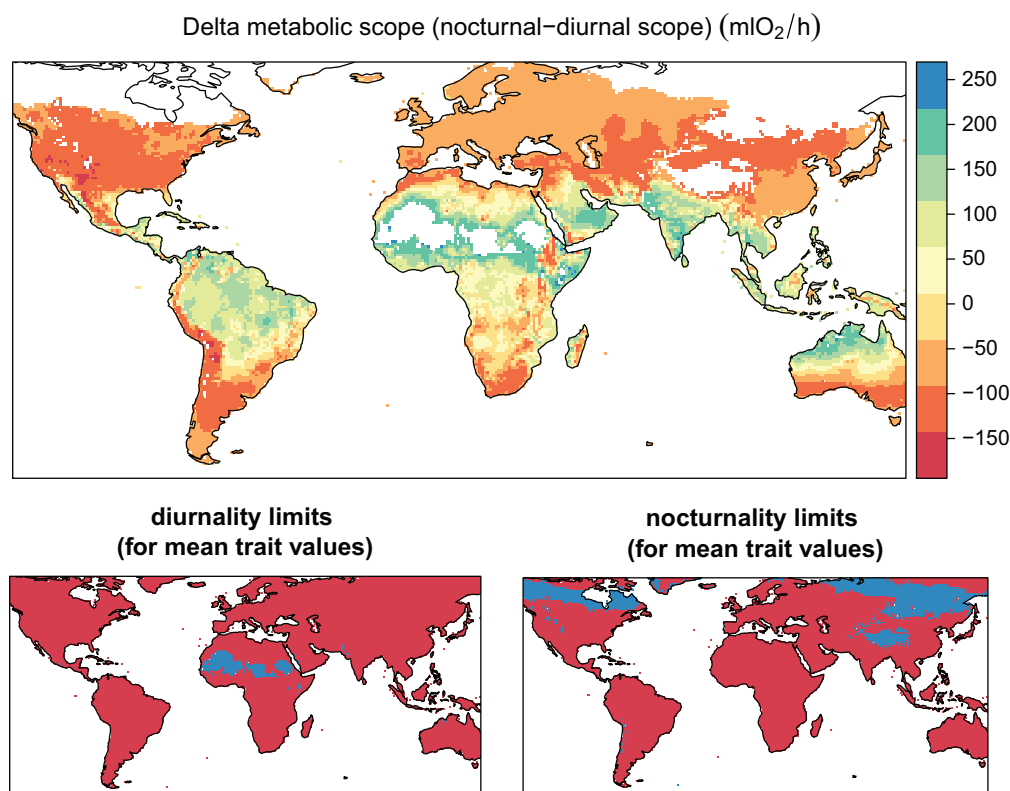
Figure 2: Delta metabolic scope (metabolic scope for nocturnal species minus metabolic scope for diurnal species) of an average rodent (mean trait values, *top*), which shows high suitability for nocturnal thermal conditions generally for low latitudes (yellows and blues) and high suitability for high latitudes (oranges and reds). Greenish blue values indicate areas where activity during nocturnal hours would result in larger metabolic scope, while reddish values indicate that diurnal activity would lead to larger scope. Some areas exceed metabolic capacity (the thermoregulatory polygon) where activity during the day is simply not possible (white areas, *top*; blue areas, *bottom left*) or activity during the night is not possible (white areas, *top*; blue areas, *bottom right*).

as body mass and thermal conductance can to some extent compensate for thermal limitations in diurnal and nocturnal niches. Finally, these ecophysiological traits also may drive differential climate change impacts for nocturnal and diurnal species as demonstrated by model projections; diurnal habitable space for mammals is lost under all warming scenarios, while nocturnal mammals tend to gain habitable space under warming unless they have low body mass or high thermal conductance. Long-term changes in climate over geologic and evolutionary timescales differentially affected diurnal and nocturnal mammals (Lovegrove 2017; Wu et al. 2017), and we provide a mechanistic basis for understanding how future climate change may have differing consequences for species as a function of diel activity. Conceptually, this was possible because recently proposed thermoregulatory polygons also take into consideration the upper metabolic ceiling where thermoregulation is possible, a subject that has been generally neglected in the more classic ecophysiological literature (Rezende and Bacigalupe 2015).

That nocturnal rodents tend to have lower thermal conductance and are more prevalent at low latitudes (fig. 4) are all consistent with studies from the field and from other taxa. For example, Ding et al. (2018) researched two sympatric gerbil species in the Gobi Desert, one nocturnal and one diurnal, and found that thermal conductance and critical temperatures were lower for the nocturnal species. And while the average rodent (mean trait values) as described by the model experiences temperatures beyond the thermoregulatory polygon in some parts of the globe (fig. 2), traits (e.g., size or thermal conductance) can make persistence in these environments possible; Cortés et al. (2003), for example, hypothesized that *Chinchilla chinchilla* likely survives as a nocturnal small mammal in the Andes (between 3,500 and 5,000 m) as a consequence of its high insulation.

Body temperature variation represents an important consideration for endothermic thermoregulation, environmental variation, and even extinction (Geiser and Turbill 2009). For example, diurnal small mammals in the tropics
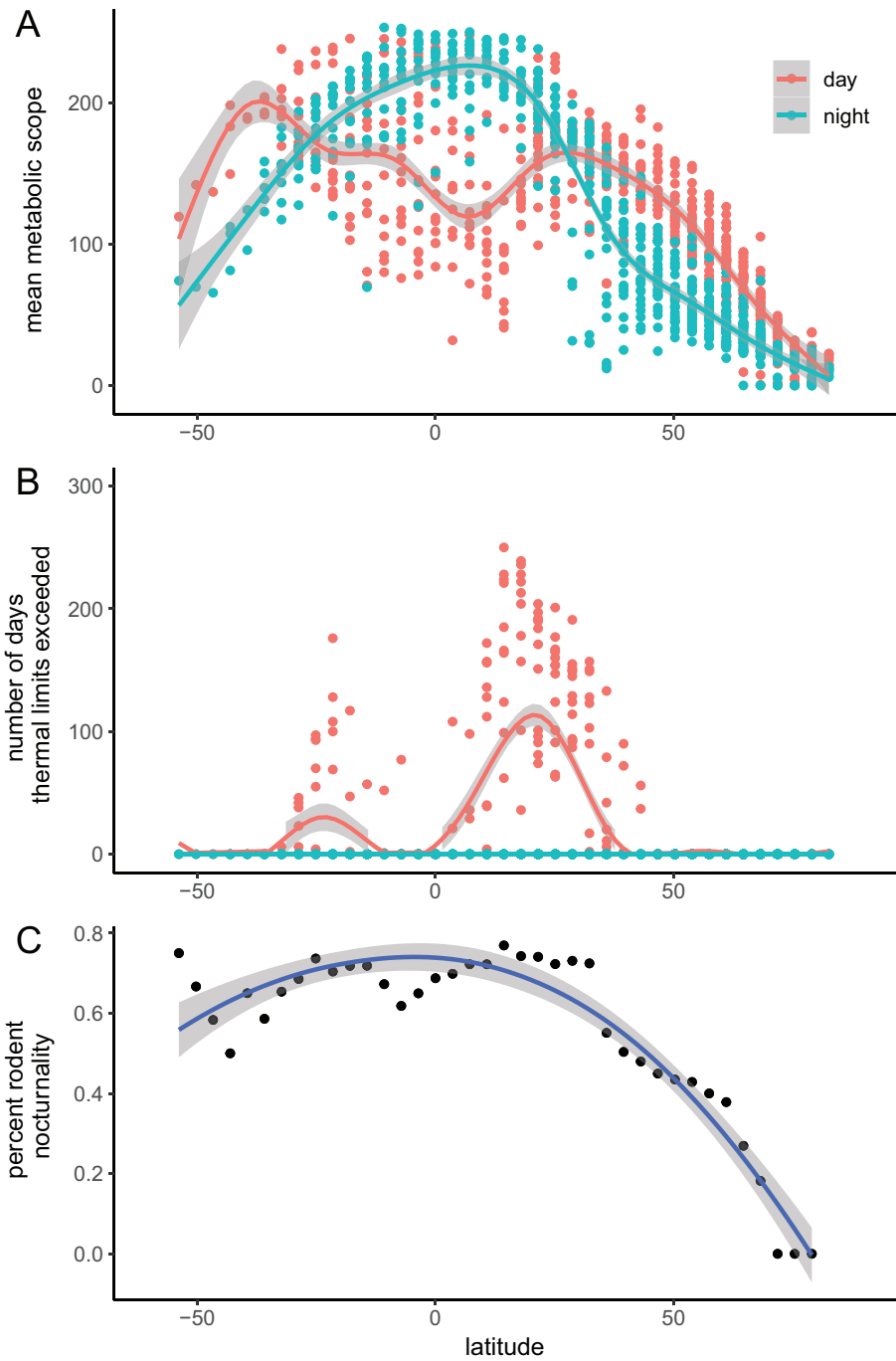
Figure 3: Delta metabolic scope (metabolic scope for nocturnal species minus metabolic scope for diurnal species) with variable body mass (minimum and maximum body sizes) and minimum thermal conductance (C_{min}; minimum and maximum C_{min} values). Some areas exceed metabolic capacity (the thermoregulatory polygon) where activity during the day or night is simply not possible (white terrestrial area in the maps, as in fig. 2).

can maintain high body temperatures during the day (the active phase), which favors passive heat dissipation (Levesque et al. 2018), and body temperature itself appears to be under selection in mammals (Clarke and Rothery 2008). Body temperature and BMR have exhibited decoupled evolutionary trajectories in mammals that have facilitated persistence in a diversity of thermal environments (Avaria-Llautureo et al. 2019). Although we kept body temperature constant in this application, the model can be easily generalized to a variable T_b range (fig. 2*C* in Rezende and Bacigalupe 2015), giving rise to broader polygons by the same range, since heat loss is directly proportional to the temperature differential according to Newton's law of cooling (see "Model and Approach"). Heat substitution (activity-generated heat) also buffers suboptimal environmental conditions in mammals (Humphries and Careau 2011) and could mitigate to some degree cold-weather constraints for nocturnal mammals as estimated here (heat substitution is unlikely to alter results for diurnal constraints, however). Daily torpor and seasonal hibernation also play key roles in mammalian thermal biology (Geiser 2004). Results from the model application using hot- and cold-quarter temperatures (figs. S1, S2) clearly show that nocturnal and diurnal habitable space during these months, respectively, are maximized. While our approach here simplifies a complex seasonal and activity variation scenario, the results give boundaries for thermal constraints on mammals while also signposting the mechanisms that allow for population persistence.

Consistently across latitude, nocturnal mammals are smaller than diurnal mammals (fig. 5), counter to our prediction (e.g., fig. 3). A number of factors could account for this strong body size difference. Body mass and scaling have significant consequences for a wide range of life-history and ecological traits (Fristoe et al. 2015), the potential impact of nocturnality on home range size may impose constraints on larger species (Clutton-Brock and Harvey 1977), and increased predation risk or competition might also force smaller lineages toward nocturnality (Kronfeld-Schor and Dayan 2003). Water balance and food requirements are particularly important for small mammals (Porter and Kearney 2009; Levy et al. 2016) and can have determining effects on body size (McNab 2010). Small endotherms are also especially vulnerable to extreme climatic events and acute dehydration (Gardner et al. 2011). Nocturnal activity or other temporal activity shifts (e.g., avoidance of hot midday hours) could then be one way for rodents and small mammals to avoid such extremes. Body size and thermal conductance can also interact with one another in complex ways not examined in this study. For example, Briscoe et al. (2015) found that fur depth changes across environmental gradients may compensate thermally for sexual dimorphic differences in body mass for koalas.

Whatever the mechanism, the fact that nocturnal mammals are smaller than diurnal species will have important climate change and thermoregulatory consequences (importantly, differences in size between nocturnal and diurnal species hold for the whole PanTHERIA data set,

Figure 4: Mean metabolic scope of an average rodent (*A*) and number of days where temperature exceeded thermal limits (*B*) calculated over daily averages (1981–2010) globally as a function of latitudinal bands across day (red) and night (light blue). *C*, Percentage of species within latitudinal bands that are nocturnal with a fitted polynomial (dark blue line).

not only for small mammals). Our warming projections showed key differences as a function of body size. Smaller body size was associated with lower loss of habitable area for diurnal species consistent with expectations of shrink-

ing mass under a warming climate for many species (Sheridan and Bickford 2011). Examining recent climate change responses in mammals across elevation, McCain and King (2014) also found that larger mammals exhibited larger
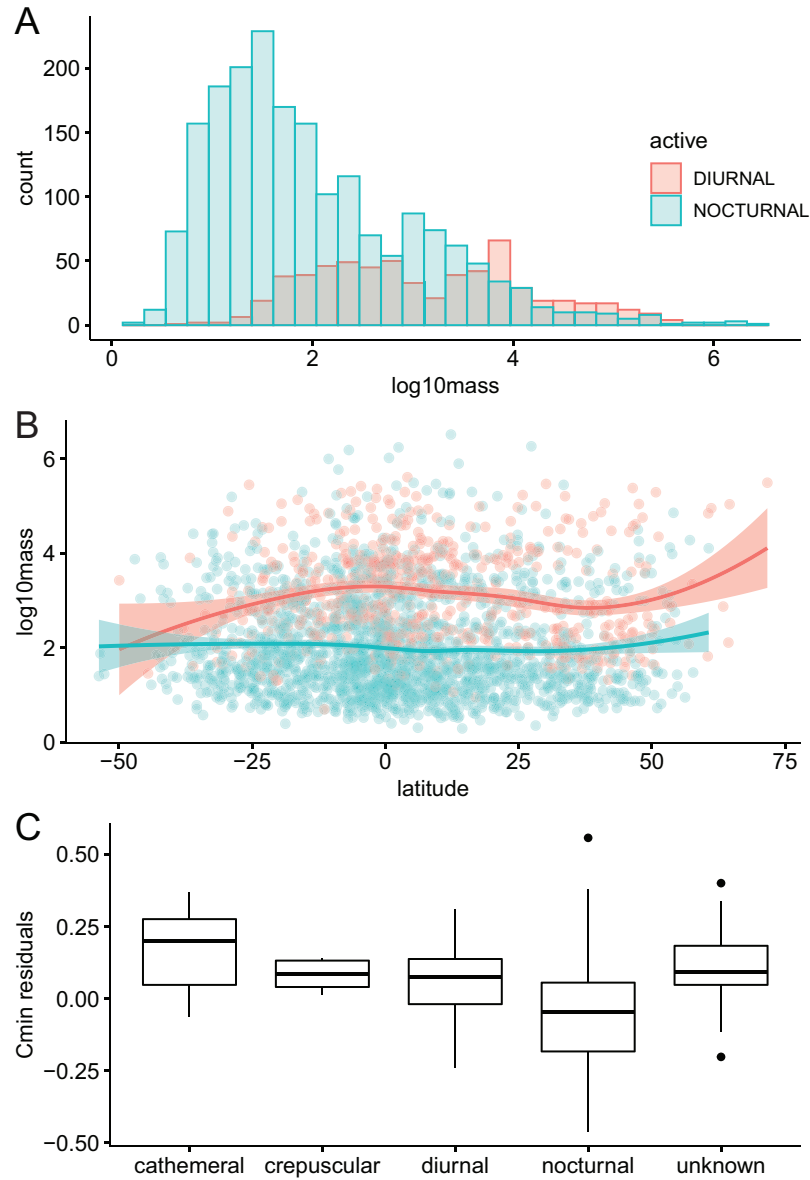
Figure 5: Histogram of body mass of mammal species across the PANtheria data set (all mammals including large species) as a function of activity (*A*) and mean body mass across latitude (*B*). Also shown is minimum thermal conductance C_{min} (residuals of body mass; *C*) of rodents from the Naya et al. (2013) data set.

responses to warming. On the other hand, nocturnal species exhibited positive habitat gains with larger body size, again emphasizing the importance of activity-time considerations for understanding climate change impacts.

How mammal species will respond to climate change will be determined by their physiology and energetics (Levesque et al. 2016). Our approach provides a mechanistic examination of how traits might contribute to distribution limits and climate change responses. Range limits of endotherms broadly are influenced by thermal tolerance (Bozi-

novic et al. 2011), but the specific mechanisms through which margins are determined appear to vary spatially and taxonomically (Khaliq et al. 2017). Thermal conductance, body size, and activity times will likely modulate relationships between mammal persistence and environmental conditions. Similarly, obligate nocturnal and diurnal species shift their distributions more than cathemeral mammals (McCain and King 2014). Given the clear distinction between the thermal regimes and unique challenges of daytime and nighttime temperatures, as well as the specific thermal adaptations
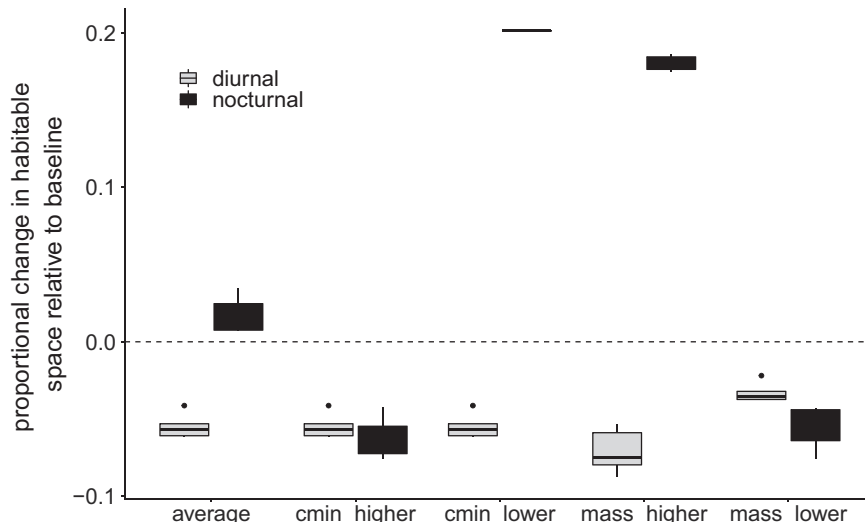
Figure 6: Projections of changes in habitable space for nocturnal and diurnal mammals under climate change (representative concentration pathway 4.5 for 2050) based on five general circulation models (GCMs; CCSM4, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM, and MPI-ESM-LR). Thermoregulatory polygons with mean trait values for small mammals were used as the baseline, and proportional change was calculated as the difference between baseline and future scenarios using each of the GCMs and variable traits (average = no change in traits; cmin_higher = 50% higher C_{min}; cmin_lower = 50% lower C_{min}; mass_higher = 50% higher m_b; mass_lower = 50% lower m_b). For reference, the 20% increase in habitable space under warming projected for low C_{min} nocturnal small mammals represents the upper limit of increase from baseline; that is, under those scenarios there was no uninhabitable space.

of diurnal and nocturnal species, stronger signals of spatial shifts would be expected for strictly nocturnal or diurnal species as a response to changing temperatures.

We show here how metabolic scope for activity may be affected by nocturnality in small mammals and endotherms broadly. The classic U-shaped metabolic curve of a typical endotherm is inadequate for such study because metabolic scope calculations require knowledge of the upper part of the thermoregulatory polygon. The putative impact of thermoregulation on activity is also ignored in the U-shaped metabolic curve. The thermoregulatory polygon approach implemented in this study therefore represents a novel type of process-based or mechanistic physiological model that can provide insights into macroecology and biogeography (Cabral et al. 2017). Projections of distributions of particular species using this approach would be limited by the lack of specific mechanisms that determine survival and reproduction. Mechanistic species distribution models, for example, can properly account for active thermoregulation and behavioral responses at high temporal resolution (Kearney and Porter 2009; Mathewson et al. 2017; Levy et al. 2019). However, the power of this approach is the simple analytical form of the model (based on Newton's law of cooling; Scholander et al. 1950) and therefore the ease of prediction and interpretation of how single factors (climate, thermal conductance, BMR, MMR, and others) can influence biogeography and climatic relationships.

There are clear thermoregulatory consequences of nocturnality, diurnality, and other activity periods in mammals. Unique challenges to daytime and nighttime temperatures drive species to adapt morphologically (body mass and thermal conductance) and physiologically (Gaston 2019). Under climate warming, one potential response to escape high temperatures, in addition to upslope or latitudinal shifts, would be to become more nocturnal (Levy et al. 2019). In large mammals, such shifts to nocturnality are widely evident as a response to human disturbance (Gaynor et al. 2018). Of course, other environmental factors need to be considered and may limit such shifts, in particular, light, which varies across latitude and limits mammal activity time (Bennie et al. 2014)—light is also changing at a historically unprecedented rate (Davies and Smyth 2018). Overall, however, mechanistic analyses of endothermic thermoregulatory strategies in variable thermal environments will help to elucidate the evolutionary history of mammals (and other vertebrates) and give clues as to their future in a changing climate.

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Statement of Authorship

T.C.B., E.L.R., and F.B. conceived and designed the study. T.C.B. and E.L.R. wrote the model script and analyzed the data. T.C.B. wrote the manuscript, and all authors contributed to reviewing and editing the manuscript.

Literature Cited

Anderson, S. R., and J. J. Wiens. 2017. Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates. Evolution 71:1944–1959.

Avaria-Llautureo, J., C. E. Hernández, E. Rodríguez-Serrano, and C. Venditti. 2019. The decoupled nature of basal metabolic rate and body temperature in endotherm evolution. Nature 10.1038/s41586-019-1476-9

Bacigalupe, L.D., E. L. Rezende, G. J. Kenagy, and F. Bozinovic. 2003. Activity and space use by degus: a trade-off between thermal conditions and food availability? Journal of Mammalogy 84:311–318.

Beaudrot, L., M. A. Acevedo, J. P. Lessard, A. Zvoleff, P. A. Jansen, D. Sheil, F. Rovero, et al. 2019. Local temperature and ecological similarity drive distributional dynamics of tropical mammals worldwide. Global Ecology and Biogeography 28:976–991.

Beever, E. A., L. E. Hall, J. Varner, A. E. Loosen, J. B. Dunham, M. K. Gahl, F. A. Smith, and J. J. Lawler. 2017. Behavioral flexibility as a mechanism for coping with climate change. Frontiers in Ecology and the Environment 15:299–308.

Bennie, J. J., J. P. Duffy, R. Inger, and K. J. Gaston. 2014. Biogeography of time partitioning in mammals. Proceedings of the National Academy of Sciences of the USA 111:13727–13732.

Bozinovic, F., P. Calosi, and J. J. Spicer. 2011. Physiological correlates of geographic range in animals. Annual Review of Ecology, Evolution and Systematics 42:155–179.

Bozinovic, F., and R. A. Vásquez. 1999. Patch use in a diurnal rodent: handling and searching under thermoregulatory costs. Functional Ecology 13:602–610.

Briscoe, N. J., A. Krockenberger, K. A. Handasyde, and M. R. Kearney. 2015. Bergmann meets Scholander: geographical variation in body size and insulation in the koala is related to climate. Journal of Biogeography 42:791–802.

Bronson, F. H. 2009. Climate change and seasonal reproduction in mammals. Philosophical Transactions of the Royal Society B 364:3331–3340.

Cabral, J. S., L. Valente, and F. Hartig. 2017. Mechanistic simulation models in macroecology and biogeography: state-of-art and prospects. Ecography 40:267–280.

Clarke, A., and P. Rothery. 2008. Scaling of body temperature in mammals and birds. Functional Ecology 22:58–67.

Clutton-Brock, T. H., and P. H. Harvey. 1977. Primate ecology and social organization. Journal of Zoology 183:1–39.

Cortés, A., C. Tirado, and M. Rosenmann. 2003. Energy metabolism and thermoregulation in *Chinchilla brevicaudata*. Journal of Thermal Biology 28:489–495.

Davies, T. W., and T. Smyth. 2018. Why artificial light at night should be a focus for global change research in the 21st century. Global Change Biology 24:872–882.

Ding, B. Y., Q. S. Chi, W. Liu, Y. L. Shi, and D. H. Wang. 2018. Thermal biology of two sympatric gerbil species: the physiological basis of temporal partitioning. Journal of Thermal Biology 74:241–248.

Faurby, S., and J. C. Svenning. 2015. A species-level phylogeny of all extant and late Quaternary extinct mammals using a novel heuristic-hierarchical Bayesian approach. Molecular Phylogenetics and Evolution 84:14–26.

Fristoe, T. S., J. R. Burger, M. A. Balk, I. Khaliq, C. Hof, and J. H. Brown. 2015. Metabolic heat production and thermal conductance are mass-independent adaptations to thermal environment in birds and mammals. Proceedings of the National Academy of Sciences of the USA 112:15934–15939.

Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming? Trends in Ecology and Evolution 26:285–291.

Gaston, K. J. 2019. Nighttime ecology: the "nocturnal problem" revisited. American Naturalist, 10.1086/702250.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science 360:1232–1235.

Geiser, F. 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. Annual Review of Physiology 66:239–274.

Geiser, F., and C. Turbill. 2009. Hibernation and daily torpor minimize mammalian extinctions. Naturwissenschaften 96:1235–1240.

Gerkema, M. P., W. I. Davies, R. G. Foster, M. Menaker, and R. A. Hut. 2013. The nocturnal bottleneck and the evolution of activity patterns in mammals. Proceedings of the Royal Society B 280:20130508.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society B 326:119–157.

Harris, I., P. D. Jones, T. J. Osborn, and D. H. Lister. 2014. Updated high-resolution grids of monthly climatic observations: the CRU TS3.10 dataset. International Journal of Climatology 34:623–642.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2004. The WorldClim interpolated global terrestrial climate surfaces. Version 1.3.

Huey, R. B., J. B. Losos, and C. Moritz. 2010. Are lizards toast? Science 328:832–833.

Humphries, M. M., and V. Careau. 2011. Heat for nothing or activity for free? evidence and implications of activity-thermoregulatory heat substitution. Integrative and Comparative Biology 51:419–431.

Humphries, M. M., J. Umbanhowar, and K. S. McCann. 2004. Bioenergetic prediction of climate change impacts on northern mammals. Integrative and Comparative Biology 44:152–162.

Humphries, M. M., S. Boutin, D. W. Thomas, J. D. Ryan, C. Selman, A. G. McAdam, D. Berteaux, and J. R. Speakman. 2005. Expenditure freeze: the metabolic response of small mammals to cold environments. Ecology Letters 8:1326–1333.

Jackson, T. P., T. J. Roper, L. Conradt, M. J. Jackson, and N. C. Bennett. 2002. Alternative refuge strategies and their relation to thermophysiology in two sympatric rodents, *Parotomys brantsii* and *Otomys unisulcatus*. Journal of Arid Environments 51:21–34.

Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648–2648.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

Kenagy, G. J., R. F. Nespolo, R. A. Vásquez, and F. Bozinovic. 2002. Daily and seasonal limits of time and temperature to activity of degus. Revista Chilena de Historia Natural 75:567–581.

Khaliq, I., K. Böhning-Gaese, R. Prinzinger, M. Pfenninger, and C. Hof. 2017. The influence of thermal tolerances on geographical ranges of endotherms. Global Ecology and Biogeography 26:650–668.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34:153–181.

Levesque, D. L., J. Nowack, and C. Stawski. 2016. Modelling mammalian energetics: the heterothermy problem. Climate Change Responses 3:7.

Levesque, D. L., A. A. Tuen, and B. G. Lovegrove. 2018. Staying hot to fight the heat-high body temperatures accompany a diurnal endothermic lifestyle in the tropics. Journal of Comparative Physiology B 188:707–716.

Levy, O., T. Dayan, W. P. Porter, and N. Kronfeld-Schor. 2016. Foraging activity pattern is shaped by water loss rates in a diurnal desert rodent. American Naturalist 188:205–218.

———. 2019. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? Ecological Monographs 89:e01334

Lovegrove, B. G. 2017. A phenology of the evolution of endothermy in birds and mammals. Biological Reviews 92:1213–1240.

Mathewson, P. D., L. Moyer-Horner, E. A. Beever, N. J. Briscoe, M. Kearney, J. M. Yahn, and W. P. Porter. 2017. Mechanistic variables can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates. Global Change Biology 23:1048–1064.

McCain, C. M., and S. R. King. 2014. Body size and activity times mediate mammalian responses to climate change. Global Change Biology 20:1760–1769.

McNab, B. K. 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. Oecologia 164:13–23.

Medina, I., E. Newton, M. R. Kearney, R. A. Mulder, W. P. Porter, and D. Stuart-Fox. 2018. Reflection of near-infrared light confers thermal protection in birds. Nature Communications 9:3610.

Mitchell, D., E. P. Snelling, R. S. Hetem, S. K. Maloney, W. M. Strauss, and A. Fuller. 2018. Revisiting concepts of thermal physiology: predicting responses of mammals to climate change. Journal of Animal Ecology 87:956–973.

Naya, D. E., L. Spangenberg, H. Naya, and F. Bozinovic. 2013. Thermal conductance and basal metabolic rate are part of a coordinated system for heat transfer regulation. Proceedings of the Royal Society B 280:20131629.

Naya, D. E., H. Naya, and C. R. White. 2018. On the interplay among ambient temperature, basal metabolic rate, and body mass. American Naturalist 192:518–524.

Porter, W. P., and M. Kearney. 2009. Size, shape, and the thermal niche of endotherms. Proceedings of the National Academy of Sciences of the USA 106:19666–19672.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Rezende, E. L., and L. D. Bacigalupe. 2015. Thermoregulation in endotherms: physiological principles and ecological consequences. Journal of Comparative Physiology B 185:709–727.

Rosenmann, M., and P. R. Morrison. 1974. Maximum oxygen consumption and heat loss facilitation in small homeotherms by He-O2. American Journal of Physiology 226:490–495.

Scholander, P. F., R. Hock, V. Walters, F. Johnson, and L. Irving 1950. Heat regulation in some arctic and tropical mammals and birds. Biological Bulletin 99:237–258.

Sheridan, J. A., and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. Nature Climate Change 1:401–406.

Sinervo, B., F. Mendez-De-La-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. Villagrán-Santa Cruz, R. Lara-Resendiz, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–899.

Tracy, C. R. 1972. Newton's law: its application for expressing heat losses from homeotherms. BioScience 22:656–659.

van der Vinne, V., J. A. Gorter, S. J. Riede, and R. A. Hut. 2015. Diurnality as an energy-saving strategy: energetic consequences of temporal niche switching in small mammals. Journal of Experimental Biology 218:2585–2593.

van der Vinne, V., S. J. Riede, J. A. Gorter, W. G. Eijer, M. T. Sellix, M. Menaker, S. Daan, V. Pilorz, and R. A. Hut. 2014. Cold and hunger induce diurnality in a nocturnal mammal. Proceedings of the National Academy of Sciences of the USA 111:15256–15260.

Voigt, C. C., and D. Lewanzik. 2011. Trapped in the darkness of the night: thermal and energetic constraints of daylight flight in bats. Proceedings of the Royal Society B 278:2311–2317.

Williams, C. M., H. A. Henry, and B. J. Sinclair. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. Biological Reviews 90:214–235.

Wu, J., T. Yonezawa, and H. Kishino. 2017. Rates of molecular evolution suggest natural history of life history traits and a post-K-Pg nocturnal bottleneck of placentals. Current Biology 27:3025–3033.

Zhu, W. L., T. Jia, X. Lian, and Z. K. Wang. 2008. Evaporative water loss and energy metabolic in two small mammals, voles (*Eothenomys miletus*) and mice (*Apodemus chevrieri*), in Hengduan mountains region. Journal of Thermal Biology 33:324–331.

Zurell, D., C. H. Graham, L. Gallien, W. Thuiller, and N. E. Zimmermann. 2018. Long-distance migratory birds threatened by multiple independent risks from global change. Nature Climate Change 8:992–996.