

ARTICLE

A mechanistic model of endotherm hibernation applied to the endangered mountain pygmy possum under climate change

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Abstract

Hibernation is an important strategy used by many endotherms to conserve energy and water. Global warming is changing species' phenology and hibernation patterns, but whether such changes are beneficial or harmful depends on the species' life history traits, physiology, morphology, and behavior. Mechanistic niche models can be used to make strong inferences on such responses by explicitly quantifying the consequences of changed hibernation patterns for energy and water requirements. However, they have yet to be adapted to heterothermic species. Here, we address this problem by extending the endotherm biophysical model of the NicheMapR package to encompass torpor. This model accurately predicts the energy requirements of hibernating mammals over a broad size range from microbats to bears. We then used this approach to assess the effect of climate change on a Critically Endangered hibernator, the Australian mountain pygmy possum (*Burramys parvus*). Specifically, we contrasted conditions for the year 2010 with two future climate-change scenarios (2 or 4°C of average warming) to identify: (i) the projected changes in energy and water requirements; (ii) the advantage conferred by hibernating for the species' energy and water requirements; and (iii) the areas across southeastern Australia that could continue to support hibernation. We projected an 11%–43% reduction in hibernation hours for the mountain pygmy possum under our two climate-change scenarios. In consequence, requirements for energy increased by 4%–21%, and for water by 10%–34%. Under current conditions, hibernation reduces annual energy requirements by 44%–52% and annual water requirements by 32%–42%, but in our projections, this energetic and hydric benefit of hibernation will decline due to climate change. The total area where hibernating and not hibernating is energetically equivalent is projected to increase by 60% under 4°C warming, preventing recovery from the species' severely restricted distribution at present. Our results show that climate change will have a profound impact on the duration and

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patterns of hibernation, a key survival strategy, for *Burramys*. Our framework for analyzing changing hibernation patterns provides a new and general way to test the vulnerability and plasticity of hibernating endotherms under global change.

KEYWORDS

biophysical ecology, climate change, hibernation, mechanistic niche models, torpor

INTRODUCTION

Climate change is affecting species distributions globally and is predicted to have large impacts on the planet's biodiversity (Parmesan & Yohe, 2003; Pecl et al., 2017), including a rise in extinction rates by the end of this century (Maclean & Wilson, 2011). To design conservation interventions that will reduce extinction risk, we need reliable forecasts of the impacts of climate change on species (Parmesan et al., 2022). Forecasting these impacts is difficult, however, because climate change affects species differently according to their life history traits, physiology, behavior, and morphology (Huey et al., 2012; McCain & King, 2014). Correlative species distribution models (SDMs) are most often applied to forecast the impacts of climate change, but this approach captures species-specific responses only implicitly (Dormann et al., 2012). Models that include processes by which climate limits species distribution are more suitable for forecasting the impacts of climate change because the mechanisms causing decline are made explicit (Briscoe et al., 2023; Urban et al., 2016). A key question when using these mechanistic models is choosing which limiting process(es) to include.

Among endotherms, an important physiological phenomenon to consider is heterothermy. Heterothermic species have physiological scope to vary their core temperature by entering torpor and thereby making energy savings. Torpor provides several benefits, the nature of which depends on the time scales over which core temperature and metabolism vary. Species that undergo daily torpor can limit foraging without incurring large energy costs, allowing them to match energy expenditure to short-term variation in food availability. Torpor also reduces the risk of predation entailed by activity (Nowack et al., 2017; Ruf & Bieber, 2023). Some species hibernate: They seasonally employ torpor for long periods that are disrupted by phases of interbout euthermia. This allows them to avoid the energy expenditure that would otherwise be required to maintain a constant core body temperature during the cold winter season. Species that use torpor also reduce the water requirements associated with metabolic rate and activity, allowing them to match water requirements to water availability.

Because of the physiological plasticity provided by the ability to enter torpor, heterotherms are expected to be better able to adjust to environmental fluctuations induced by climate change than homeotherms, which maintain a constant high core body temperature (Canale & Henry, 2010; Nowack et al., 2017). On the other hand, increased environmental temperatures can increase energy requirements while an animal is in a torpid state, thereby reducing the benefits of torpor, but this can be modulated by the extent to which the temperature varies temporally (Boyles & McKechnie, 2010). Higher environmental temperatures have already shortened the duration of hibernation in some species, due to earlier emergence and later immergence, together with increased frequency of bouts of euthermia during hibernation, due to more extreme burrow temperatures (Findlay-Robinson et al., 2023; French, 1982; Wells et al., 2022). Reduction in hibernation entails increased activity, higher annual requirements for water and energy, and more competition with or predation by homeotherms (Ruf & Bieber, 2023). However, if these energetic and interaction effects can be overcome, hibernators may increase their litter size due to increased energy availability (Findlay-Robinson et al., 2023, Wells et al., 2022).

Currently, our ability to model how hibernators will respond to climate change is limited. Here, we present a framework to quantitatively project when or where changes in energy and water requirements will occur under climate change for a given species. We demonstrate how species-specific predictions of the effect of climate change on hibernation can be made using the endotherm model of NicheMapR (Kearney, Briscoe, et al., 2021; Kearney & Porter, 2017). This model finds solutions to the energy balance model of an endotherm under different microclimates given the species' potential behavioral and physiological responses (e.g., changed posture, increased blood flow, panting). In previous releases, the thermoregulatory algorithm catered for homeothermic species only, that is, those that predominantly defend a narrow range of high body temperatures. The new algorithm presented here instead attempts to balance the heat budget by reducing body temperature to a specified minimum, capturing the close coupling of core body and ambient temperatures witnessed in

hibernating endotherms (Boyles et al., 2011). The approach can be applied to any heterothermic species that enters torpor under cold conditions. It can also capture the newly discovered phenomenon of “hot torpor” by modeling a dynamic response of minimum metabolic rate (Reher & Dausmann, 2021). We illustrate the general approach by comparing laboratory measurements with the model’s predictions for four mammal species—hoary bat (*Lasiurus cinereus*), mountain pygmy possum (*Burramys parvus*), alpine marmot (*Marmota marmota*), and black bear (*Ursus americanus*)—that cover a wide mass range from 27.6 g to 66 kg.

We then selected the mountain pygmy possum (hereafter *Burramys*) as a case study because its metabolism and its relationship to temperature have been well researched (Fleming, 1985; Geiser et al., 1990; Geiser & Broome, 1991, 1993; Geiser & Körtner, 2004). This case study also serves to expand hibernation research for southern hemisphere hibernators, which have been identified as being understudied (Wells et al., 2022).

Burramys is Australia’s only alpine marsupial and the only seasonally hibernating marsupial (Mansergh & Broome, 1994). It is a small-bodied (35–80 g), insectivore-granivore-frugivore that is Critically Endangered according to the International Union for Conservation of Nature (Department of Environment, 2016; Mansergh & Broome, 1994; Menkhorst et al., 2008). In the recent past, the major threats to the species have been habitat loss due to ski resort expansion in the Australian Alps and predation from the introduced feral cat (*Felis catus*) and red fox (*Vulpes vulpes*) (Department of Environment, 2016). Climate change is expected to present major challenges for the species in the future (Department of Environment, 2016). The area of the Australian Alps with currently at least 100 days of annual snow cover has been projected to reduce by 60%–100% with a 1–3°C increase in temperatures above 1990 levels (Hennessy et al., 2003). Decreased snow cover resulting from climate change is expected to affect *Burramys* by shortening and interrupting its current hibernation pattern (Geiser & Broome, 1991, 1993; Kortner & Geiser, 1998), increasing interactions with low-elevation species, both competitors and predators, likely to occupy higher areas from which they were previously excluded by snow cover in winter (Broome et al., 2012). Climate change may also reduce the availability of *Burramys*’ two main food sources, the Bogong moth (*Agrotis infusa*) and the mountain plum pine (*Podocarpus lawrencei*) through reduced winter survival for the moth and increased fire frequency for the pine (Gibson et al., 2018).

Our research had four main aims: (1) extend the NicheMapR framework to include heterothermy and

show this model’s applicability across a wide range of species; (2) apply the model to compare the energy and water requirements of *Burramys* in the present day with that projected for the future, for 2°C and 4°C warming scenarios, at its four major population sites; (3) quantify the energetic and hydric savings conferred by hibernation at the same four sites; and (4) use spatially projected energy and water requirements across southeastern Australia to identify where it is advantageous for *Burramys* to hibernate and how that distribution will change with climate warming.

METHODS

Modeling heterothermy

The endotherm model of NicheMapR is a modularized R (R Core Team, 2023) implementation of the “Niche Mapper” endotherm model originally developed by Porter and colleagues (Kearney, Briscoe, et al., 2021; Mathewson et al., 2017; Porter et al., 1994). It has been used to model the bioenergetics of a wide range of endotherms, including the night parrot (Kearney et al., 2016), koala (Briscoe et al., 2016), and grizzly bear (Rogers et al., 2021). It computes the required metabolic heat production (under cold conditions) or evaporative water loss (under hot conditions, from panting or sweating) to maintain a specified core body temperature given environmental conditions and functional traits (Kearney, Jusup, et al., 2021). This body temperature is the set point (T_{set}) that an organism attempts to maintain, which is regulated in vivo by the hypothalamus (Heller et al., 1977). The relevant traits include body size and shape, pelage properties, and physiological characteristics such as basal metabolic rate, Q_{10} temperature coefficient (i.e., the factor by which a rate, here metabolism, changes with a 10°C change in body temperature), oxygen extraction efficiency, and the presence of fat. The model allows the organism to adjust its behavior (by posture change) and physiology (by changes to flesh conductivity, panting, sweating) to maintain the T_{set} given the minimum permissible metabolic heat production (the basal metabolic rate) and may allow the core temperature to rise to an individual-specific value (T_{max}) in the process. This process of responding to changes in environmental conditions is typical of a homeotherm and was, until now, the only way an endotherm in NicheMapR could be modeled.

We have added the argument TORPOR to the *endoR* function in NicheMapR, the default setting of 0 employing the original homeotherm model (Kearney, Briscoe, et al., 2021), hereafter referred to as the

“standard” model. Our new algorithm can be run by setting the parameter TORPOR to 1 and we will refer to this model as the “torpor” model (GitHub link for updated *endoR* function <https://github.com/mrke/NicheMapR/blob/master/R/endoR.R>). This torpor algorithm requires only one additional parameter, the minimum core temperature the animal can tolerate (T_{\min}). For most animals, torpor reduces energy requirements by lessening the temperature differential defended between ambient temperature and the animal’s core temperature (Geiser, 2004). Both the standard and torpor algorithms start by predicting the metabolic rate for T_{set} given animal characteristics and environmental conditions (for a visualization of the algorithm, see Appendix S1: Figure S1). While the standard algorithm does not allow the animal’s core temperature to drop below T_{set} or the predicted metabolic rate to go below the basal metabolic rate, the torpor model reduces the core temperature, consequently lowering the basal metabolic rate to a new torpid basal metabolic rate according to the Q_{10} effect. The torpor algorithm then re-predicts the metabolic rate based on the newly reduced core temperature and basal metabolic rate, and will continue to drop the core temperature by a user-specified interval, and re-predict until the predicted metabolic rate is less than or equal to the new torpid basal metabolic rate, or the core temperature reaches T_{\min} (whichever happens first).

However, two aspects of torpor require greater model complexity. First, as ambient temperatures decline well below T_{\min} , a point is reached where metabolic heat generation must rise to defend this lower body temperature. That is, it must switch back to the standard algorithm but with T_{\min} as the new target core temperature. We set this transition to occur when the calculated energy balance deviates from zero (i.e., steady state). We chose the threshold of less than 5% of the current value of metabolic heat generation. Second, larger mammals that undergo torpor (e.g., black bears) cannot rely on the Q_{10} effect alone to reduce their metabolic rate, so they actively downregulate it (Geiser, 2004). For these species, the basal metabolic rate should be set to the metabolic rate observed in torpid individuals (the same approach could be used to simulate “hot torpor”).

To assess the performance of our new algorithm, we compared model predictions of the metabolic rate and core temperature to laboratory observations from metabolic chambers for four species across the class Mammalia and spanning several orders of magnitudes of mass (Figure 1). These were the hoary bat, mountain pygmy possum, alpine marmot, and black bear, weighing 27.5 g, 44.3 g, 3.87 kg, and 66 kg, respectively. We used physiological parameters taken from the literature (see Appendix S1: Tables S1–S4) and simulated each species

exposed to air temperatures between -30 and 40°C at 1°C increments and dry still air (relative humidity values of 15% and wind speed at 0.1 m/s). The simulated metabolic rates were then compared with those from laboratory data taken from the literature (Appendix S1: Table S5). To account for variation in physiological parameters, a sensitivity analysis was run with physiological parameters varying 10% above and below their initial value, using Latin hypercube sampling (following Morris et al., 2024) (see of Appendix S1: Figures S2–S9, Section S1).

Microclimate modeling

We used the *micro_era5* function from the *NicheMapR* package to simulate the microclimate (Kearney, 2020; Kearney & Porter, 2017; Klinges et al., 2022). This function works in three steps. First, the *mcera5* package (Klinges et al., 2022) is used to obtain the macroclimate data from the ERA5 climate dataset (ECMWF Re-Analysis 5; Hersbach et al., 2020). ERA5 data are available at an hourly temporal resolution from 1950 to 5 days from present (pre-1978 data are currently classified as preliminary) at a 0.25° spatial resolution. Second, the *elevatr* package (Hollister et al., 2017) and *microclima* package (Maclean et al., 2019) topographically adjust temperature along with other terrain corrections (e.g., shading) at meso- and micro-scales. Lastly, the microclimate model is run on these macroclimatic data. This model takes as inputs these hourly weather conditions including air temperature, wind speed, and relative humidity at 1–2 m above the ground, cloud cover, and rainfall, as well as the physical properties of the habitat, and computes hourly microclimatic conditions above- and belowground, including soil temperature and moisture, at multiple depths, and snow cover and its influence on the soil heat budget (Kearney & Porter, 2017; Kearney, 2020; see Appendix S2 for a vignette showing the code and providing a brief description of how the microclimate works and how it interacts with the endotherm model).

Key input parameters for this study were the locations of modeled populations, the height above ground at which the animal is typically positioned, the bulk density of the soil, the time period, and the level of shading (0%–100%) at the site. For our more detailed study of *Burramys*, the site coordinates we chose were those of the four known *Burramys* population sites: Kosciusko (148.25° , -36.45°), Bogong (147.16° , -36.95°), Buller (146.42° , -37.14°), and Snow Ridge (148.40° , -35.95°) (Broome et al., 2012; Schulz et al., 2012a, 2012b). For our landscape-scale study across southeastern Australia, we chose locations at a 0.25° spatial resolution between 141.7° and 150.9° longitude and -34.1 and -43.6 latitude.

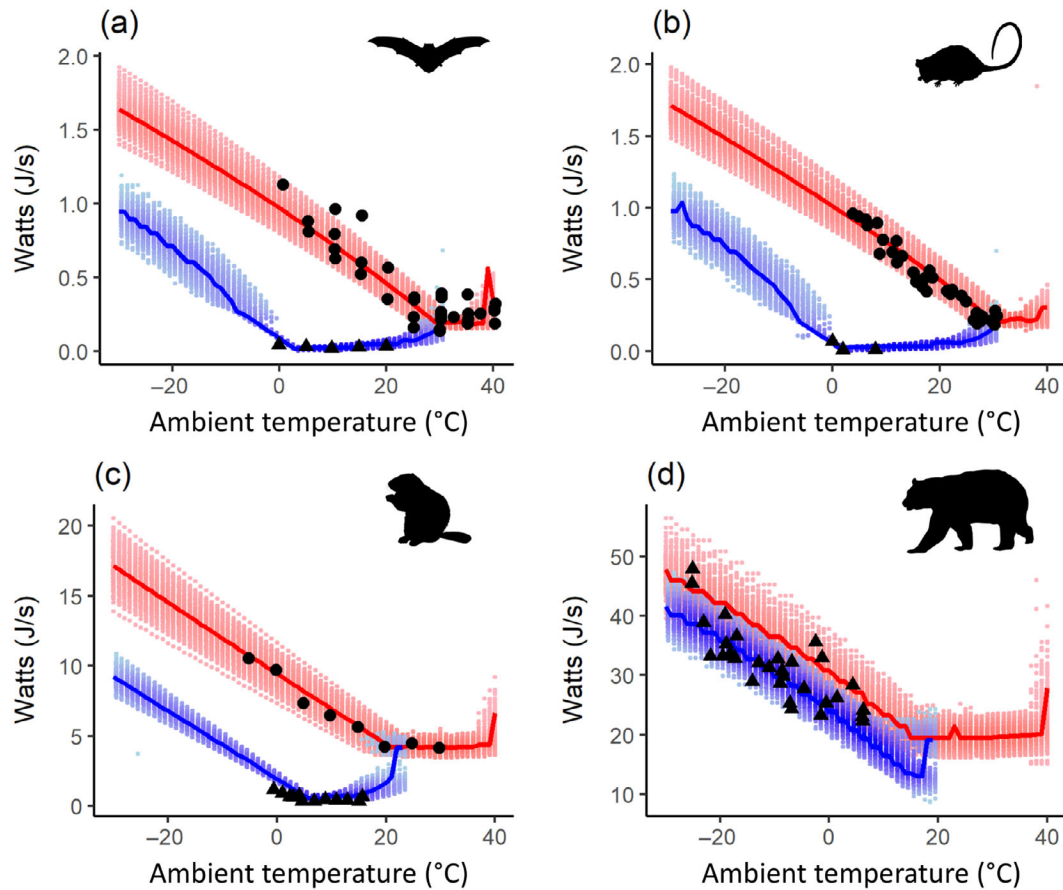


FIGURE 1 Comparison of predicted and observed outputs for regular and hibernating metabolic activity for the (a) hoary bat, (b) mountain pygmy possum, (c) alpine marmot, and (d) black bear. Black circles and triangles are values from laboratory experiments performed on these non-hibernating and hibernating animals, respectively (see Appendix S1: Table S5 for references). No data for non-hibernating black bears could be found. Red and blue lines are predictions from the standard and torpor models, respectively, while the colored dots represent predictions from models with different physiological parameters. As only cold torpor was being modeled, the torpor model was not simulated once the homeotherm thermoneutral zone was reached. Animal silhouette for (b) was created by Shane D. Morris; silhouettes in (a–d) are from www.phylopic.org under a CC0 1.0 Universal Public Domain license.

The height above ground was chosen at 2.5 cm, as this is roughly midheight of *Burramys* while prone (measured from a specimen) and bulk density was 2.56 Mg/m^3 to simulate boulder fields inhabited by *Burramys* (Broome, 2001). The year chosen was 2010 because empirical data on microclimates used by *Burramys* (Shi et al., 2015) exist for Mount Kosciuszko National Park (see coordinate above). We tested our microclimate output to select the appropriate shading input parameter and soil depth profile (see Appendix S1: Section S2 for detailed explanation, with Figures S10 and S11). *Burramys* forages near the surface at night and sleeps belowground during the day, so we selected “near-surface” (depth at 2.5 cm and 70% shade) and “burrow” (depth at 15 cm and 80% shade) microclimatic conditions (Broome, 2001).

We chose the TerraClimate (Qin et al., 2020) future scenarios of 2 and 4°C above global mean pre-industrial

temperatures to simulate climate change, using the scenario parameter in the `micro_era5` function. The TerraClimate future scenarios use the observational records from 1985 to 2015 to ascertain the monthly degree of change in climatic conditions a 2 or 4°C mean global increase in temperature would cause in these years (Abatzoglou et al., 2018). It does this while accounting for the spatial variation in climatic effects from such increases in global mean temperatures. The `micro_era5` function requires the changes in temperature (minimum and maximum), solar radiation, precipitation, vapor pressure, and soil moisture to predict future warming. As we choose 2010 as our baseline year (because we could validate it), our modeled future scenarios depict the local climate at our sites in 2010 if that year experienced a mean global increase in temperature of 2 or 4°C. In summary, we simulated the burrow and near-surface conditions for all hours for the year 2010, 2010 plus 2°C, and 2010 plus

4°C, at each of the four sites (Kosciuszko, Bogong, Buller, and Snow Ridge) and at a 0.25° spatial resolution across southeastern Australia.

Modeling *Burramys*

To quantify how environmental conditions affect the energetic requirements of *Burramys*, rules were created to have the endotherm heat budget models interact with the appropriate microclimate outputs at the appropriate times (for the schematic of modeling procedure, see Figure 2). Simulated active animals were modeled to interact with the near-surface outputs only, while simulated inactive and hibernating animals interacted only with the burrow outputs.

To simulate nocturnal activity energy costs, when *Burramys* is active, the target metabolic rate was double the basal metabolic rate. This activity multiplier generally ranges between $\times 1.56$ and 4.5 for mammals (Mathewson et al., 2020; Rogers et al., 2021), but our value ($\times 2$) was chosen to be lower than that of the summer value ($\times 3$) of a physiological and ecologically similar, yet diurnal and more active species, the American pika (*Ochotona princeps*) (Mathewson et al., 2017). We ran our analyses with higher activity values (2.5 and 3) to confirm that our choice of activity multiplier did not significantly impact our results (see in Appendix S1: Figures S12–S14, Section S3).

The factors responsible for initiating hibernation are synergistic and complex. The mechanisms suggested to control hibernation in *Burramys* are photoperiod, food availability, and temperature (Geiser & Broome, 1991). Photoperiod will not shift with climate change, and effects on food availability cannot be forecast at the necessary resolution, so temperature was chosen as the cue used to induce hibernation in our modeling. Changes in air temperature (with no change in photoperiod) have been deemed to be the main factor controlling the emergence date of the meadow jumping mouse (*Zapus hudsonius*), European edible dormouse (*Glis glis*), and yellow-bellied marmot (*Marmota flaviventris*) (Findlay-Robinson et al., 2023). The torpor model was invoked immediately after temperatures in the burrow microclimate were below 8°C for 24 consecutive hours. We chose an ambient temperature threshold of 8°C because this is the highest temperature at which *Burramys* can undergo prolonged torpor (Geiser & Broome, 1993). We considered 24 consecutive hours to be a period of time that would reasonably trigger multiday hibernation rather than bouts of torpor lasting less than 1 day (see Appendix S1: Figures S15–S16, Section S4 for testing of 1 h threshold). Temporary rewarming

(interbout euthermia) was incorporated by reverting to the standard endotherm model and was simulated to occur every 8 days (192 h), in bouts lasting 19 h (Broome & Geiser, 1995), throughout hibernation.

The energetic and water requirements for a hibernating and non-hibernating *Burramys* could be compared by making hibernation possible or impossible when the above conditions were met. This was done for the four sites for the present conditions (2010) and the two future-warming scenarios, with the results displayed temporally and for the southeast of Australia for which results are displayed at a 0.25° spatial resolution.

RESULTS

Our models matched past laboratory data closely. Pearson correlation coefficients were 0.98, 0.98, and 0.99 for the standard models of the hoary bat, *Burramys*, and alpine marmot, respectively, and 0.86, 0.89, 0.92, and 0.81 for the torpor model of the hoary bat, *Burramys*, alpine marmot, and black bear, respectively (Figure 1). The root mean squared errors (RMSEs) were 0.07, 0.06, and 0.35 W (joules per second) for the standard models of the hoary bat, *Burramys*, and alpine marmot, respectively, and 0.02, 0.01, 0.52, and 3.51 W for the torpor model of the hoary bat, *Burramys*, alpine marmot, and black bear, respectively (Figure 1).

Our simple rule for the initiation of hibernation (burrow air temperature $< 8^{\circ}\text{C}$ for > 24 h) predicted the observed current hibernation period for *Burramys* at Kosciuszko, starting in April or May and ending in October or November (Kortner & Geiser, 1998) (Figure 3). Climate change was predicted to cause a reduction in snow depth (Appendix S1: Figure S3) and hibernation hours at all four sites (Figure 3). Buller had the largest reduction in hibernation hours for both warming scenarios (Figure 3). Increased fragmentation of the hibernation period caused by more frequent incidences of arousal occurred at all sites (Figure 3). These arousals were additional to the programmed arousals for interbout euthermia. The use of a 1-h hibernation threshold changed the results quantitatively, but not qualitatively (Appendix S1: Figures S15 and S16).

The amount of energy required by *Burramys* in the summer months (December–February) declined at all sites due to climate change (Figure 4). This did not lead to increased water requirements (Figure 4), indicating that *Burramys* will not encounter summer heat stress. Monthly energy requirements just prior to hibernation increased at all sites with climate warming, particularly for the 4°C scenario, to values exceeding any calculated for the present-day sites (Figure 4). Buller, Kosciuszko,

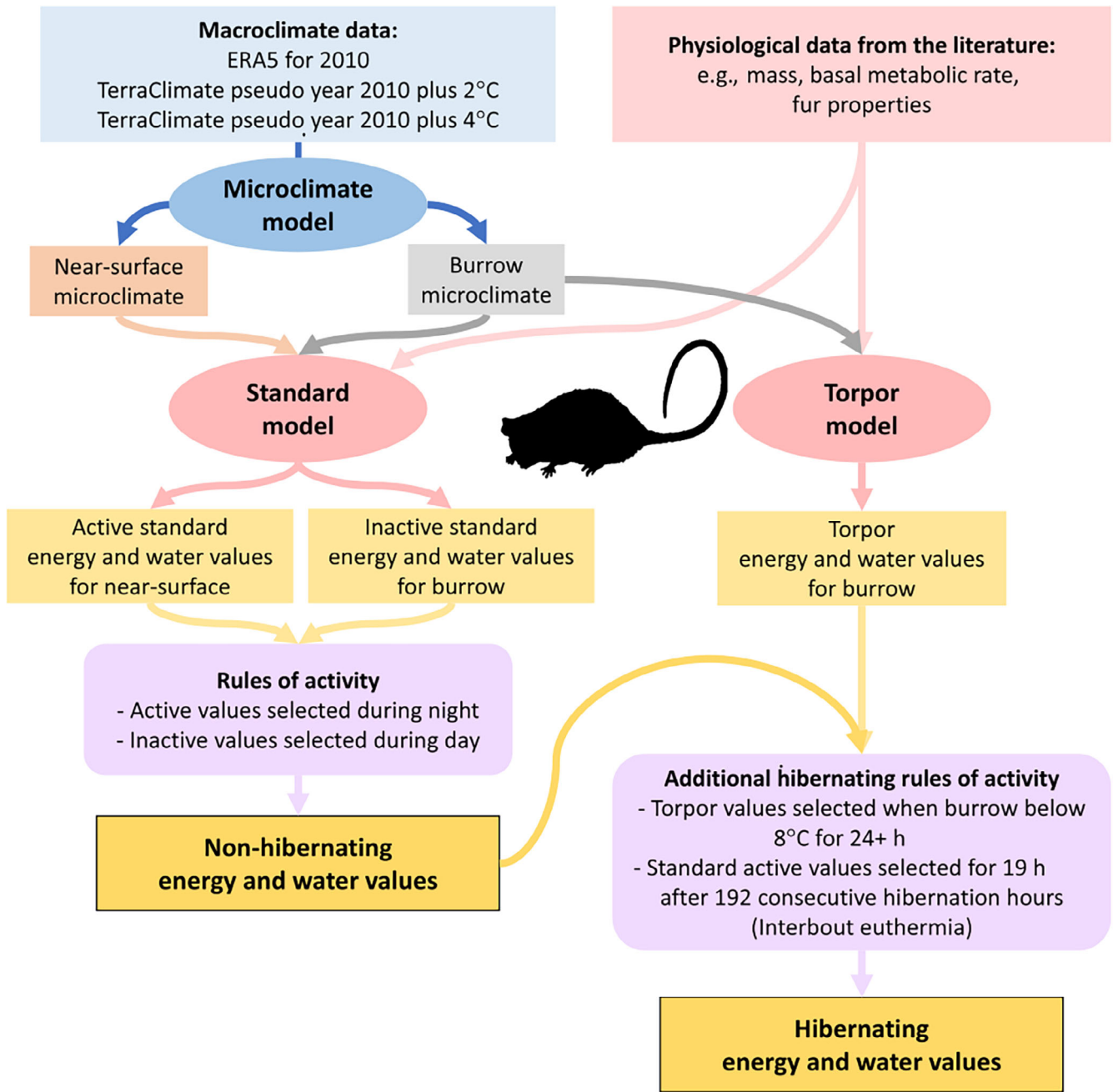


FIGURE 2 Outline of modeling procedure to calculate the non-hibernating and hibernating energy and water values for *Burramys parvus* given different climatic conditions. *Burramys* silhouette created by Shane D. Morris.

and Snow Ridge had increased energy requirements post-hibernation with climate change (Figure 4).

Energy and water requirements for a hibernating *Burramys* were projected to increase with temperature at all sites when considered on an annual basis (Figure 4). However, the magnitude of the energy and water savings from hibernation decreased with a warming climate (Figure 4). In 2010, *Burramys* would need to consume between 77% and 110% more energy annually at its four main sites if it did not hibernate (Figure 4). This

decreased to 57%–86% with 2°C warming and further declined to 36%–66% with 4°C warming. These decreases were caused by the reduction in hibernation hours (Figure 3). Water savings did not decline as sharply, non-hibernators needing 48%–72% more at present, 37%–55% more with 2°C warming, and 25%–42% more with 4°C warming.

The energy savings accrued by invoking hibernation in our simulated *Burramys* decreased with projected increased temperatures across southeastern Australia

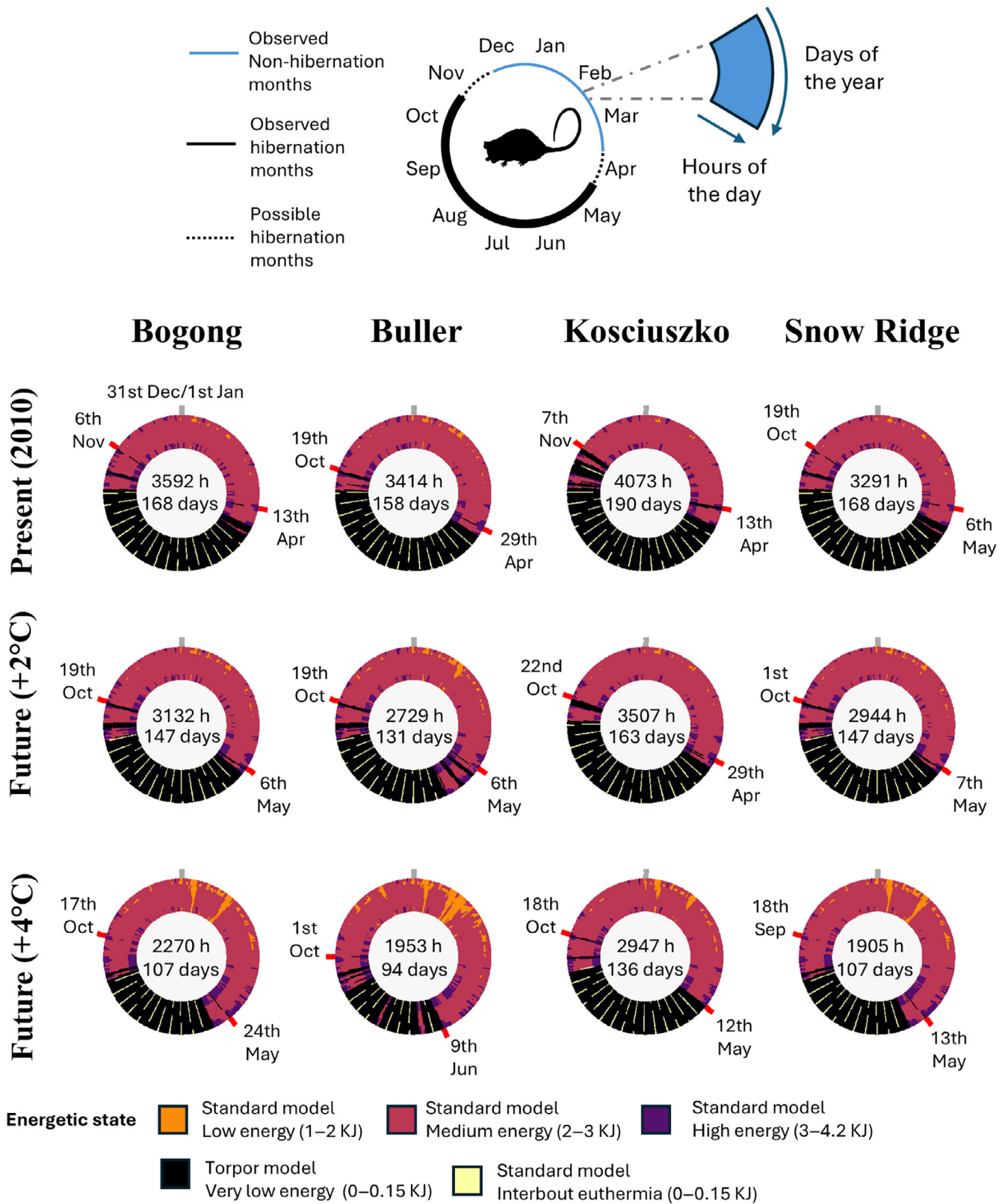


FIGURE 3 The observed hibernation period for *Burramys parvus* at Kosciuszko National Park (Kortner & Geiser, 1998) and the simulated hibernation period and hourly energy requirements at four sites—Kosciuszko, Bogong, Buller, and Snow Ridge—for 2010 and two future climate-warming scenarios (2 and 4°C increase, respectively). Black represents extremely low energy usage associated with hibernation. Spikes of high energy use during hibernation, which are yellow lines within the black section, represent arousals for interbout euthermia. These were programmed to occur and therefore do not increase with warming temperatures. This is in comparison to the dark pink sections within the black sections (see Buller with a 4°C increase) that are arousals caused by increased ambient temperatures. *Burramys* silhouette created by Shane D. Morris.

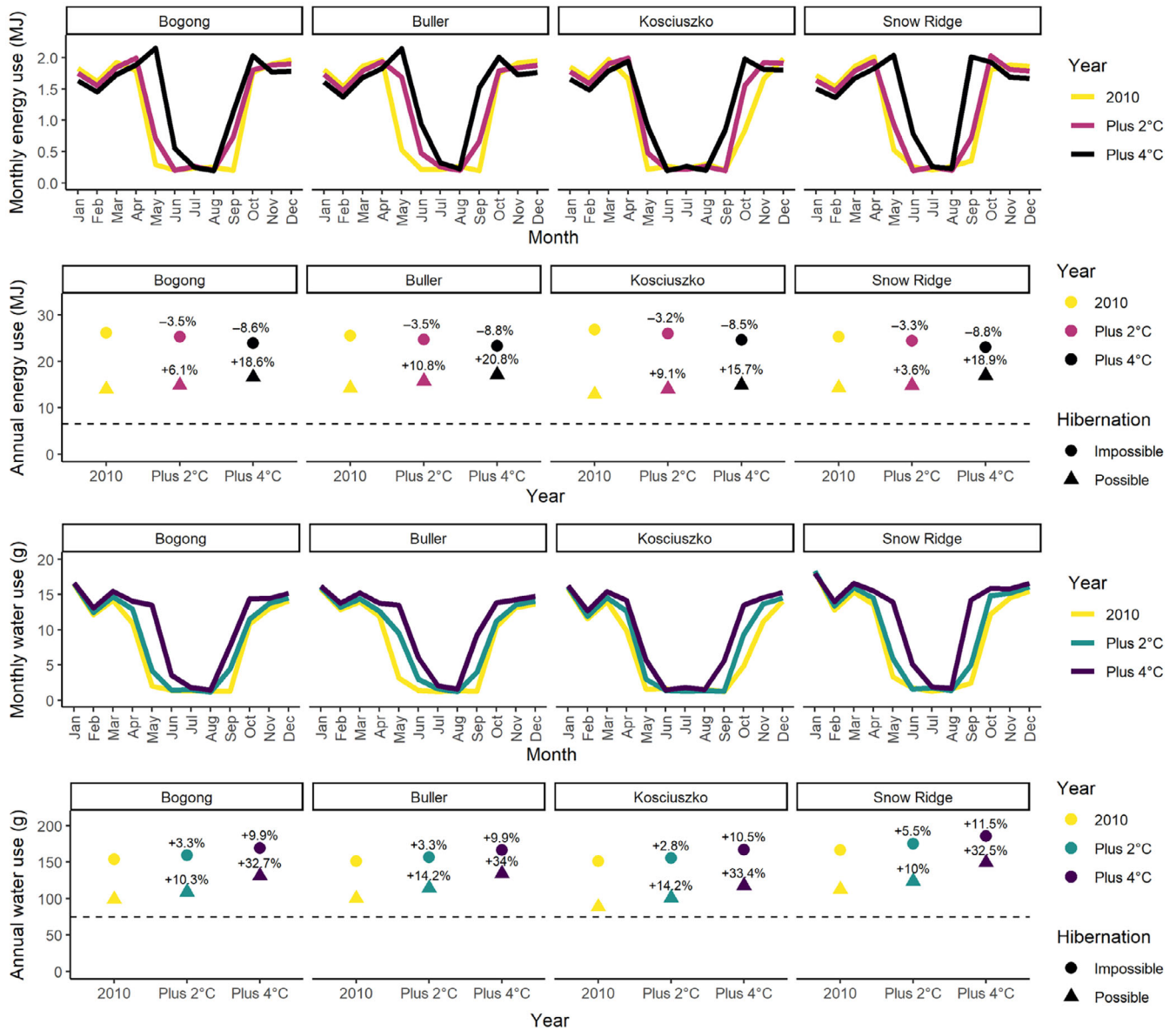


FIGURE 4 The monthly and annual energy and water requirements for *Burramys parvus* at four sites—Kosciuszko, Bogong, Buller, and Snow Ridge—across southeastern Australia for 2010 and two future climate-warming scenarios (2 and 4°C increase, respectively). The annual requirement graphs compare outputs when hibernation is possible versus impossible. The percentages denote the increase or decrease in energy or water requirements in the future scenarios in comparison to the present. The dashed line in the annual requirement graphs represents the theoretical minimum energy and water a strictly homeothermic *Burramys parvus* could use in a year.

(Figure 5). The 2°C warming scenario caused a 29% increase in the areas where hibernation has no value as an energy-saving mechanism (i.e., 100% of energy used with hibernation possible vs. hibernation impossible). The areas lost were primarily to the west and north of currently occupied areas. Under the 4°C warming scenario, there was a 60% increase in the area where hibernating and non-hibernating are equivalent, thus limiting the places where hibernation is beneficial in saving energy to areas of the Australian Alps and the highlands of Tasmania (Figure 5).

DISCUSSION

Our study shows that it is possible to use biophysical models to quantify the impact of climate change on torpor, including hibernation. We found strong agreement between the model-predicted torpid metabolic rates for species ranging from microbats to bears (Figure 1), and between the simulated current hibernation pattern and the observed pattern for *Burramys* (Figure 3). Our detailed analyses of hibernation in *Burramys* support predictions that hibernation periods will shorten due to

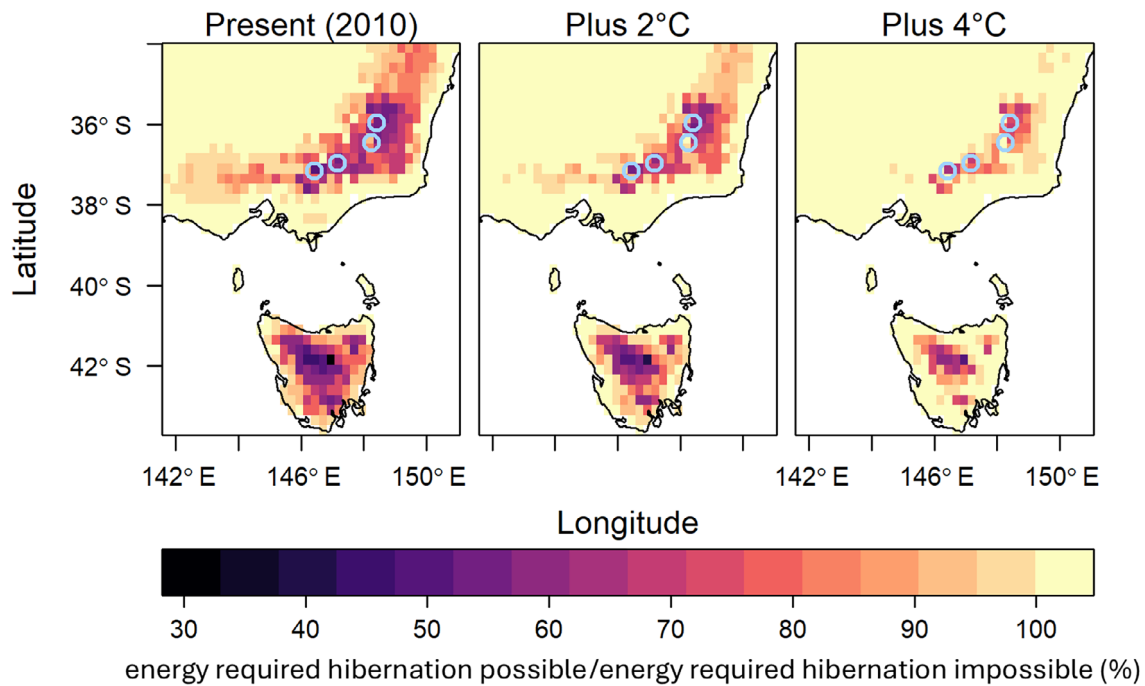


FIGURE 5 The energy required by *Burramys parvus* across southeastern Australia when hibernation is possible expressed as a percentage of that required is impossible, that is, 100% indicates that hibernation did not occur. The values for the present and two future climate-warming scenarios (2 and 4°C increase, respectively) are shown. The light blue circles show the location of the four sites (Buller, Bogong, Kosciuszko, and Snow Ridge from west to east) where *Burramys parvus* is currently found.

climate change (Findlay-Robinson et al., 2023; Inouye et al., 2000; Wells et al., 2022), leading to reductions in the energetic and hydric advantage of hibernation. Therefore, the value of hibernation as a life history strategy will be compromised, with consequences for fitness that include higher energy and water requirements and increased exposure to predators (Ruf & Bieber, 2023).

Warming temperatures were projected to cause *Burramys* to hibernate less at all four of the sites at which it is currently present (Figure 3). This was a consequence of more variable burrow temperatures resulting from lower snow cover (Appendix S1: Figure S11). Juvenile alpine marmots have low survival under similar conditions (Rézouki et al., 2016), suggesting that small-bodied individuals (<100 g) are particularly susceptible to reduced snow cover. Small-bodied animals are vulnerable to low temperature due to their high surface-area-to-volume ratios and small energy reserves (Kooijman, 1986). Climate change might have less impact on adults of larger species but could still reduce juvenile survival.

The magnitude of site-specific impacts of climate change depended strongly on the climate-change scenario. The percentage of hibernation hours lost for Bogong and Kosciuszko doubled between the 2 and 4°C warming scenarios, tripled for Buller, and almost quadrupled for Snow Ridge (Figure 3). This highlights the

nonlinear responses of physiological and behavioral responses to climate change (Huey et al., 2012), which may not be captured with more descriptive approaches to forecasting climate change impacts.

Hibernation is often interpreted as an energy-saving strategy, but our study highlights the value of hibernation in also reducing water requirements. Under present-day conditions at Kosciuszko, a free-living *Burramys* capable of heterothermy has a water requirement similar to the theoretical minimum for a strictly homeothermic *Burramys* (Figure 4); this latter value is a physical impossibility because it assumes that the energy and water demands are met with zero activity or digestion. We found that climate change reduced both the energetic and hydric advantages of hibernation (Figure 4). The difference in energy requirements for a hibernating and non-hibernating *Burramys* reduced for three reasons. First, there were fewer hours cold enough to induce hibernation; second, the hibernation period was disrupted more often by temperature fluctuations; and third, higher winter temperature reduced the need for non-hibernating animals to generate heat to maintain body temperature. Although water requirements barely increased in the summer under climate warming for both the hibernators and non-hibernators (hibernation does not occur in the summer months), water demands increased in hibernators due to their reduced ability to save water because of fewer overall hours hibernating.

The challenges posed for *Burramys* by higher energy demands are twofold: finding enough food to meet this demand and avoiding predators while foraging for this extra food. These challenges are magnified by the recent decline in its Bogong-moth food source (Green et al., 2021), potentially requiring prey-switching to less-abundant arthropods or the less nutritious mountain plum pine, and imposing additional physiological costs (Hooker et al., 2017). The timing of energy demands is important, as the largest increase in energy requirements came just prior to hibernation, when moths are unlikely to be available (Green et al., 2021). Increased foraging needs will lead to increased activity time, and therefore exposure to competitors and predators. At the same time, predator activity will be less constrained as a result of the decrease in snow cover. Increased predation caused by decreased snow depth and duration is well documented across the northern hemisphere (Pedersen et al., 2017).

The current energetic and hydric advantage to *Burramys* of hibernation extends across much of south-eastern Australia, primarily along the Great Dividing Range and in Tasmania (Figure 5). Intriguingly, hibernation is predicted to be advantageous in locations far from where *Burramys* currently occurs, and as far north as Wombeyan Caves, New South Wales (-34.31° S, 149.97° E), a site of Pleistocene fossil deposits that contain *Burramys* remains (Lundelius, 1983). This widespread advantage is projected to contract due to climate change. This could have serious consequences for the viability of *Burramys*. Not only would a key environmental response that is currently adopted by the species lose its benefit throughout its entire range but also no new areas would emerge where hibernation becomes possible (Figure 5), so the species will be unable to increase its range from the highly restricted area that it currently occupies. This prognosis assumes that hibernation is a key aspect of *Burramys*' current adaptive strategy. Although hibernation is highly adaptive in specific climatic conditions, and populations may have different capacities to adapt to climate change based on the characteristics of their habitat, diet, genetics, life history, etc. (Boyles et al., 2011), there is no compelling evidence to suggest that the species would be competitive without the advantage of hibernation.

Only a small area of the Australian Alps retains areas where hibernation would remain possible in a warming climate. The most substantial areas that will continue to provide environmental conditions suited to hibernation by *Burramys* are in Tasmania. *Burramys* does not occur in Tasmania, presumably because of dispersal limitation, but the island could serve as a climatic refuge for *Burramys* in the future. This would be the case if conditions other than climate that influence the suitability of

habitat for *Burramys*, and which include the characteristics of habitat, food resources, predators, and competitors, are also satisfied in Tasmania.

Improving the predictive accuracy of mechanistic models for *Burramys* would create numerous opportunities for future research, from the physiological to the ecosystem level. More knowledge about the mechanisms that induce activity and hibernation would provide increased realism in the modeling of this life history strategy, although the simple rules we used approximated observed hibernation patterns remarkably well. Physiological plasticity could be included in future work, especially since other southern hemisphere hibernators (e.g., other pygmy possums [*Cercartetus* spp.]) have highly variable interindividual and interannual torpor patterns (Turner, Körtner, et al., 2012; Turner, Warnecke, et al., 2012). Another way to increase realism would be to include social effects; species such as *Burramys* often do not hibernate alone and often huddle to retain heat (Fleming, 1985). This would extend the range of environments in which hibernation is physically possible. Information on the frequency of huddling and the number of individuals involved could lead to better predictions, if the phenomenon is common. High-resolution dietary and food availability data would allow predictions of the feasibility of meeting future energy and water increases and allow these models to better inform efforts to conserve the species. Knowledge of the extent to which *Burramys* caches food would be of particular interest, as this can greatly affect hibernation duration (Humphries et al., 2003). Detailed data on feeding, along with data on water intake in the wild, would allow surplus energy and water to be calculated and *Burramys*-specific data on milk composition, and the resultant conversion to offspring weaned would allow reproduction rates to be estimated. Additional information on site characteristics could further improve the approximation of the microhabitat conditions in the Australian Alps, which could be used for other species. Similarly, improvements in the availability of subcontinental level approximations of soil type, structure, and shading would allow for more heterogeneous input data, further increasing realism with little increase in computational requirements.

Although the potential negative effect of climate change on hibernators has been highlighted previously (Geiser, 2013), methods to quantify these effects, based on the underlying ecophysiological mechanisms, have previously been lacking. Our new process-driven methodology is highly flexible and can be used for species across size classes and on the whole spectrum of heterothermy from those that exhibit daily torpor to hibernation periods several months in duration. This can allow us to not only gain new insights into the advantages of

heterothermy, but also how these will change with a warming climate.

AUTHOR CONTRIBUTIONS

All authors contributed to the study design. Michael R. Kearney and Shane D. Morris developed the torpor algorithm. Shane D. Morris performed the analysis and wrote the manuscript, with significant input from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Morris et al., 2025) are available in Zenodo at <https://doi.org/10.5281/zenodo.17119843>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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