Ecological consequences of temperature regulation: Why might the mountain pygmy possum *Burramys parvus* need to hibernate near underground streams?

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Abstract

The mountain pygmy possum (*Burramys parvus*) is an endangered marsupial restricted to boulder fields in the Australian Alps, where it hibernates under the snow during
winter. Understanding its habitat requirements is essential for conservation, so we examine here ecological implications of the thermal consequences of maintaining water balance during the hibernation season. Hibernating mountain pygmy possums arousing to consume water must either drink liquid water or consume snow. If they drink water, then the energy required to warm that water to body temperature (4.18 J g\(^{-1}\) °C\(^{-1}\)) increases linearly with mass ingested. If they eat snow, then the energy required melt the snow (latent heat of fusion = 332 J g\(^{-1}\)) and then warm it to body temperature is much higher than just drinking. For mountain pygmy possums, these energetic costs are a large proportion (up to 19%) of their average daily metabolic rate during the hibernation period and may dramatically shorten it. If mountain pygmy possums lose water equivalent to 5% of body mass before arousing to rehydrate, then the potential hibernation period is reduced by 30 days for consuming snow compared to 8.6 days for drinking water. The consequences of ingesting snow rather than liquid water are even more severe for juvenile possums. A reduction in the hibernation period can impact on the overwinter survival, a key factor determining demographics and population size. Therefore, habitats with subnivean access to liquid water during winter, such as those with subterranean streams running under boulder fields, may be of particular value.

**Keywords:** relative water economy, latent heat of fusion, specific heat of water, eating snow, warming food

The mountain pygmy possum (*Burramys parvus*) is the Australian mammal most threatened by global warming, as it is the only species restricted to limited high altitude refugia within the Australian Alps (1,2). Understanding its habitat requirements is essential for effective conservation, so we examine here the thermal consequences of mountain pygmy possums
maintaining water balance by eating snow during the hibernation season, and the implications of thermal biology for the ecology and habitat requirements of this species.

The habitat of the mountain pygmy possum consists of boulder fields above the winter snowline (usually 1370m) in a few alpine areas within Victoria and New South Wales, southeastern Australia (1,3), with a total habitat area of only some 10 km² (4). Overwinter survival of mountain pygmy possums is closely correlated with the depth and duration of winter snow cover; 150 days of snow cover is optimal for survival (2). Early snowmelt in spring is particularly problematic, as this reduces temperatures in hibernacula and increases the duration and frequency of arousals from hibernation (5). Snowmelt beginning before the arrival of their primary spring food-source, migratory Bogong moths (*Agrotis infusa*), means that pygmy possums undergo their final arousal from hibernation before they have access to this food (2). Snow depth and duration has been decreasing in the Australian Alps over the last 40 years, with more severe reductions, and increasing early spring snow melt predicted to occur by 2050-2070 (6,7).

Identification of all extant populations of mountain pygmy possums, and a thorough understanding of their habitat requirements, is necessary if extinction of this species in the wild is to be prevented. Acclimatisation of mountain pygmy possums to cool lowland habitats, reflecting their historical distribution as revealed by the fossil record, is one proposed strategy to mitigate the extinction threat posed by climate change (2). Recent research has identified some previously unknown populations of mountain pygmy possums in New South Wales, further north than previously known populations and at lower-than-predicted altitudes of 1180-1300m (8-10). These lower altitude populations may have persisted due to good snow cover in the year proceeding the survey (8). Interestingly, studies of these new populations suggest that mountain pygmy possums may have a preference for boulder fields with close proximity to permanently flowing streams (9,11). Previous
physiological research has focussed on the energy and thermal requirements of mountain pygmy possums (4,12-14) and we know nothing of their water requirements. Surprisingly, maintaining water balance might be problematic for hibernating mammals (15,16) so we present here a model of water balance for hibernating mountain pygmy possums. This model explains why availability of liquid water during the hibernation period may enhance survival, and therefore why permanently flowing streams may be an important component of current and future habitat.

Mountain pygmy possums hibernate from late summer to early spring, for five (juveniles) to seven (adults) months, when they inhabit hibernacula located under the snow within spaces between boulders (13). Their hibernacula are insulated from the surrounding environment by snow, vegetation and soil, with ambient temperatures within the hibernacula remaining constant at around 1.5 to 2.5°C, while air temperature varies from approximately -8 to 20°C (4). For hibernating mammals, including marsupials (17,18), the typical hibernation period consists of bouts of torpor interrupted by brief periods of arousal to eutermia (4). During torpor, the body temperature of the mountain pygmy possum may decrease to 1.8 ºC, with a pronounced reduction in metabolic rate from a basal metabolic rate of 1.12 ml O$_2$ g$^{-1}$ h$^{-1}$ to as low as 0.020 ml O$_2$ g$^{-1}$ h$^{-1}$ (12). Arousing periodically from hibernation to eutermia is energetically costly. In the laboratory, one day of eutermia for mountain pygmy possums uses up to 1.85g fat, more than half the fat reserves used by a torpid possum over 155 days (12). Why hibernators undergo these costly periodic arousals is not well understood, although it is assumed that arousal is necessary to restore some aspect(s) of physiological homeostasis perturbed during long periods of torpor (18). Amongst the various hypotheses that have been proposed (see ref. 18) is the suggestion that evaporative water loss during hibernation may result in dehydration and so mammals are required to arouse to drink (15). Indeed, a number
of recent studies suggest that maintenance of water balance is a critical factor determining hibernation duration and success (19-22).

For torpid mammals, the only avenues of water gain and loss are metabolic water production and evaporative water loss. The ratio of these, relative water economy (relative water economy = metabolic water production/evaporative water loss), is therefore an index of the state of water balance for a torpid mammal (16). Many small mammals, even tropical and mesic species, have a favourable relative water economy (i.e. they make more metabolic water than they lose by evaporation) when euthermic at moderate to low ambient temperatures (e.g. 23-26). However during torpor, their metabolic rate (and therefore metabolic water production) decreases proportionally more than their evaporative water loss, and so the relative water economy becomes more unfavourable, and water balance is typically negative (e.g. 16,27-30). Water loss equivalent to about 5% body mass appears to be a critical limit requiring arousal from torpor (31), and so it is likely that hibernating mammals reaching this limit must arouse to drink. For another hibernating marsupial, the monito del monte (*Dromiciops gliroides*), rates of mass loss calculated from RWE during torpor correlated with observed periodicity of arousals in the field (16), indicating that maintenance of water balance may indeed be an important function of periodic arousals during hibernation.

Mammals arousing from hibernation to drink must warm ingested water to body temperature. For hibernators in cold environments, this can have a significant energetic cost, especially if the ingested water is ice and must be melted then warmed, but the cost is rarely considered when assessing the energetic consequences of arousals. Mountain pygmy possums consuming water to offset that lost by evaporative water loss during hibernation could drink liquid water if it is available (e.g. from streams running beneath boulder fields), or eat frozen water in the form of snow or ice. Here we determine the potential impact of availability of
liquid compared to frozen water on the energy budget of hibernating mountain pygmy possums, and thus assesses the ecological consequences of temperature regulation for this endangered species.

We model the energetic costs of mountain pygmy possums ingesting liquid water or eating snow based on physical constants for heat requirements of warming of water (specific heat capacity of water = 4.19 J g$^{-1}$ °C$^{-1}$; ref. 32) and melting of snow (latent heat of fusion = 334 J g$^{-1}$; ref. 32). We assume that euthermic pygmy possums attain a body temperature of 35°C during periodic arousals from torpor (4), that ingested liquid water is the same temperature as the ambient temperature within a hibernaculum under the snow (2°C; ref. 4) and that the temperature of ingested snow is 0°C. Calculations are based on a mean body mass for adult possums of 57g, and 30g for juveniles, after ref. 4, with torpor metabolic rates of 0.025 ml O$_2$ g$^{-1}$ h$^{-1}$ for adult possums and 0.022 ml O$_2$ g$^{-1}$ h$^{-1}$ for juveniles (12); ml O$_2$ were converted to joules assuming 20.1 ml O$_2$ J$^{-1}$ (32). We base our calculations of overall energetic costs of replenishing evaporated water on there being 20 arousals during the hibernation period (33), and the assumption that possums must replace the equivalent of between 1 and 10% of their body mass (5% being most likely; 16,31) in water during each arousal.

Mountain pygmy possums may cache seeds in their subnivean hibernacula for consumption during periodic arousals (3,5). Like water, ingested food must also be warmed to body temperature, but the specific heat of dry food is much lower than water, and there is no latent heat of fusion (34). Seeds have little preformed water (< 20%; 35), so warming of seeds from an ambient temperature of 2°C to a body temperature of 35°C is insignificant compared to the much greater costs of warming liquid and especially frozen water (34,37).
The energy required to warm ingested liquid water from 2°C to a euthermic body temperature of 35°C is 138 J g⁻¹. Therefore the energetic cost for an adult possum (57 g) of ingesting between 1 and 10% body mass of liquid water and warming it to 35°C ranges from 78.8 to 788 J respectively, and for a juvenile possum (30 g) from 41.5 to 415 J. Ingesting 5% of body mass as liquid water at 2°C requires 394 J for adults and 207 J for juveniles (Figure 1).

The total energetic cost of ingesting snow is much higher than for liquid water, as the snow must first be melted at high energetic cost (i.e. latent heat of fusion = 334 J g⁻¹), and then warmed from 0 °C to a euthermic body temperature of 35°C at a lower energetic cost (i.e. specific heat of water x temperature increase = 146 J g⁻¹). For an adult mountain pygmy possum, this equates to an energetic cost of between 274 and 2740 J for ingesting between 1 and 10% body mass of snow, and for juvenile possums between 144 and 1442 J. Ingesting 5% of body mass as snow requires 1370 J for adult possums and 721 J for juveniles (Figure 1).

To put these heat requirements in perspective, warming ingested liquid water to euthermic body temperature is equivalent to the energy used by an adult mountain pygmy possum during 2.8 (1% of body mass ingested) to 28 (10% of body mass ingested) hours of torpor. Ingesting and warming a volume of water equivalent to 5% of body mass consumes as much energy as 13 hours of torpor. For juvenile possums the relative costs are slightly higher; ingesting a volume of liquid water equivalent to 1 and 10% of body mass consumes as much energy as 3.1 to 31 hours of torpor and water that is 5% of body mass would require the energy of 16 hours of torpor.

For frozen water, the torpor energy equivalents are even higher. Melting and then warming ingested snow to a euthermic body temperature requires as much energy as 9.6 to 96 hours of torpor for an adult pygmy possum (for 1 to 10% of body mass ingested...
respectively). Ingesting the equivalent of 5% of body mass requires energy sufficient for 48
hours. For juvenile possums, ingesting between 1 and 10% body mass as snow requires the
energy of 11 to 109 hours of torpor respectively. A snow intake equivalent to 5% of body
mass would require equivalent energy of 54 hours torpor.

The energetic consequences of warming water and snow potentially affect torpor
duration. If mountain pygmy possums undergo 20 arousals during the hibernation period and
drink liquid water or eat snow to rehydrate during each arousal, then the energetic costs of
warming this water are substantial compared to the energetic costs of hibernation. For adult
possums, warming liquid water during 20 arousals will use as much energy a 2.3 to 23 days
of torpor, while melting and warming snow is energetically equivalent to 8.0 to 80 days of
torpor (range calculated for ingesting 1 to 10% body mass of snow or water during each
arousal; Figure 2). Ingesting 5% of body mass per arousal is energetically equivalent to 11.5
days of torpor for drinking liquid water and 40 days of torpor for eating snow. For juveniles,

drinking liquid water is equivalent to 2.6 to 26 days of torpor and eating snow 9.1 to 91 days
(ingesting 1 to 10% of body mass). Ingesting 5% of body mass is energetically equivalent to
13 days of torpor for drinking liquid water and 45 days of torpor for eating snow.

There is growing evidence that unfavourable water balance during hibernation at least
ccontributes to the necessity for periodic arousals to euthermia by hibernating mammals, and
that factors affecting water balance during hibernation can impact on hibernation success (15,
19-22). Here we determine for the endangered mountain pygmy possum the thermal,
n energetic and ecological consequences of ingesting water to overcome these hygric
imbances during hibernation. If hibernating mountain pygmy possums arouse to replenish
their body water, then they must either drink liquid water or consume frozen water (snow or
ice) while euthermic. There are significant energetic costs associated with warming ingested
food and water to body temperature, especially during winter in alpine or tundra
environments. Water has a particularly high specific heat capacity and therefore warming of drinking water is of energetic significance. Ingesting frozen water has even higher additional thermal costs as the water must first be melted, then warmed (34,37).

Estimates of the energetic costs of warming ingested water for several euthermic small mammals inhabiting subnivean environments are variable. Holleman et al.\textsuperscript{36} estimated the energetic costs of eating ice to be 140 J g\textsuperscript{0.8} day\textsuperscript{-1} or 2% of average daily metabolic rate for red-backed voles (\textit{Clethrionomys rutilus}). Whitney\textsuperscript{38} suggested that half of the ingested food of red-backed voles and tundra voles (\textit{Microtus oeconomus}) during winter would be frozen water, and that melting and warming this water would require 4 kJ day\textsuperscript{-1}, or 7% of average daily metabolic rate. Berteaux\textsuperscript{34} estimated that meadow voles (\textit{Microtus pennsylvanicus}) in a subnivean environment would expend between 4.7 and 12.9% of their winter average daily metabolic rate warming ingested liquid and frozen water respectively.

Our calculations for hibernating adult mountain pygmy possums suggest that the energetic cost of warming ingested liquid water of 7.88 kJ (394 J to warm liquid water equivalent to 5% body mass x 20 arousals) is 7.5% of the energetic cost of remaining torpid (104.5 kJ; 12) for 155 days. If we include costs of arousal to euthermia of 68.5 J arousal\textsuperscript{-1} (12) for 20 arousals to predict an overall energy cost of 1475 kJ for 155 days of the hibernation period, then the percentage cost of warming liquid water is much lower (about 0.5%), reflecting the high energetic costs of arousal. Similar calculations for costs of consuming frozen water (1370 J to melt and warm the water) indicate that eating snow would account for 26% of the energetic cost of remaining torpid (27.36 kJ) and 19% of the overall energy required (including periodic arousals) for winter hibernation of 155 days.

The magnitude of the energetic costs for heating ingested water is determined by the temperature differential between the animal and the food/water, the quantity of food/water ingested, and the specific heat capacity of the food/water (34). For hibernating mountain
pygmy possums these costs are a particularly high proportion of their average daily metabolic rate, compared to other mammals in subnivean environments. This relatively high cost is despite a relatively moderate subnivean microclimate for pygmy possums resulting in a much smaller body to ice temperature differential (e.g. 0 to 35°C compared to -30 to 40 °C for subarctic voles; 38). It is also possible that mountain pygmy possums could drink before they reached their euthermic body temperature of 35 °C, further reducing their body to water temperature differential. However, as mountain pygmy possums consistently achieve body temperatures of 35 °C during arousals (4) the ingested water would still ultimately be warmed to 35 °C even if initially ingested at a lower body temperature. Ingestion during the cooling phase of torpor entry is unlikely, as torpor is entered during short wave sleep (39). Our model for mountain pygmy possums ingesting water equivalent to 5% of body mass (2.8 g for adults) during a hibernation period of 155 days is for an average water consumption of 0.37g day\(^{-1}\), much less than the 2.2g day\(^{-1}\) for Alaskan voles (36), 7.5g day\(^{-1}\) predicted for red-backed voles and tundra voles (38) and 30.8g day\(^{-1}\) measured for meadow voles (34).

Particularly high proportions of energy expenditure calculated to warm ingested water for hibernating mountain pygmy possums do not reflect a more extreme environment, drinking before full arousal, or higher water intake, but rather the very low torpor metabolic rate of a hibernating marsupial compared with the high metabolic rates of euthermic rodents.

The average daily metabolic rate of various vole species in winter ranges from 118 kJ day\(^{-1}\) (meadow voles; 34) to 244 kJ day\(^{-1}\) (tundra voles; 38), much higher than that calculated for mountain pygmy possums during the hibernation period (9.5 kJ day\(^{-1}\); calculated from data of Geiser and Broome\(^{12}\), even after accounting for their energetically costly arousals.

The substantial energetic cost of consuming cold or frozen water is of particular significance for a hibernator compared to a euthermic rodent. For meadow voles average daily metabolic rate was 22.7% higher in winter than summer, with 60% of this difference
attributed to eating frozen rather than liquid water (34). Euthermic animals clearly meet these extra costs by simply consuming more energy. However, for hibernators, which can’t take in more energy during hibernation, the consequence is severe - a reduction in the overall time that they can potentially hibernate. For adult mountain pygmy possums, consuming 5% of body mass as snow during each of 20 arousals requires the energy equivalent to 30 days of hibernation, and even for drinking liquid water, the cost is 8.6 days of hibernation.

A reduction in the hibernation period has the potential to dramatically impact on the overwinter survival of mountain pygmy possums, which in turn is a key factor determining the demographics and overall population size of this endangered species (40). The annual survival of mountain pygmy possums is low at about 40%,(40) with insufficient energy reserves to sustain hibernation until the arrival of Bogong moths in spring likely a factor contributing to overwinter mortality, highlighting the significance of energy conservation during the winter hibernation period (40). Indeed, in years of early snow melt, when possums are forced to arouse earlier in the spring, populations of mountain pygmy possums decline (2). Habitat where hibernating pygmy possums have access to liquid water, such as boulderfields with permanently flowing subterranean streams, may therefore be important in allowing pygmy possums to balance their water budget without the excessive energetic costs of eating snow or ice to obtain water. Access to liquid water may prolong the hibernation period approximately three weeks, and this could impact substantially on overwinter survival and population persistence.

The consequences of eating snow rather than drinking frozen water are even more significant for juvenile mountain pygmy possums. Smaller body mass and lower mass-specific torpor metabolic rates of juveniles (12) mean that the impacts of warming water are a bigger proportion of the energy budget than for adults. The hibernation period of juvenile possums is already shorter than that of adults (five compared to seven months), being limited
by their ability to accrue sufficient fat reserves prior to hibernation (12), and overwinter survival is reduced compared to adults (40). Therefore habitat providing access to liquid water may be of particular importance for recruitment of juveniles into the population.

We have demonstrated here how thermoregulatory costs of maintaining water balance have important consequences for the ecological requirements of an endangered marsupial. Our results suggest that mountain pygmy possum habitats with subnivean access to liquid water during winter, such as those with subterranean streams running under boulder fields, should be considered when prioritising habitat conservation. Attempts to translocate mountain pygmy possums to new habitats for conservation and management purposes should include water availability as an important habitat characteristic.

Disclosure of Potential Conflicts of Interest

There are no potential conflicts of interest.

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References


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Figure 1: The energy required for a mountain pygmy possum to warm liquid water from 2°C to 35°C (SH; specific heat; dashed line), and the energy required to melt (LHF; latent heat of fusion) and warm the resulting water (SH; specific heat; thin black line) when eating snow (thick black line). The torpid and euthermic metabolic rates of mountain pygmy possums are shown for comparison (grey lines; values from 12). Note the break in the y axis.
Figure 2: Consequences of the energetic costs of eating snow (solid lines) compared to drinking liquid water (dashed lines) on the energy reserves available for hibernation for juvenile (grey lines) and adult (black lines) mountain pygmy possums (*Burramys parvus*). The ellipse indicates the costs of ingesting water equivalent to 5% of body mass, a likely estimate of the degree of dehydration triggering an arousal for a hibernating mammal.