

Ecological consequences of temperature regulation

Why might the mountain pygmy possum *Burramys parvus* need to hibernate near underground streams?

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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 ($4.18 \text{ J g}^{-1} \text{ }^{\circ}\text{C}^{-1}$) 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 with 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.

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 1370 m) 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 d 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 past 40 y, 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 1180–1300 m.^{8–10} These lower altitude populations may have persisted due to good snow cover in the year preceding 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}

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Previous physiological research has focused 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 5 (juveniles) to 7 (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 euthermia.⁴ During torpor, the body temperature of the mountain pygmy possum may decrease to 1.8 °C, with a pronounced reduction in metabolic rate from a basal metabolic rate of 1.12 ml O₂ g⁻¹ h⁻¹ to as low as 0.020 ml O₂ g⁻¹ h⁻¹.¹² Arousing periodically from hibernation to euthermia is energetically costly. In the laboratory, one day of euthermia for mountain pygmy possums uses up to 1.85 g fat, more than half the fat reserves used by a torpid possum over 155 d.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 Among 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 favorable relative water economy (i.e., they make more metabolic water than they lose by evaporation) when euthermic at moderate to low ambient temperatures.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 unfavorable, and water balance is typically negative.^{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 with 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 57 g, and 30 g for juveniles, after ref. 4, with torpor metabolic rates of 0.025 ml O₂ g⁻¹ h⁻¹ for adult possums and 0.022 ml O₂ g⁻¹ h⁻¹ for juveniles¹²; ml O₂ were converted to joules assuming 20.1 ml O₂ 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; refs. 16 and 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 with 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 (Fig. 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

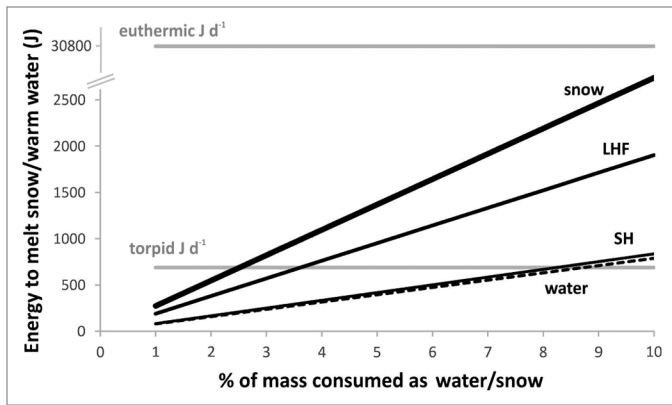


Figure 1. The energy required for a mountain pygmy possum to warm liquid water from 2 to 35 °C (SH; specific heat; dashed line), and the energy required to melt (LHF; latent heat of fusion) and warm the resulting water (SH; specific heat; thin black line) when eating snow (thick black line). The torpid and euthermic metabolic rates of mountain pygmy possums are shown for comparison (gray lines; values from 12). Note the break in the y axis.

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 (Fig. 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 h 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 h of torpor and water that is 5% of body mass would require the energy of 16 h 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 h 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 h. For juvenile possums, ingesting between 1 and 10% body mass as snow requires the energy of 11 to 109 h of torpor respectively. A snow intake equivalent to 5% of body mass would require equivalent energy of 54 h 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 with the energetic costs of hibernation. For adult possums, warming liquid water during 20 arousals will use as much energy a 2.3 to 23 d of torpor, while melting and warming snow is energetically equivalent to 8.0 to 80 d of torpor (range calculated for ingesting 1 to 10% body mass of snow or water during each arousal; Fig. 2). Ingesting 5% of body mass per arousal is energetically equivalent to 11.5 d of torpor for drinking liquid water and 40 d of torpor

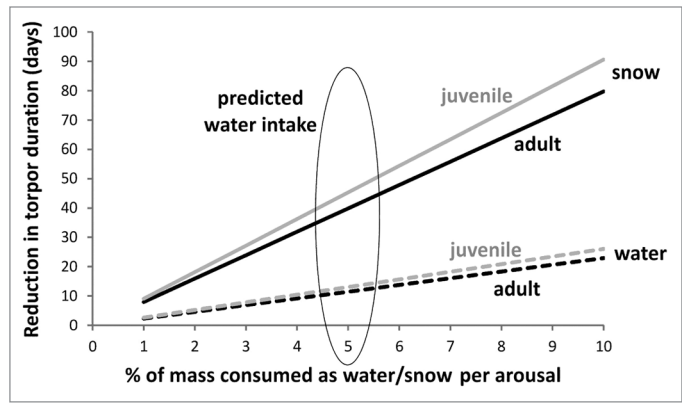


Figure 2. Consequences of the energetic costs of eating snow (solid lines) compared with drinking liquid water (dashed lines) on the energy reserves available for hibernation for juvenile (gray lines) and adult (black lines) mountain pygmy possums (*Burrmys parvus*). The ellipse indicates the costs of ingesting water equivalent to 5% of body mass, a likely estimate of the degree of dehydration triggering an arousal for a hibernating mammal.

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

There is growing evidence that unfavorable water balance during hibernation at least contributes 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, energetic and ecological consequences of ingesting water to overcome these hygric imbalances 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.³⁶ estimated the energetic costs of eating ice to be 140 J g^{-0.8} day⁻¹ or 2% of average daily metabolic rate for red-backed voles (*Clethrionomys rutilus*). Whitney³⁸ suggested that half of the ingested food of red-backed voles and tundra voles (*Microtus oeconomus*) during winter would be frozen water, and that melting and warming this water would require 4 kJ day⁻¹, or 7% of average daily metabolic rate. Berteaux³⁴ estimated that meadow voles (*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 \times 20 arousals) is 7.5% of the energetic cost of remaining torpid (104.5 kJ; 12) for 155 d. If we include costs of arousal to euthermia of 68.5 J per arousal¹² for 20 arousals to predict an overall energy cost of 1475 kJ for 155 d 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 d.

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 with 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 with -30 to 40 °C for subarctic voles; ref. 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 arousals⁴ 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 d is for an average water consumption of 0.37 g day⁻¹, much less than the 2.2 g day⁻¹ for Alaskan voles,³⁶ 7.5 g day⁻¹ predicted for red-backed voles and tundra voles³⁸ and 30.8 g 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 Broome¹²), 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 with 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 d of hibernation, and even for drinking liquid water, the cost is 8.6 d 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 within sufficient 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 3 wk, 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 juveniles¹² 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 (5 compared with 7 mo), being limited by their ability to accrue sufficient fat reserves prior to hibernation,¹² and overwinter survival is reduced compared with 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

No potential conflicts of interest were disclosed.

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References

- Broome L, Archer M, Bates H, Shi H, Geiser F, MacAllan B, Heinze D. H and SM, Evans T, Jackson S. A brief review of the life history of, and threats to, *Burramys parvus* with a prehistory-based proposal for ensuring that it has a future. In: Lunney D and Hutchings P, eds. *Wildlife and Climate Change: Towards Robust Conservation Strategies for Australian Fauna*. Royal Zoological Society of NSW: Mosman, 2012; 114-26
- Broome L. Density, home range, seasonal movements and habitat use of the mountain pygmy-possum *Burramys parvus* (Marsupialia: Burramyidae) at Mount Blue Cow. Kosciuszko National Park. *Aust Ecol* 2001; 26:275-92; <http://dx.doi.org/10.1046/j.1442-9993.2001.01114>
- Heinze D, Broome L, Mansergh I. A review of the ecology and conservation of the mountain pygmy-possum *Burramys parvus*. In Goldingay RL, Jackson SM eds. *The Biology of Possums and Gliders*. Surrey Beatty and Sons 2004 pg 254-67
- Körtner G, Geiser F. Ecology of natural hibernation in the marsupial Mountain Pygmy-possum (*Burramys parvus*). *Oecologia* 1998; 113:170-8; <http://dx.doi.org/10.1007/s00442005036>
- Smith AP, Broome L. The effects of season, sex and habitat on the diet of the mountain pygmy possum (*Burramys parvus*). *Wildl Res* 1992; 19:755-68; <http://dx.doi.org/10.1071/WR92075>
- Whetton PH, Haylock MR, Galloway R. Climate change and snow-cover duration in the Australian Alps. *Clim Change* 1996; 32:447-79; <http://dx.doi.org/10.1007/BF0014035>
- Hennessey K, Whetton P, Smith I, Bathols J, Hutchinson M, Sharples J. The impact of climate change on snow conditions in mainland Australia. A report for the Victorian Department of Sustainability and Environment, Victorian Greenhouse Office, New South Wales National Parks and Wildlife Service, New South Wales Department of Infrastructure, Planning and Natural Resources, Australian Greenhouse Office and Australian Ski Areas Association. CSIRO Atmospheric Research, 2003
- Schulz M, Wilks G, Broome L. Occupancy of spoil sumps by the Mountain Pygmy-possum *Burramys parvus* in Kosciuszko National Park. *Ecol Manage Restor* 2012; 13:290-6; <http://dx.doi.org/10.1111/j.1442-8903.2012.00659>
- Schulz M, Wilks G, Broome L. An uncharacteristic new population of the Mountain Pygmy-possum *Burramys parvus* in New South Wales. *Aust Zool* 2012; 36:22-
- Broome L, Ford F, Dawson M, Green K, Little D, McElhinney N. Re-assessment of mountain pygmy-possum *Burramys parvus* population size and distribution of habitat in Kosciuszko National Park. *Aust Zool* 2013; 36:381-403; <http://dx.doi.org/10.7882/AZ.2013.00>
- Broome L, Schulz M, Bates H, Shi H. Good news for the Alps: A recovery in numbers and extension of known range for the mountain pygmy-possum. 58th Scientific Meeting, Aust Mam Soc 2012
- Geiser F, Broome LS. Hibernation in the mountain pygmy possum *Burramys parvus* (Marsupialia). *J Zool (Lond)* 1991; 223:593-602; <http://dx.doi.org/10.1111/j.1469-7998.1991.tb04390>
- Broome LS, Geiser F. Hibernation in free-living mountain pygmy-possums, *Burramys parvus* (Marsupialia: Burramyidae). *Aust J Zool* 1995; 43:373-9; <http://dx.doi.org/10.1071/ZO995037>
- Körtner G, Song X, Geiser F. Rhythmicity of torpor in a marsupial hibernator, the mountain pygmy-possum (*Burramys parvus*), under natural and laboratory conditions. *J Comp Physiol B* 1998; 168:631-8; PMID:9871346; <http://dx.doi.org/10.1007/s00360005018>
- Thomas DW, Geiser F. Periodic arousals in hibernating mammals: is evaporative water loss involved? *Funct Ecol* 1997; 11:585-91; <http://dx.doi.org/10.1046/j.1365-2435.1997.00129>
- Withers PC, Cooper CE, Nespolo RF. Evaporative water loss, relative water economy and evaporative partitioning of a heterothermic marsupial, the monito del monte (*Dromiciops gliroides*). *J Exp Biol* 2012; 215:2806-13; PMID:22837452; <http://dx.doi.org/10.1242/jeb.07043>
- Geiser F. Hibernation in pygmy possums (Marsupialia: Burramyidae). *Comp Biochem Physiol A Comp Physiol* 1985; 81:459-63; PMID:2863034; [http://dx.doi.org/10.1016/0300-9629\(85\)91009-](http://dx.doi.org/10.1016/0300-9629(85)91009-)
- Humphries MM, Thomas DW, Kramer DL. The role of energy availability in Mammalian hibernation: a cost-benefit approach. *Physiol Biochem Zool* 2003; 76:165-79; PMID:12794670; <http://dx.doi.org/10.1086/36795>
- Park KJ, Jones G, Ransome RD. Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). *Funct Ecol* 2000; 14:580-8; <http://dx.doi.org/10.1046/j.1365-2435.2000.r01-1-00460>
- Németh I, Nyitrai V, Németh A, Altbäcker V. Diuretic treatment affects the length of torpor bouts in hibernating European ground squirrels (*Spermophilus citellus*). *J Comp Physiol B* 2010; 180:457-64; PMID:19956957; <http://dx.doi.org/10.1007/s00360-009-0426->
- Willis CKR, Menzies AK, Boyles JG, Wojciechowski MS. Evaporative water loss is a plausible explanation for mortality of bats from white-nose syndrome. *Integr Comp Biol* 2011; 51:364-73; PMID:21742778; <http://dx.doi.org/10.1093/icb/icr07>
- Muñoz-García A, Ben-Hamo M, Pinshov B, Williams JB, Korine C. The relationship between cutaneous water loss and thermoregulatory state in Kuhl's pipistrelle *Pipistrellus kuhlii*, a Vespertilionid bat. *Physiol Biochem Zool* 2012; 85:516-25; PMID:22902380; <http://dx.doi.org/10.1086/66698>
- Cooper CE, Cruz-Neto AP. Metabolic, hygric and ventilatory physiology of a hypermetabolic marsupial, the honey possum (*Tarsipes rostratus*). *J Comp Physiol B* 2009; 179:773-81; PMID:19365634; <http://dx.doi.org/10.1007/s00360-009-0358->
- Cooper CE, Withers PC, Cruz-Neto AP. Metabolic, ventilatory, and hygric physiology of the gracile mouse opossum (*Gracilinanus agilis*). *Physiol Biochem Zool* 2009; 82:153-62; PMID:19199558; <http://dx.doi.org/10.1086/59596>
- Cooper CE, Withers PC, Cruz-Neto AP. Metabolic, ventilatory and hygric physiology of a South American marsupial, the long-furred woolly mouse opossum. *J Mammal* 2010; 91:1-10; <http://dx.doi.org/10.1644/09-MAMM-A-138R>
- Barker JM, Cooper CE, Withers PC, Cruz-Neto AP. Thermoregulation by an Australian murine rodent, the ash-grey mouse (*Pseudomys albocinereus*). *Comp Biochem Physiol A Mol Integr Physiol* 2012; 163:336-42; PMID:22871479; <http://dx.doi.org/10.1016/j.cbpa.2012.07.01>
- Cooper CE, McAllan BM, Geiser F. Effect of torpor on the water economy of an arid-zone marsupial, the stripe-faced dunnart (*Sminthopsis macroura*). *J Comp Physiol B* 2005; 175:323-8; PMID:15864500; <http://dx.doi.org/10.1007/s00360-005-0488->
- Withers PC, Cooper CE. Thermal, metabolic, hygric and ventilatory physiology of the sandhill dunnart (*Sminthopsis psammophila*; Marsupialia, Dasyuridae). *Comp Biochem Physiol A Mol Integr Physiol* 2009; 153:317-23; PMID:19285566; <http://dx.doi.org/10.1016/j.cbpa.2009.03.00>
- Withers PC, Cooper CE. The metabolic and hygric physiology of the little red kaluta. *J Mammal* 2009; 90:752-60; <http://dx.doi.org/10.1644/08-MAMM-A-286R>
- Pusey H, Cooper CE, Withers PC. Metabolic, hygric and ventilatory physiology of the red-tailed phascogale (*Phascogale calura*; Marsupialia; Dasyuridae): adaptations to aridity or arboreality? *Mamm Biol* 2013; 78:397-405; <http://dx.doi.org/10.1016/j.mambio.2012.11.00>
- Kallen FC. Some aspects of water balance in the hibernating bat. *Ann Acad Sci Fenn Ser 4* 1964; 71:57-267
- Withers PC *Comparative Animal Physiology*. Saunders College Publishing 1992
- Geiser F, Broome LS. The effect of temperature on the pattern of torpor in a marsupial hibernator. *J Comp Physiol B* 1993; 163:133-7; PMID:8320351; <http://dx.doi.org/10.1007/BF0026359>
- Berteaux D. Energetic cost of heating ingested food in mammalian herbivores. *J Mammal* 2000; 81:683-90; [http://dx.doi.org/10.1644/1545-1542\(2000\)081<0683:ECOHI2.3.CO](http://dx.doi.org/10.1644/1545-1542(2000)081<0683:ECOHI2.3.CO)
- Morton SR, MacMillen RE. Seeds as sources of preformed water for desert-dwelling granivores. *J Arid Environ* 1982; 5:61-
- Holleman DF, White RG, Feist DD. Seasonal energy and water metabolism in free-living Alaskan voles. *J Mammal* 1982; 63:293-6; <http://dx.doi.org/10.2307/138064>
- Chappell MA. Thermal energetics and thermoregulatory costs of small arctic mammals. *J Mammal* 1980; 61:278-91; <http://dx.doi.org/10.2307/138004>
- Whitney P. Seasonal maintenance and net production of two sympatric species of subarctic microtine rodents. *Ecology* 1977; 58:314-25; <http://dx.doi.org/10.2307/193560>
- Heller HC, Ruby NF. Sleep and circadian rhythms in mammalian torpor. *Annu Rev Physiol* 2004; 66:275-89; PMID:14977404; <http://dx.doi.org/10.1146/annurev.physiol.66.032102.11531>
- Broome L. Intersite differences in population demography of Mountain Pygmy-possums *Burramys parvus* Broom (1986-1998): implications for metapopulation conservation and ski resorts in Kosciuszko National Park, Australia. *Biol Conserv* 2001; 102:309-23; [http://dx.doi.org/10.1016/S0006-3207\(01\)00105-](http://dx.doi.org/10.1016/S0006-3207(01)00105-)