1 Ecological consequences of temperature regulation: Why might the mountain pygmy possum

2 *Burramys parvus* need to hibernate near underground streams?

3

4 Christine E. Cooper* and Philip C. Withers

5

6 *Corresponding author

7 Department of Environment and Agriculture, Curtin University, PO Box U1987 Perth

8 Western Australia

9 Zoology, School of Animal Biology M092, University of Western Australia, Crawley

10 Western Australia 6009

11

12 *Contact details:

13 Dr Christine Cooper

14 Department of Environmental Biology

15 Curtin University of Technology

16 PO Box U1987

17 Perth, Western Australia

18 Ph +61 8 9266 7965

19 Fax +61 8 9266 2495

20 e-mail C.Cooper@curtin.edu.au

21

22

23 **Abstract**

24   The mountain pygmy possum (*Burramys parvus*) is an endangered marsupial

25 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} $^{\circ}$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.

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

50   maintaining water balance by eating snow during the hibernation season, and the implications

51   of thermal biology for the ecology and habitat requirements of this species.

52   The habitat of the mountain pygmy possum consists of boulder fields above the

53   winter snowline (usually 1370m) in a few alpine areas within Victoria and New South Wales,

54   southeastern Australia (1,3), with a total habitat area of only some 10 km^2 (4). Overwinter

55   survival of mountain pygmy possums is closely correlated with the depth and duration of

56   winter snow cover; 150 days of snow cover is optimal for survival (2). Early snowmelt in

57   spring is particularly problematic, as this reduces temperatures in hibernacula and increases

58   the duration and frequency of arousals from hibernation (5). Snowmelt beginning before the

59   arrival of their primary spring food-source, migratory Bogong moths (*Agrotis infusa*), means

60   that pygmy possums undergo their final arousal from hibernation before they have access to

61   this food (2). Snow depth and duration has been decreasing in the Australian Alps over the

62   last 40 years, with more severe reductions, and increasing early spring snow melt predicted to

63   occur by 2050-2070 (6,7).

64   Identification of all extant populations of mountain pygmy possums, and a thorough

65   understanding of their habitat requirements, is necessary if extinction of this species in the

66   wild is to be prevented. Acclimatisation of mountain pygmy possums to cool lowland

67   habitats, reflecting their historical distribution as revealed by the fossil record, is one

68   proposed strategy to mitigate the extinction threat posed by climate change (2). Recent

69   research has identified some previously unknown populations of mountain pygmy possums in

70   New South Wales, further north than previously known populations and at lower-than-

71   predicted altitudes of 1180-1300m (8-10). These lower altitude populations may have

72   persisted due to good snow cover in the year proceeding the survey (8). Interestingly, studies

73   of these new populations suggest that mountain pygmy possums may have a preference for

74   boulder fields with close proximity to permanently flowing streams (9,11). Previous

75 physiological research has focussed on the energy and thermal requirements of mountain

76 pygmy possums (4,12-14) and we know nothing of their water requirements. Surprisingly,

77 maintaining water balance might be problematic for hibernating mammals (15,16) so we

78 present here a model of water balance for hibernating mountain pygmy possums. This model

79 explains why availability of liquid water during the hibernation period may enhance survival,

80 and therefore why permanently flowing streams may be an important component of current

81 and future habitat.

82   Mountain pygmy possums hibernate from late summer to early spring, for five

83 (juveniles) to seven (adults) months, when they inhabit hibernacula located under the snow

84 within spaces between boulders (13). Their hibernacula are insulated from the surrounding

85 environment by snow, vegetation and soil, with ambient temperatures within the hibernacla

86 remaining constant at around 1.5 to 2.5ºC, while air temperature varies from approximately -

87 8 to 20ºC (4). For hibernating mammals, including marsupials (17,18), the typical hibernation

88 period consists of bouts of torpor interrupted by brief periods of arousal to euthermia (4).

89 During torpor, the body temperature of the mountain pygmy possum may decrease to 1.8 ºC,

90 with a pronounced reduction in metabolic rate from a basal metabolic rate of 1.12 ml O_2 g^{-1} h^{-1}

91 ^{1} to as low as 0.020 ml O_2 g^{-1} h^{-1} (12). Arousing periodically from hibernation to euthermia is

92 energetically costly. In the laboratory, one day of euthermia for mountain pygmy possums

93 uses up to 1.85g fat, more than half the fat reserves used by a torpid possum over 155 days

94 (12). Why hibernators undergo these costly periodic arousals is not well understood, although

95 it is assumed that arousal is necessary to restore some aspect(s) of physiological homeostasis

96 perturbed during long periods of torpor (18). Amongst the various hypotheses that have been

97 proposed (see ref. 18) is the suggestion that evaporative water loss during hibernation may

98 result in dehydration and so mammals are required to arouse to drink (15). Indeed, a number

99   of recent studies suggest that maintenance of water balance is a critical factor determining

100   hibernation duration and success (19-22).

101   For torpid mammals, the only avenues of water gain and loss are metabolic water

102   production and evaporative water loss. The ratio of these, relative water economy (relative

103   water economy = metabolic water production/evaporative water loss), is therefore an index of

104   the state of water balance for a torpid mammal (16). Many small mammals, even tropical and

105   mesic species, have a favourable relative water economy (i.e. they make more metabolic

106   water than they lose by evaporation) when euthermic at moderate to low ambient

107   temperatures (e.g. 23-26). However during torpor, their metabolic rate (and therefore

108   metabolic water production) decreases proportionally more than their evaporative water loss,

109   and so the relative water economy becomes more unfavourable, and water balance is

110   typically negative (e.g. 16,27-30). Water loss equivalent to about 5% body mass appears to be

111   a critical limit requiring arousal from torpor (31), and so it is likely that hibernating mammals

112   reaching this limit must arouse to drink. For another hibernating marsupial, the monito del

113   monte (*Dromiciops gliroides*), rates of mass loss calculated from RWE during torpor

114   correlated with observed periodicity of arousals in the field (16), indicating that maintenance

115   of water balance may indeed be an important function of periodic arousals during

116   hibernation.

117   Mammals arousing from hibernation to drink must warm ingested water to body

118   temperature. For hibernators in cold environments, this can have a significant energetic cost,

119   especially if the ingested water is ice and must be melted then warmed, but the cost is rarely

120   considered when assessing the energetic consequences of arousals. Mountain pygmy possums

121   consuming water to offset that lost by evaporative water loss during hibernation could drink

122   liquid water if it is available (e.g. from streams running beneath boulder fields), or eat frozen

123   water in the form of snow or ice. Here we determine the potential impact of availability of

124   liquid compared to frozen water on the energy budget of hibernating mountain pygmy

125   possums, and thus assesses the ecological consequences of temperature regulation for this

126   endangered species.

127   We model the energetic costs of mountain pygmy possums ingesting liquid water or

128   eating snow based on physical constants for heat requirements of warming of water (specific

129   heat capacity of water = 4.19 J g^{-1} $°C^{-1}$; ref. 32) and melting of snow (latent heat of fusion =

130   334 J g^{-1}; ref. 32). We assume that euthermic pygmy possums attain a body temperature of

131   35°C during periodic arousals from torpor (4), that ingested liquid water is the same

132   temperature as the ambient temperature within a hibenaculum under the snow (2°C; ref. 4)

133   and that the temperature of ingested snow is 0°C. Calculations are based on a mean body

134   mass for adult possums of 57g, and 30g for juveniles, after ref. 4, with torpor metabolic rates

135   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

136   converted to joules assuming 20.1 ml O_2 J^{-1} (32). We base our calculations of overall

137   energetic costs of replenishing evaporated water on there being 20 arousals during the

138   hibernation period (33), and the assumption that possums must replace the equivalent of

139   between 1 and 10% of their body mass (5% being most likely; 16,31) in water during each

140   arousal.

141   Mountain pygmy possums may cache seeds in their subnivean hibernacula for

142   consumption during periodic arousals (3,5). Like water, ingested food must also be warmed

143   to body temperature, but the specific heat of dry food is much lower than water, and there is

144   no latent heat of fusion (34). Seeds have little preformed water (< 20%; 35), so warming of

145   seeds from an ambient temperature of 2ºC to a body temperature of 35ºC is insignificant

146   compared to the much greater costs of warming liquid and especially frozen water (34,37).

147

148   The energy required to warm ingested liquid water from 2ºC to a euthermic body

149   temperature of 35ºC is 138 J g^{-1}. Therefore the energetic cost for an adult possum (57 g) of

150   ingesting between 1 and 10% body mass of liquid water and warming it to 35ºC ranges from

151   78.8 to 788 J respectively, and for a juvenile possum (30 g) from 41.5 to 415 J. Ingesting 5 %

152   of body mass as liquid water at 2ºC requires 394 J for adults and 207 J for juveniles (Figure

153   1).

154   The total energetic cost of ingesting snow is much higher than for liquid water, as the

155   snow must first be melted at high energetic cost (i.e. latent heat of fusion = 334 J g^{-1}), and

156   then warmed from 0 ºC to a euthermic body temperature of 35ºC at a lower energetic cost

157   (i.e. specific heat of water x temperature increase = 146 J g^{-1}). For an adult mountain pygmy

158   possum, this equates to an energetic cost of between 274 and 2740 J for ingesting between 1

159   and 10% body mass of snow, and for juvenile possums between 144 and 1442 J. Ingesting

160   5% of body mass as snow requires 1370 J for adult possums and 721 J for juveniles (Figure

161   1).

162   To put these heat requirements in perspective, warming ingested liquid water to

163   euthermic body temperature is equivalent to the energy used by an adult mountain pygmy

164   possum during 2.8 (1% of body mass ingested) to 28 (10% of body mass ingested) hours of

165   torpor. Ingesting and warming a volume of water equivalent to 5% of body mass consumes as

166   much energy as 13 hours of torpor. For juvenile possums the relative costs are slightly higher;

167   ingesting a volume of liquid water equivalent to 1 and 10% of body mass consumes as much

168   energy as 3.1 to 31 hours of torpor and water that is 5% of body mass would require the

169   energy of 16 hours of torpor.

170   For frozen water, the torpor energy equivalents are even higher. Melting and then

171   warming ingested snow to a euthermic body temperature requires as much energy as 9.6 to 96

172   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 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

198   environments. Water has a particularly high specific heat capacity and therefore warming of

199   drinking water is of energetic significance. Ingesting frozen water has even higher additional

200   thermal costs as the water must first be melted, then warmed (34,37).

201   Estimates of the energetic costs of warming ingested water for several euthermic

202   small mammals inhabiting subnivean environments are variable. Holleman et al.[36] estimated

203   the energetic costs of eating ice to be 140 J $g^{-0.8}$ day^{-1} or 2% of average daily metabolic rate

204   for red-backed voles (*Clethrionomys rutilus*). Whitney[38] suggested that half of the ingested

205   food of red-backed voles and tundra voles (*Microtus oeconomus*) during winter would be

206   frozen water, and that melting and warming this water would require 4 kJ day^{-1}, or 7% of

207   average daily metabolic rate. Berteaux[34] estimated that meadow voles (*Microtus*

208   *pennsylvanicus*) in a subnivean environment would expend between 4.7 and 12.9 % of their

209   winter average daily metabolic rate warming ingested liquid and frozen water respectively.

210   Our calculations for hibernating adult mountain pygmy possums suggest that the energetic

211   cost of warming ingested liquid water of 7.88 kJ (394 J to warm liquid water equivalent to

212   5% body mass x 20 arousals) is 7.5% of the energetic cost of remaining torpid (104.5 kJ; 12)

213   for 155 days. If we include costs of arousal to euthermia of 68.5 J $arousal^{-1}$ (12) for 20

214   arousals to predict an overall energy cost of 1475 kJ for 155 days of the hibernation period,

215   then the percentage cost of warming liquid water is much lower (about 0.5%), reflecting the

216   high energetic costs of arousal. Similar calculations for costs of consuming frozen water

217   (1370 J to melt and warm the water) indicate that eating snow would account for 26% of the

218   energetic cost of remaining torpid (27.36 kJ) and 19% of the overall energy required

219   (including periodic arousals) for winter hibernation of 155 days.

220   The magnitude of the energetic costs for heating ingested water is determined by the

221   temperature differential between the animal and the food/water, the quantity of food/water

222   ingested, and the specific heat capacity of the food/water (34). For hibernating mountain

223 pygmy possums these costs are a particularly high proportion of their average daily metabolic

224 rate, compared to other mammals in subnivean environments. This relatively high cost is

225 despite a relatively moderate subnivean microclimate for pygmy possums resulting in a much

226 smaller body to ice temperature differential (e.g. 0 to 35ºC compared to -30 to 40 ºC for

227 subarctic voles; 38). It is also possible that mountain pygmy possums could drink before they

228 reached their euthermic body temperature of 35 ºC, further reducing their body to water

229 temperature differential. However, as mountain pygmy possums consistently achieve body

230 temperatures of 35 ºC during arousals (4) the ingested water would still ultimately be warmed

231 to 35 ºC even if initially ingested at a lower body temperature. Ingestion during the cooling

232 phase of torpor entry is unlikely, as torpor is entered during short wave sleep (39). Our model

233 for mountain pygmy possums ingesting water equivalent to 5% of body mass (2.8 g for

234 adults) during a hibernation period of 155 days is for an average water consumption of 0.37g

235 day^{-1}, much less than the 2.2g day^{-1} for Alaskan voles (36), 7.5g day^{-1} predicted for red-

236 backed voles and tundra voles (38) and 30.8g day^{-1} measured for meadow voles (34).

237   Particularly high proportions of energy expenditure calculated to warm ingested water

238 for hibernating mountain pygmy possums do not reflect a more extreme environment,

239 drinking before full arousal, or higher water intake, but rather the very low torpor metabolic

240 rate of a hibernating marsupial compared with the high metabolic rates of euthermic rodents.

241 The average daily metabolic rate of various vole species in winter ranges from 118 kJ day^{-1}

242 (meadow voles; 34) to 244 kJ day^{-1} (tundra voles; 38), much higher than that calculated for

243 mountain pygmy possums during the hibernation period (9.5 kJ day^{-1}; calculated from data of

244 Geiser and Broome[12]), even after accounting for their energetically costly arousals.

245   The substantial energetic cost of consuming cold or frozen water is of particular

246 significance for a hibernator compared to a euthermic rodent. For meadow volesaverage daily

247 metabolic rate was 22.7% higher in winter than summer, with 60% of this difference

248 attributed to eating frozen rather than liquid water (34). Euthermic animals clearly meet these

249 extra costs by simply consuming more energy. However, for hibernators, which can't take in

250 more energy during hibernation, the consequence is severe - a reduction in the overall time

251 that they can potentially hibernate. For adult mountain pygmy possums, consuming 5% of

252 body mass as snow during each of 20 arousals requires the energy equivalent to 30 days of

253 hibernation, and even for drinking liquid water, the cost is 8.6 days of hibernation.

254 A reduction in the hibernation period has the potential to dramatically impact on the

255 overwinter survival of mountain pygmy possums, which in turn is a key factor determining

256 the demographics and overall population size of this endangered species (40). The annual

257 survival of mountain pygmy possums is low at about 40%,(40) withinsufficient energy

258 reserves to sustain hibernation until the arrival of Bogong moths in spring likely a factor

259 contributing to overwinter mortality, highlighting the significance of energy conservation

260 during the winter hibernation period (40). Indeed, in years of early snow melt, when possums

261 are forced to arouse earlier in the spring, populations of mountain pygmy possums decline

262 (2). Habitat where hibernating pygmy possums have access to liquid water, such as

263 boulderfields with permanently flowing subterranean streams, may therefore be important in

264 allowing pygmy possums to balance their water budget without the excessive energetic costs

265 of eating snow or ice to obtain water. Access to liquid water may prolong the hibernation

266 period approximately three weeks, and this could impact substantially on overwinter survival

267 and population persistence.

268 The consequences of eating snow rather than drinking frozen water are even more

269 significant for juvenile mountain pygmy possums. Smaller body mass and lower mass-

270 specific torpor metabolic rates of juveniles (12) mean that the impacts of warming water are a

271 bigger proportion of the energy budget than for adults. The hibernation period of juvenile

272 possums is already shorter than that of adults (five compared to seven months), being limited

273   by their ability to accrue sufficient fat reserves prior to hibernation (12), and overwinter

274   survival is reduced compared to adults (40). Therefore habitat providing access to liquid

275   water may be of particular importance for recruitment of juveniles into the population.

276   We have demonstrated here how thermoregulatory costs of maintaining water balance

277   have important consequences for the ecological requirements of an endangered marsupial.

278   Our results suggest that mountain pygmy possum habitats with subnivean access to liquid

279   water during winter, such as those with subterranean streams running under boulder fields,

280   should be considered when prioritising habitat conservation. Attempts to translocate

281   mountain pygmy possums to new habitats for conservation and management purposes should

282   include water availability as an important habitat characteristic.

283

284   **Disclosure of Potential Conflicts of Interest**

285   There are no potential conflicts of interest.

286

287   **Acknowledgements**

290

291

References

1. 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.

2. 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.

3. 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.

4. Körtner G, Geiser F. Ecology of natural hibernation in the marsupial Mountain Pygmy-possum (*Burramys parvus*). Oecologia 1998; 113:170-78.

5. Smith AP, Broome L. The effects of season, sex and habitat on the diet of the mountain pygmy possum (*Burramys parvus*) Wild Res 1992; 19:755-68.

6. Whetton PH, Haylock MR, Galloway R. Climate change and snow-cover duration in the Australian Alps. Clim Change 1996; 32:447-79.

7. 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.

317   8. Schulz M, Wilks G, Broome L. Occupancy of spoil sumps by the Mountain Pygmy-
318   possum *Burramys parvus* in Kosciuszko National Park. Ecol Manag Rest 2012; 13:290-
319   96.

320   9. Schulz M, Wilks G, Broome L. An uncharacteristic new population of the Mountain
321   Pygmy-possum *Burramys parvus* in New South Wales. Aust Zool 2012; 36:22-28.

322   10. Broome L, Ford F, Dawson M, Green K, Little D, McElhinney N. Re-assessment of
323   mountain pygmy-possum *Burramys parvus* population size and distribution of habitat in
324   Kosciuszko National Park. Aust Zool 2013; 36:381-403.

325   11. Broome L, Schulz M, Bates H, Shi H. Good news for the Alps: A recovery in numbers
326   and extension of known range for the mountain pygmy-possum. 58th Scientific Meeting,
327   Aust Mam Soc 2012.

328   12, Geiser F, Broome LS. Hibernation in the mountain pygmy possum *Burramys parvus*
329   (Marsupialia). J Zool Lond 1991; 223:593-602.

330   13. Broome, LS and Geiser F. Hibernation in free-living mountain pygmy-possums,
331   *Burramys parvus* (Marsupialia: Burramyidae). Aust J Zool 1995; 43:373-9.

332   14. Körtner G, Song X, Geiser F. Rhythmicity of torpor in a marsupial hibernator, the
333   mountain pygmy-possum (*Burramy parvus*) under natural and laboratory conditions. J
334   Comp Physiol B 1998; 168:631-38.

335   15. Thomas DW, Geiser F. Periodic arousals in hibernating mammals: is evaporative water
336   loss involved? Funct Ecol 1997; 11:585–91.

337   16. Withers PC, Cooper CE, Nespolo RF. Evaporative water loss, relative water economy and
338   evaporative partitioning of a heterothermic marsupial, the Monito del Monte
339   (*Dromiciops gliroides*). J Exp Biol 2012; 215: 2806-13.

340   17. Geiser F. Hibernation in pygmy possums (Marsupialia: Burramyidae). Comp Biochem
341   Physiol 1985; 81A: 459-63.

342   18. Humphries MM, Thomas DW, Kramer DL. The role of energy availability in mammalian

343   hibernation: A cost-benefit approach. Physiol Biochem Zool 2003; 76:165–79.

344   19. Park KJ, Jones G, Ransome RD. Torpor, arousal and activity of hibernating greater

345   horseshoe bats (*Rhinolophus ferrumequinum*). Func Ecol 2000; 14:580–8.

346   20. Németh I, Nyitrai V, Németh A, Altbächer V. Diuretic treatment affects the length of

347   torpor bouts in hibernating European ground squirrels (*Spermophilus citellus*). J Comp

348   Phys B 2010; 180:457–64.

349   21. Willis CKR, Menzies AK, Boyles JG, Wojciechowski MS. Evaporative water loss is a

350   plausible explanation for mortality of bats from white-nose syndrome. Int Comp Biol

351   2011; 51:364–73.

352   22. Muñoz-Garcia A, Ben-Hamo M, Pinshow B, Williams JB, Korine C. The relationship

353   between cutaneous water loss and thermoregulatory state in Kuhl's pipistrelle

354   *Pipistrellus kuhlii*, a vespertillionid bat. Physiol Biochem Zool 2012; 85:516-25.

355   23. Cooper CE, Cruz-Neto AP. Metabolic, hygric and ventilatory physiology of a

356   hypermetabolic marsupial, the honey possum (*Tarsipes rostratus*). J Comp Physiol B

357   2009; 179:773-81.

358   24. Cooper CE, Withers PC, Cruz-Neto AP. Metabolic, ventilatory and hygric physiology of

359   the gracile mouse opossum (*Gracilinanus agilis*). Physiol Biochem Zool 2009; 82:153–

360   62.

361   25. Cooper CE, Withers PC, Cruz-Neto AP. Metabolic, ventilatory and hygric physiology of

362   a South American marsupial, the long-furred woolly mouse opossum. J Mamm 2010; 91:

363   1–10.

364   26. Barker JM, Cooper CE, Withers PC and Cruz-Neto AP. Thermoregulation by an

365   Australian murine rodent, the ash-grey mouse (*Pseudomys albocinereus*). Comp

366   Biochem Physiol A 2012; 163:336-342.

367   27. Cooper CE, Geiser F, McAllan B. Effect of torpor on the water economy of an arid-zone

368   dasyurid, the stripe-faced dunnart (*Sminthopsis macroura*) J Comp Physiol B 2005;

369   175:323-28.

370   28. Withers PC, Cooper CE Thermal, metabolic, hygric and ventilatory physiology of the

371   sandhill dunnart (*Sminthopsis psammophila* Marsupialia, Dasyuridae) Comp Physiol

372   Biochem 2009; 153:317-23.

373   29. Withers PC, Cooper CE The metabolic and hygric physiology of the little red kaluta. J

374   Mamm 2009; 90:752–760.

375   30. Pusey H, Cooper CE, Withers PC. Metabolic, hygric and ventilatory physiology of the

376   red-tailed phascogale (*Phascogale calura*; Marsupialia; Dasyuridae): adaptations to

377   aridity or arboreality? Mamm Biol 2013; 78:397-405.

378   31. Kallen FC. Some aspects of water balance in the hibernating bat. Ann Acad Sci Fenn Ser

379   4 1964; 71:57-267.

380   32. Withers PC Comparative Animal Physiology. Saunders College Publishing 1992.

381   33. Geiser F, Broome LS The effect of temperature on the pattern of torpor in a marsupial

382   hibernator. J Comp Physiol B 1993; 163:133-37.

383   34. Berteaux D. Energetic cost of heating ingested food in mammalian herbivores. J Mamm

384   2000; 81:683-90.

385   35. Morton SR, MacMillen RE. Seeds as sources of preformed water for desert-dwelling

386   granivores. J Arid Environ 1982; 5:61-67.

387   36. Holleman DF, White RG, Feist DD. Seasonal energy and water metabolism in free-living

388   Alaskan voles. J Mamm 1982; 63:293-96.

389   37. Chappell MA Thermal energetics and thermoregulatory costs of small arctic mammals. J

390   Mamm 1980 61:278-91.

391 38. Whitney P Seasonal maintenance and net production of two sympatric species of

392   subarctic microtine rodents. Ecology 1977; 58:314-25.

393 39. Heller HC, Ruby NR. Sleep and circadian rhythms in mammalian torpor. Ann Rev

394   Physiol. 2004; 66:275–89.

395 40. Broome L. Intersite differences in population demography of Mountain Pygmy-possums

396   *Burramys parvus* Broom (1986-1998): implications for metapopulation conservation and

397   ski resorts in Koskiuszko National Park, Australia. Biol Cons 2001, 102:309-23.
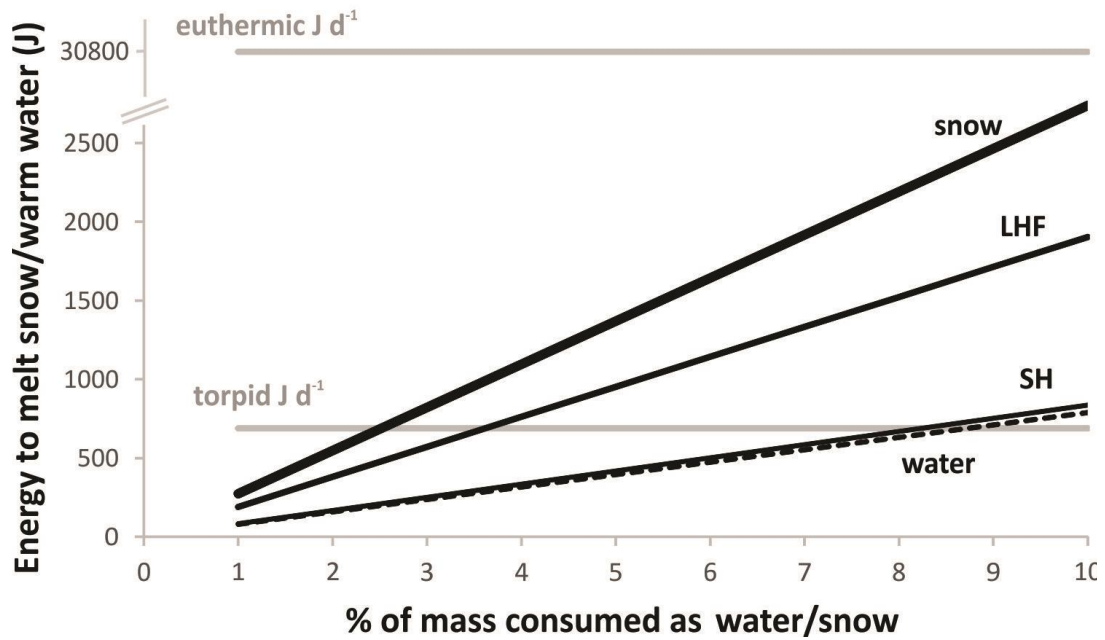
398

399

400

401

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 show for comparison (grey lines; values from 12). Note the break in the y axis.
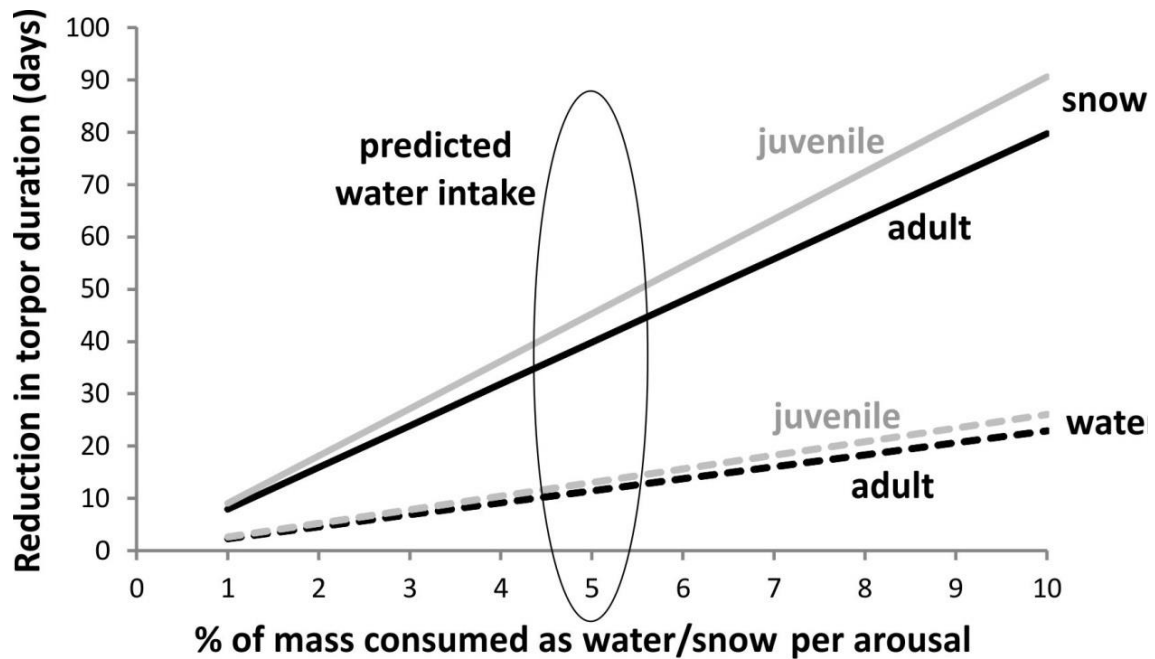
427

428

429

430

431

432

433

434

435

436

437

438

439 **Figure 2:** Consequences of the energetic costs of eating snow (solid lines) compared to

440 drinking liquid water (dashed lines) on the energy reserves available for hibernation for

441 juvenile (grey lines) and adult (black lines) mountain pygmy possums (*Burramys parvus*).

442 The ellipse indicates the costs of ingesting water equivalent to 5% of body mass, a likely

443 estimate of the degree of dehydration triggering an arousal for a hibernating mammal.

444