

CLASSICS

Conserving energy during hibernation



Fritz Geiser discusses the impact of Barbara Snapp and Craig Heller's classic paper 'Suppression of metabolism during hibernation in ground squirrels (*Citellus lateralis*)', published in *Physiological Zoology* in 1981.

How hibernators manage to reduce their high metabolic rate – and therefore energy expenditure – from times when they are active to small almost immeasurable fractions during hibernation has attracted scientific inquiry for over a century. This problem was also the subject of the classic study by Barbara D. Snapp and H. Craig Heller published in 1981, which presented detailed measurements of different well-identified physiological states as a function of temperature (Snapp and Heller, 1981). It remains a landmark paper in the analysis of metabolic rate reduction during rodent hibernation because it provided measurements of physiological variables over a wide temperature range rather than the narrow ranges that had been previously covered. The paper sparked new interest in the mechanisms of metabolic rate reduction during hibernation and their ecological implications, and resulted in renewed attempts to resolve them.

It is truly astonishing that many mammalian and one avian species can hibernate and are able to turn down the endothermic furnace within minutes to extremely low values, which approach

those of ectothermic amphibians or reptiles, allowing these 'heterothermic' endotherms to survive for weeks or even months without eating. One major controversy regarding the metabolic rate reduction during torpor was whether the fall of metabolism was entirely due to the falling body temperature or whether other influences are involved. Hibernators reduce body temperature from normothermia (high body temperatures of ~35–40°C) to torpor by ~30°C on average (Ruf and Geiser, 2015), and in some species it can fall by more than 40°C (Barnes, 1989). Over this entire temperature range, body temperature falls in line with the environmental temperature (i.e. hibernating animals are said to be thermo-conforming), although body temperature during torpor can be regulated at even lower values, often near 0°C, to prevent tissue damage (Heller et al., 1977). As biochemical reactions in the tissues of living organisms are strongly temperature dependent, the fall of metabolic rate therefore may simply be explained by the effects on tissue metabolic rate of this body temperature reduction. To determine whether the reduction of metabolic rate that is associated with torpor is simply a result of the fall in temperature, scientists have calculated the factor by which the metabolic rate changes over a 10°C change in temperature – known as the Q_{10} value.

Snapp and Heller applied this approach to golden-mantled ground squirrels (*Citellus lateralis* or *Spermophilus lateralis* presently *Callospermophilus lateralis*), a medium-sized (200 g) hibernator that expresses prolonged torpor bouts of up to 3 weeks and reduces its body temperature to near 0°C. In their detailed study, Snapp and Heller measured oxygen consumption and carbon dioxide production via open-flow respirometry and collected hypothalamic temperatures for core body temperature readings. They compared the animals' basal metabolic rate (which represents the minimum cost of living during normothermia measured at high ambient temperatures where heat loss is minimal) of normothermic individuals (body temperature ~37°C) with the

minimum metabolic rate during deep torpor, when the body temperature was below 10°C. They did this after the metabolism and body temperature of hibernating animals had reached steady-state minima. Over this body temperature range they found the metabolic rate fell by a Q_{10} of 2.3 on average, although some Q_{10} values as high as 2.8 were observed. To put this in context, many biochemical reaction rates change between 2- and 2.5-fold over a 10°C change in temperature (i.e. they have a Q_{10} between 2 and 2.5); therefore, if the Q_{10} for metabolic rate during torpor was between 2 and 2.5, the reduction in body temperature would entirely explain the measured reduction in metabolic rate. However, if the Q_{10} was above 2.5 or even 3.0, other mechanisms in addition to temperature effects must be involved, resulting in an even more pronounced reduction in the metabolic rate.

Snapp and Heller also examined retention of carbon dioxide during hibernation. It had been suggested previously that carbon dioxide storage could be a potential inhibitor of metabolism during hibernation. However, their comparative data on carbon dioxide production relative to oxygen consumption did not strongly support this hypothesis; hence, carbon dioxide storage was not considered to be a major contributor to metabolic inhibition.

The overall conclusion from their study was that the effect of temperature on tissue metabolism explained the metabolic rate reduction during hibernation in ground squirrels to a large extent. However, most of their calculations were derived from comparing the basal metabolic rate at normothermic body temperatures with the torpor metabolic rate at low body temperatures (below 10°C) in a medium-sized hibernator, which, as recognized by Snapp and Heller (1981), is not representative of all hibernating species. Hibernators range in size from about 4 g bats to 100,000 g bears, with a median mass of 68 g, and not all hibernate at body temperatures below 10°C (Ruf and Geiser, 2015): many hibernators therefore have to deal with different energetic challenges because of differences in size and thermal conditions. Indeed, recent

Classics is an occasional column, featuring historic publications from the literature. These articles, written by modern experts in the field, discuss each classic paper's impact on the field of biology and their own work.

studies have established that at high body temperature or during torpor entry, hibernators not only switch off thermoregulatory heat production, which results in the initial fall of metabolic rate and body temperature at torpor entry described above (Heller et al., 1977), but also actively inhibit enzyme activity and therefore metabolism, as shown more recently (Storey and Storey, 1990; Geiser, 2004). Therefore, if Q_{10} values are calculated for torpid animals at high body temperatures, the values will be high, because both temperature effects and metabolic inhibition are involved in the metabolic rate reduction. However, as further reductions in metabolic rate at lower body temperatures mainly involve temperature effects with little metabolic inhibition, the overall Q_{10} will become smaller the lower the body temperature falls, which explains most of the results reported by Snapp and Heller (1981).

One inherent problem with the comparison of Q_{10} in endotherms, which also was recognized by Snapp and Heller (1981), is that Q_{10} calculations must be made for animals that are in equivalent physiological states – as the calculation assumes that temperature is the major underlying reason for the change in metabolic rate. However, some researchers have compared values between non-equivalent physiological states, which has caused controversy. A common example is the comparison of resting metabolic rates at low environmental temperatures that require a thermoregulatory increase for body temperature regulation with metabolic rates that do not include a thermoregulatory component, like those in thermo-conforming torpid individuals. Obviously, this results in artificially increased Q_{10} values, because of the high metabolic rates required for thermoregulation, and has contributed to some unwarranted questioning of the validity of the Q_{10} approach in endotherms.

Importantly, not all high Q_{10} values reported are due to erroneous Q_{10}

calculations, as shown by Snapp and Heller (1981). Many have been derived from valid comparisons, usually between basal metabolic rate and the steady-state metabolic rate during torpor in individuals in which the body temperature had fallen in line with the temperature of their surroundings. Both of these do not contain a thermoregulatory component and only reflect cost of living at the respective body temperatures. Interestingly, species that have high Q_{10} values ($Q_{10} > 4$) include many small hibernators such as marsupials, bats and rodents on the one hand and large bears on the other (Geiser, 2004; Tøien et al., 2011). The observation of high Q_{10} values in small and large hibernators may appear paradoxical at first glance, but they make functional sense. Small species must suppress their metabolism to maximize energy savings in order to survive the hibernation season, which usually lasts for about 6 months from autumn to spring, because they only have relatively small energy reserves in the form of fat. As their minimum body temperature is limited by the freezing point of body fluids, a reduction of body temperature much below 0°C to eek out their energy reserves further is not possible. Therefore, the only avenue for small hibernators appears to be to maximize metabolic inhibition in order to minimize the metabolic rate – reflected in high Q_{10} values – to values as little as 1 or 2% of the basal metabolic rate (Ruf and Geiser, 2015). Medium-sized hibernators like ground squirrels often also have low body temperatures, although they are not forced to lower metabolism to the same extent as small species because they can store ample amounts of fat and many also store seeds for later consumption. In large bears, the observed high Q_{10} values are also explained to some extent by body temperature, in this case the high minimum body temperature of around 30°C, which hibernating bears maintain by thermoregulation (Tøien et al., 2011). Simply because of their size, bears also have a much lower metabolic rate per unit body mass when at their normal body temperature (Tattersall et al., 2012) and therefore it is relatively easy for them to

reach the low metabolic rate values during torpor of ~25% of basal metabolism. However, a body temperature reduction of about 7°C is not sufficient for bears to reduce their metabolic rate by temperature effects alone and therefore massive metabolic inhibition is required.

Clearly, hibernators are extremely efficient in reducing their metabolic rates during torpor. This enormous reduction in energy expenditure is perhaps best illustrated by the fact that many hibernating mammals can survive entirely on body fat gained during pre-hibernation fattening, often for 6 months and up to 1 year. Snapp and Heller contributed to the understanding of how this metabolic rate reduction during hibernation is achieved in their 1981 publication, providing the impetus for further studies that substantially enhanced the understanding of the mechanisms involved in minimizing energy expenditure during hibernation.

Fritz Geiser
University of New England
fgeiser@une.edu.au

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