

Metabolic Rate Reduction During Hibernation and Daily Torpor

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Abstract. Mechanisms causing the substantial reduction of metabolic rates (MR) during torpor (TMR) in mammals and birds remain controversial. It has been suggested that body temperature (T_b), metabolic inhibition, the small differential between T_b and ambient temperature (T_a), or low thermal conductance are responsible for the low TMR. Available data suggest that MR reduction depends on patterns of torpor, state of torpor, and body mass. Daily heterotherms (species displaying daily torpor exclusively) appear to rely to a large extent on the fall of T_b for MR reduction, perhaps with the exception of very small species and at high T_b during torpor, where some metabolic inhibition may be used. In contrast, hibernators (species capable of prolonged torpor bouts) rely extensively on metabolic inhibition, in addition to T_b effects, to reduce MR to a fraction of that observed in daily heterotherms. In small hibernators metabolic inhibition and the large fall of T_b are employed to maximise energy conservation, whereas in large hibernators metabolic inhibition appears to be employed to facilitate MR and T_b reduction at torpor onset. Over the T_a range where torpid heterotherms are thermo-conforming, the $T_b - T_a$ differential is more or less constant despite a decline of TMR with T_a . However, in thermo-regulating torpid individuals, the $T_b - T_a$ differential is maintained by a proportional increase of TMR as during normothermia, albeit at a lower T_b . Thermal conductance in most torpid thermo-regulating individuals is similar to that in normothermic individuals despite the substantially lower TMR in the former; however, conductance is low when deeply torpid animals are thermo-conforming, likely because of peripheral

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vasoconstriction. Consequently most of the apparently contradictory hypotheses that have been proposed to explain metabolic rate reduction appear to be correct. However, not all hypotheses match the measured data of all species in all stages of torpor.

Introduction

Most researchers working on daily torpor and hibernation agree that the reduction of MR during torpor is substantial and is pivotal for survival in many species. Nevertheless, the mechanisms of how the MR is reduced remain controversial. Several and at first glance mutually exclusive hypotheses attempting to explain the MR reduction during torpor have been proposed. These hypotheses suggest that MR is reduced: (1) via temperature effects (Hammel et al., 1968; Snapp and Heller, 1981), (2) by physiological inhibition in addition to temperature effects (Malan, 1986; Geiser, 1988; Storey and Storey, 1990), (3) by the small $T_b - T_a$ differential (Heldmaier and Ruf, 1992), or (4) the low apparent thermal conductance (C) in torpid individuals (Snyder and Nestler, 1990). These hypotheses are examined here in relation to patterns of torpor, state of torpor, and body mass, because these attributes appear important in determining MR and T_b during torpor.

Data Selection and Analysis

Data on MR, T_b , and body mass of heterothermic mammals and birds were collected from the literature. Basal MR (BMR) was used as a reference point for the TMR of thermo-conforming torpid individuals because in both physiological states metabolism is used for maintenance only, without extra energy expenditure for thermoregulation (Bucher and Chappell, 1997; Wang and Lee, 2000). TMR data were statistically analysed in different T_b bins of 0.0–9.9° C, 10.0–14.9° C, 15.0–24.9° C, and 24.0–32.9° C and the TMR and the Q_{10} (the change in rate caused by 10° C change in temperature) was calculated between BMR (MR_1) and TMR (MR_2) at corresponding T_b s ($Q_{10} = MR_1/MR_2^{10/(T_{b1}-T_{b2})}$) and analysed as a function of body mass. Data for torpid individuals were collected at T_a below and above the T_b set point (T_{set}) during torpor to examine relations between MR and T_b , MR and C, and MR and the $T_b - T_a$ differential in daily heterotherms and hibernators (further details and data in Geiser, 2004).

Torpor Entry

At torpor entry the T_{set} falls faster than T_b facilitated by thermal inertia (Heller et al., 1977). Since most species enter torpor at low T_a , well below the thermoneutral zone (TNZ), the fall of T_{set} should result in a fall from resting MR (RMR) to \sim BMR, because heat production for normothermic thermoregulation will cease (Withers 1992). In sugar gliders, *Petaurus breviceps*, a $\sim 4^\circ\text{C}$ drop from a nocturnal T_b to a diurnal resting normothermic T_b results in a precipitous drop from RMR to \sim BMR, which superficially appears to be a torpor entry (Fig. 1), supporting the theoretical prediction.

The initial reduction of MR at torpor onset at low T_a in most species will follow a similar pattern (Song et al., 1996). However, because the T_{set} is reduced by $> 4^\circ\text{C}$, the substantial fall in T_b that must follow the reduction from RMR to

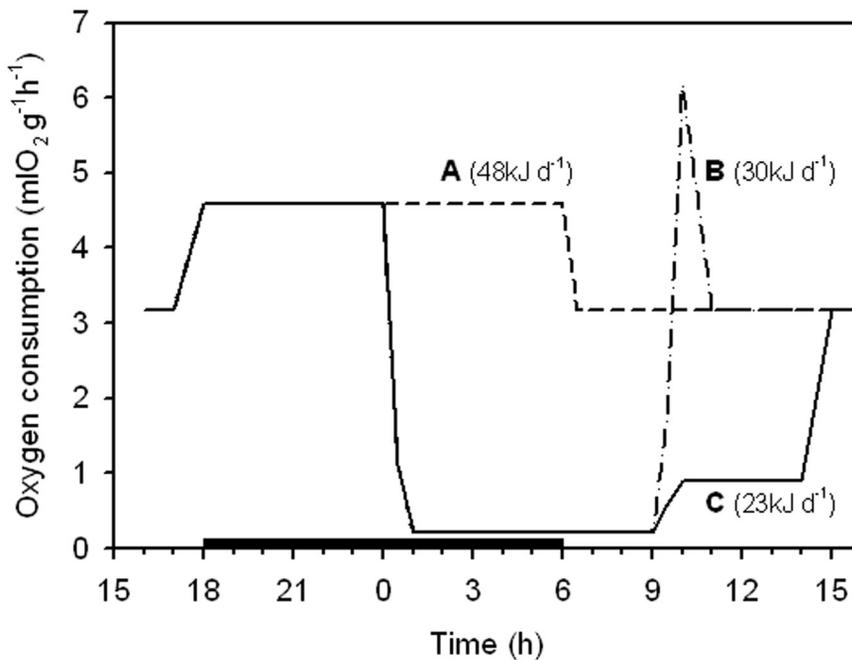


Fig. 1. Oxygen consumption of a sugar glider (*Petaurus breviceps*, 120 g) exposed to T_a 10°C during the activity phase at night (dark bar) and the rest phase at daytime. Note the transient, precipitous drop of oxygen consumption to near BMR during the cooling phase from activity phase to rest phase body temperatures near lights on, followed by a return to RMR after the cooling phase (Holloway, 1998).

-BMR at torpor onset of most heterothermic species is one of the reasons why MR can fall to well below the BMR.

Obviously, the scope for the reduction of RMR depends on size. Small mammals and birds (10 g) have a high RMR at low T_a and a fall of T_{set} will result in a large reduction of MR from RMR to BMR (Fig. 2). The substantial reduction of MR together with the large relative surface area of small heterotherms will result in high cooling rate, and the fast fall of T_b will in turn affect MR. In contrast, in medium (250 g) or large heterotherms (5,000 g) the TNZ extends to a lower T_a , RMR at low T_a increases only little above BMR (Fig. 2), and their small relative surface area will result in a slow cooling rate. Very large species, such as bears, are under thermoneutral conditions even at T_a near 0° C (Scholander et al., 1950) and a fall of T_{set} under thermoneutral conditions should have no effect on MR.

Thus, physiological mechanisms employed for MR reduction during torpor entry must differ between small and large heterotherms. Small species are able to reduce MR with a fall of T_b . In contrast, large species cannot rely on T_b , at least not in the initial phase of torpor entry, and metabolic inhibition for MR reduction appears unavoidable.

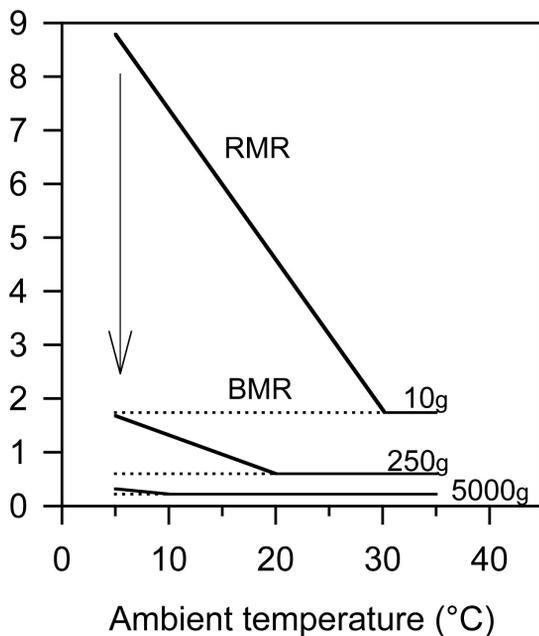


Fig. 2. Resting metabolic rate within the TNZ (BMR) and below the TNZ (RMR) in endotherms of different body mass. Note the wide TNZ and the small increase from BMR to RMR in the large in comparison to the small species. This difference will affect MR reduction at torpor onset (arrow).

Allometry of Steady-state BMR and TMR of Thermo-conforming Torpid Animals

Different approaches to MR reduction as a function of size are not only observed during torpor entry but also are reflected in the steady-state TMR and the Q_{10} between BMR and TMR. Moreover, TMR differs between daily heterotherms and hibernators.

In daily heterotherms at all T_b ranges examined, the regression lines for TMR as a function of body mass declined in parallel with T_b (Fig. 3A). However, the elevation (y-intercept) differed between BMR and TMR at T_b 25–33° C, and also between TMR at T_b 25–33° C and T_b 15–25° C (ANCOVA: $p < 0.001$).

Hibernators also reduce MR as a function of mass from BMR to TMR in parallel from normothermic T_b down to T_b 15–25° C (Fig. 3B). At high T_b s the slopes of the regression for BMR and TMR were indistinguishable, but at $T_b < 10°$ C the slope for the regression of TMR vs mass became significantly smaller ($p < 0.024$; ANCOVA). Above T_b 15° C, the slopes for mass-specific TMR versus body mass ranged from -0.214 to -0.304 ; below T_b 10° C, the slope was \sim half (-0.128) because in this T_b range the reduction of TMR relative to BMR in the small species is more pronounced than in the large species.

When the TMR in the T_b bins of daily heterotherms (Fig. 3A) and hibernators (Fig. 3B) were compared, all differed significantly in elevation (ANCOVA $p < 0.0001$) at T_b 25–33° C, T_b 15–25° C, and T_b 10–15° C. These differences were not due to differences in T_b , because mean T_b s were indistinguishable.

The Q_{10} Between BMR and TMR in Thermo-conforming Torpid Animals

The relationships between TMR and body mass are reflected in the Q_{10} (Fig. 4). As the TMR in daily heterotherms was relatively high, the Q_{10} values between BMR and TMR at all T_b during torpor were significantly smaller than in hibernators. In daily heterotherms the Q_{10} values were similar among the different T_b ranges (T_b 10–15° C, $Q_{10} = 2.0 \pm 0.2$; T_b 15–25° C, $Q_{10} = 2.4 \pm 0.7$; T_b 25–33° C, $Q_{10} = 2.3 \pm 0.7$) and the overall mean Q_{10} was 2.3 ± 0.6 ($n = 49$ species) close to those typical for biochemical reactions. The Q_{10} values for hibernators ranged from 2 to 27 (2 to 9.7 without the bear [*Ursus americanus*], which appears an overestimate). In hibernators, Q_{10} values increased with T_b (T_b 10–15° C, $Q_{10} = 3.4 \pm 0.8$; T_b 15–25° C, $Q_{10} = 3.9 \pm 1.1$; T_b 25–33° C, $Q_{10} = 7.9 \pm 7.0$) and the overall Q_{10} was 3.9 ± 3.7 ($n = 43$ species; 3.4 ± 0.9 without the bear), well above those typical for biochemical reactions. The Q_{10} values differed

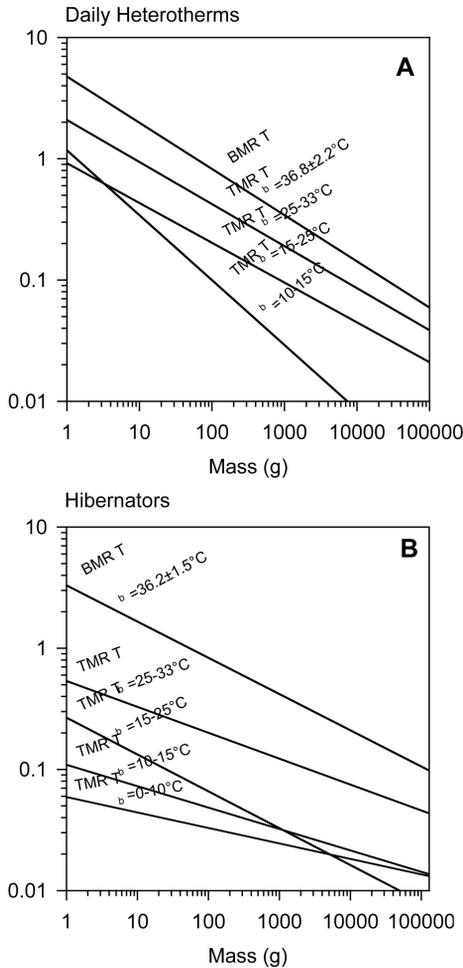


Fig. 3. MR as a function of body mass for daily heterotherms (A) and hibernators (B) at different T_b . Only regression lines are shown for clarity. All regressions are significant with the exception of that for hibernators at T_b 10–15°C ($r^2 = 0.24$, $p = 0.09$). Note the big differences in elevation (y-intercept) between A and B for regression lines fitted to torpid individuals at $T_b < 33^\circ\text{C}$.

significantly between daily heterotherms and hibernators in the three T_b ranges (Fig. 4) as well as the overall Q_{10} for the 92 species examined ($p < 0.001$).

At $T_b < 10^\circ\text{C}$, the Q_{10} values of hibernators were negatively related to body mass ($r^2 = 0.28$), reflecting a greater reduction of steady-state TMR below BMR in the small species in comparison to the large species at low T_b (Fig. 3B). At T_b 10–15°C and T_b 15–25°C, Q_{10} values between BMR and TMR of hibernators were not affected by body mass.

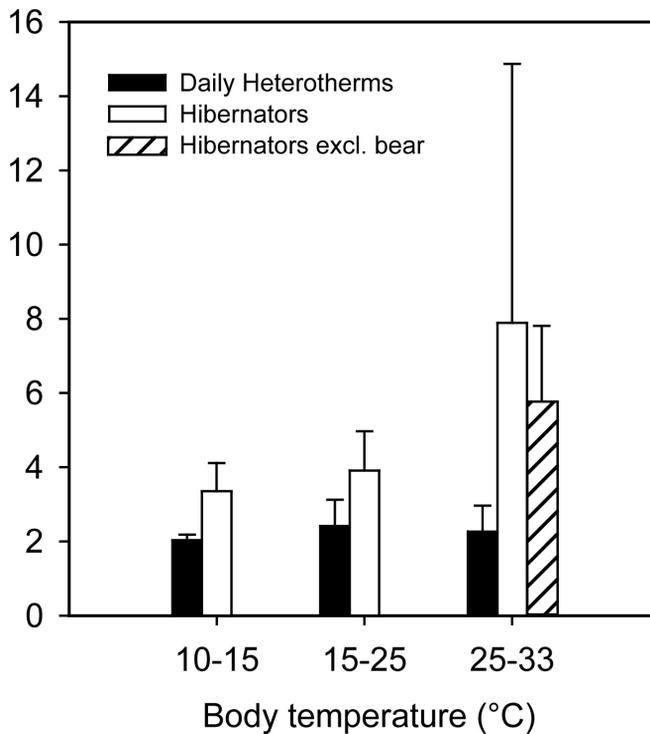


Fig. 4. Q_{10} values for daily heterotherms and hibernators between BMR and TMR measured at different T_b . Q_{10} values for daily heterotherms were not affected by T_b and were close to those typical for biochemical reactions (average $Q_{10} = 2.3 \pm 0.6$). In contrast, Q_{10} values in hibernators increased with T_b from $Q_{10} = 3.4 \pm 0.8$ at low T_b to $Q_{10} = 7.9 \pm 7.0$ ($Q_{10} = 5.8 \pm 2.0$ excl. bear) and the average Q_{10} was 3.4 ± 0.9 (excl. bear).

TMR and the $T_b - T_a$ Differential

Thermo-regulating torpid individuals at T_a below the T_{set} for T_b maintain TMR according to the $T_b - T_a$ differential, albeit at a lower T_b than during normothermia (Hainsworth and Wolf, 1970). Obviously, regulation of T_b even during torpor will result in a proportional heat loss as during normothermia, which must be compensated for by an increase in heat production.

In contrast to thermo-regulating torpid individuals, the $T_b - T_a$ differential in thermo-conforming individuals is often constant (~ 1 to 3°C) or changes little with T_a , although TMR shows a significant decline with T_a and consequently

T_b (Hock, 1951; Henshaw 1968; Song et al., 1997; Buck and Barnes, 2000; Wang and Lee 2000). These observations show that above the T_{set} the $T_b - T_a$ differential does not determine steady-state TMR in thermo-conforming torpid heterotherms.

Apparent Thermal Conductance (C) and TMR

Snyder and Nestler (1990) proposed that a low C rather than a change of T_b allows endotherms to markedly reduce MR without abandoning regulation of T_b during torpor. This argument has several problems: (1) C during torpor in most species is lower only when torpid animals are thermo-conforming and apparently do not regulate T_b , (2) the reduction of C from RMR to TMR is small in comparison to the large difference in metabolism, (3) exposure to 21% oxygen in helium, which is a more conductive atmosphere than air and will increase C, does not result in an increase in TMR (Geiser et al., 1996), (4) C of most thermo-regulating animals is the same during torpor and normothermia (Song et al., 1997; Geiser, 2004), but the TMR even in thermoregulating individuals is only a fraction of that during normothermia. Thus, a low C cannot be the reason for the low MR (Nicol et al., 1992), but appears to be a consequence of the low TMR and peripheral vasoconstriction.

Are Q_{10} Calculations Meaningful in Endotherms?

As for all other physiological measurements, common sense must be applied to the calculation of Q_{10} (Wang and Lee, 2000). This is especially important in heterothermic endotherms, which exhibit pronounced changes in their physiological state. If meaningful calculations for Q_{10} are to be made, changes of MR with T_b that are based on equivalent performance at different T_b s appear most appropriate (Wang and Lee, 2000). Thus, in the present comparison, Q_{10} values were calculated between BMR and TMR in thermo-conforming individuals because both states do not include a thermoregulatory energetic component and reflect maintenance metabolism only at different T_b . Calculations of Q_{10} values between TMR at different T_b during torpor in thermo-conforming individuals also are appropriate. In contrast, comparisons of thermo-regulating individuals (apples plus oranges) with thermo-conforming individuals (apples) are not likely to provide a meaningful Q_{10} values, because a change of state rather than the effects of temperature on rates are examined. Similarly, calculations of Q_{10} during torpor entry can be meaningless if they fail to consider that the initial decline of MR is often not related to a reduction of T_b , but a reduction of T_{set} .

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