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
vasoconstriction. Consequently most of the apparently contradictive 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 \( (Q_{10} = \frac{MR_1}{MR_2}^{10/T_{b1}-T_{b2}}) \) 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 ~BMR, because heat production for normothermic thermoregulation will cease (Withers 1992). In sugar gliders, *Petaurus breviceps*, a ~4°C drop from a nocturnal $T_b$ to a diurnal resting normothermic $T_b$ results in a precipitous drop from RMR to ~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 $>4^\circ C$, the substantial fall in $T_b$ that must follow the reduction from RMR to

![Graph](image)

*Fig. 1. Oxygen consumption of a sugar glider (Petaurus breviceps, 120 g) exposed to $T_a 10^\circ C$ 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 −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 ± 0.2; T_b 15–25°C, Q_{10} = 2.4 ± 0.7; T_b 25–33°C, Q_{10} = 2.3 ± 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 ± 0.8; T_b 15–25°C, Q_{10} = 3.9 ± 1.1; T_b 25–33°C, Q_{10} = 7.9 ± 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
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 $T_b < 10^\circ$ 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$^\circ$ C and $T_b$ 15–25$^\circ$ C, $Q_{10}$ values between BMR and TMR of hibernators were not affected by body mass.
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's. 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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References


