

Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition?

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Accepted December 14, 1987

Summary. The present study addresses the controversy of whether the reduction in energy metabolism during torpor in endotherms is strictly a physical effect of temperature (Q_{10}) or whether it involves an additional metabolic inhibition. Basal metabolic rates (BMR; measured as oxygen consumption, \dot{V}_{O_2}), metabolic rates during torpor, and the corresponding body temperatures (T_b) in 68 mammalian and avian species were assembled from the literature ($n=58$) or determined in the present study ($n=10$). The Q_{10} for change in \dot{V}_{O_2} between normothermia and torpor decreased from a mean of 4.1 to 2.8 with decreasing T_b from 30 to <10 °C in hibernators (species that show prolonged torpor). In daily heterotherms (species that show shallow, daily torpor) the Q_{10} remained at a constant value of 2.2 as T_b decreased. In hibernators with a $T_b <10$ °C, the Q_{10} was inversely related to body mass. The increase of mass-specific metabolic rate with decreasing body mass, observed during normothermia (BMR), was not observed during torpor in hibernators and the slope relating metabolic rate and mass was almost zero. In daily heterotherms, which had a smaller Q_{10} than the hibernators, no inverse relationship between the Q_{10} and body mass was observed, and consequently the metabolic rate during torpor at the same T_b was greater than that of hibernators. These findings show that the reduction in metabolism during torpor of daily heterotherms and large hibernators can be explained largely by temperature effects, whereas a metabolic inhibition in addition to temperature effects may be used by small hibernators to reduce energy expenditure during torpor.

Abbreviation: BMR basal metabolic rate

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Introduction

Torpor in mammals and birds is expressed by a reduction of body temperature (T_b) and metabolism. During hibernation (prolonged torpor) T_b may be lowered by more than 35 °C and heat production is only a small fraction of that in normothermic animals which have a T_b of 30–40 °C (Kayser 1961; Lyman et al. 1982). The torpor bouts of these hibernators last for one or two weeks and are interrupted by spontaneous arousals with short normothermic (<24 h) periods throughout the hibernation period (Twente et al. 1977; French 1982; Barnes et al. 1986). In contrast to hibernation, daily torpor always lasts for less than a day, and both T_b and metabolic rate of these daily heterotherms are maintained at higher values than in hibernators (MacMillen 1965; Morhardt 1970; Nagel 1985; Geiser 1986a).

The reduction of energy metabolism during torpor is substantial. Malan (1980; 1986) argues that the low values of metabolism cannot be explained by temperature effects alone, because the Q_{10} of 3.6 (Q_{10} is the change of rate over a 10 °C temperature range) for oxygen consumption rates between normothermia and hibernation in the mammalian species measured by Kayser (1964), is considerably greater than the Q_{10} of 2–3 that characterises biological reactions in general. In his opinion the low metabolic rates during torpor can only be explained by an additional inhibition to the temperature-induced reduction of metabolism. However, Snapp and Heller (1981) who carefully analyzed temperature effects on energy metabolism in hibernating ground squirrels obtained “normal” biological Q_{10} 's between 2 and 3 and concluded that temperature alone explains the reduction of metabolism during torpor.

To resolve these opposing views I compared

metabolic rates during normothermia with those in torpor of a large number of heterothermic mammal and bird species to determine if specific differences in Q_{10} may explain the apparent contradiction. To resolve whether there is some pattern to interspecific differences I divided the species into two groups: (i) the hibernators, which have a very substantial reduction of metabolism during torpor and (ii) the daily heterotherms which have relatively high metabolic rates during periods of torpor. Because high Q_{10} 's were observed mainly in small species and in animals that were in torpor at relatively high body temperatures, the metabolic rates and Q_{10} 's in hibernators and daily heterotherms were also compared for correlations between body mass and the reduction of metabolism during torpor, and for changes of Q_{10} with body temperature during torpor.

Material and methods

Body temperatures (T_b) and rates of oxygen consumption (\dot{V}_{O_2}) during normothermia and torpor in 60 mammalian and 8 avian species were compared in the present study. Data from measurements obtained in the present study were combined with values from the literature (Appendices 1–3). Animals were divided into 'hibernators' (species that show prolonged torpor, $n=36$) and 'daily heterotherms' (species that show shallow, daily torpor, $n=32$).

The \dot{V}_{O_2} of normothermic animals were used in the comparison only if they had been determined within the thermoneutral zone (basal metabolic rate, BMR). In those mammals for which no BMR data were available, the standard metabolic rate was calculated for the given mass using the equations of Hayssen and Lacy (1985) for the corresponding order or, where possible, family. In several species BMR data were available for individuals that differed in body mass from those used in the measurement of \dot{V}_{O_2} during torpor. In these cases BMR values were mass-corrected:

$$\log_{10} \text{BMR}_1 = b (\log_{10} \text{Mass}_1 - \log_{10} \text{Mass}_2) + \log_{10} \text{BMR}_2 \quad (1)$$

where '2 subscript' corresponds to the measured value of BMR (ml O_2 /g h) and body mass (g) and '1' to the body mass to which BMR was corrected; the slope b was taken from the equations of Hayssen and Lacy (1985) for the particular order or, where possible, family.

BMR, T_b of normothermic resting animals, and \dot{V}_{O_2} of animals that were torpid at different air temperatures (T_a) and T_b 's were used to calculate the Q_{10} between normothermia and torpor. Only species that lower T_b below 30 °C and decrease \dot{V}_{O_2} during torpor below BMR were included in the comparison. The \dot{V}_{O_2} 's of torpid animals were used in the comparison only if they were steady state values and had been determined within a T_a range in which T_b was not actively regulated (i.e. \dot{V}_{O_2} was not increased for thermoregulation during torpor) (see Heller and Hammel 1972). Metabolic rates were placed into 10 °C body temperature intervals over the respective range of T_b during torpor of each group (hibernators, 0–30 °C; daily heterotherms 10–30 °C). The Q_{10} for the change in \dot{V}_{O_2} between different T_b 's during torpor were also determined (Appendix 3). In those torpid hibernators for which \dot{V}_{O_2} and T_a but no T_b measurements were available, T_b was assumed to be 1 °C above

T_a because this value represents the difference between T_b and T_a (ΔT) during prolonged torpor in many species (Lyman et al. 1982). A ΔT of 1 °C was also assumed for torpid hummingbirds (Hainsworth and Wolf 1970). In all other daily heterotherms only T_b 's that had been measured were included because the ΔT in daily torpor is more variable than during hibernation (Morhardt 1970; Geiser and Baudinette 1987). The Q_{10} 's of \dot{V}_{O_2} between two body temperatures (T_{b1} and T_{b2}) were calculated using the equation:

$$Q_{10} = \frac{R_1 \frac{10}{T_{b1} - T_{b2}}}{R_2} \quad (2)$$

where R_1 and R_2 are the \dot{V}_{O_2} in ml O_2 /g h at the two different T_b 's.

Because metabolic rate during torpor appears to be related to body mass (exponent 0.92) (Kayser 1961) rather than surface area (exponent 0.67) (Bartholomew 1982) implying a lack of increase in mass-specific metabolism with decreasing mass during torpor, I investigated whether this is a general feature of torpor. For this comparison, the \dot{V}_{O_2} in those hibernators in which \dot{V}_{O_2} was determined at $T_b < 10$ °C ('deep' hibernation) were corrected to $T_b = 5$ °C using the corresponding Q_{10} between normothermia and torpor of that particular species and T_b . The \dot{V}_{O_2} of all hibernators, regardless of the T_b during torpor, was corrected to $T_b = 20$ °C and compared with the same values of the daily heterotherms. The Q_{10} for the change of \dot{V}_{O_2} between normothermia and torpor in each species and temperature was used to correct to the \dot{V}_{O_2} at $T_b = 20$ °C. If several measurements were available for one species the mean value was used for the statistical analyses.

The \dot{V}_{O_2} and T_b of marsupials measured in the present study were determined as described by Geiser (1986b); the rodents were measured as described by Geiser and Kenagy (1987).

Results

The Q_{10} 's for the change of oxygen consumption between normothermia and torpor in hibernators changed significantly with body temperature during torpor (Table 1). The lowest Q_{10} of 2.85 was observed in hibernators that had T_b 's between 0 and 10 °C. The Q_{10} increased when T_b during torpor was > 10 °C. The Q_{10} of \dot{V}_{O_2} between two different T_b 's during torpor in hibernators ($Q_{10} = 2.3 \pm 0.6$; SD; Appendix 3) was significantly smaller than the smallest Q_{10} determined between normothermia and torpor at $T_b < 10$ °C ($P < 0.01$; t -test). In contrast to the hibernators, no significant differences in the Q_{10} for \dot{V}_{O_2} between normothermia and in torpor at different T_b 's could be detected in the daily heterotherms and the Q_{10} was less than in hibernators (Table 1). The Q_{10} 's for \dot{V}_{O_2} between two different T_b 's during torpor in daily heterotherms ($Q_{10} = 2.6 \pm 0.9$; Appendix 3) was indistinguishable from hibernators ($Q_{10} = 2.3 \pm 0.6$).

The Q_{10} for the change of \dot{V}_{O_2} between normothermia and torpor in hibernators that were torpid at $T_b < 10$ °C showed an allometric relation-

Table 1. The Q_{10} for the change of oxygen consumption between normothermia and torpor in heterothermic endotherms

Group	T_b -range in torpor ($^{\circ}$ C)	Q_{10}	n
Hibernators	0.1–10.0	2.85 ± 0.58	29
	10.1–20.0	3.71 ± 1.22	12
	20.1–30.0	4.11 ± 1.49	5
Daily heterotherms	10.1–20.0	2.35 ± 0.57	20
	20.1–30.0	2.24 ± 0.70	16
	10.1–30.0	2.22 ± 0.57	33

The Q_{10} for the change of \dot{V}_{O_2} of hibernators (mean \pm SD) that were in torpor at different T_b 's differed significantly (one-way ANOVA: $F=6.87$; $df=2,45$; $P<0.01$). Because no such difference could be observed in the daily heterotherms ($P>0.1$; t -test) the Q_{10} of all measurements were combined for further analyses. The smallest Q_{10} of the hibernators at T_b 0.1–10.0 $^{\circ}$ C was significantly greater than that in the daily heterotherms ($P<0.001$; t -test). If several measurements were available for one species the mean value was used for the statistical analysis. Data from Appendices 1 and 2. n =number of species

ship with body mass (Fig. 1, Table 2). Most Q_{10} 's were between 2 and 3 although the Q_{10} increased significantly with decreasing body mass. Only at a body mass <100 g, Q_{10} 's greater than 3 were observed. In contrast, the Q_{10} of daily heterotherms showed no significant correlation with body mass. Because the slope for Q_{10} and body mass was almost zero it was assumed that it was smaller than in the hibernators. However, birds that enter daily torpor may differ from mammals and small birds may have higher Q_{10} 's than larger species (Table 2). If the very large badger (*Taxidea taxus*) was excluded from the analysis the slope for Q_{10} and body mass in mammalian daily heterotherms was not affected.

Mass-specific BMR as a function of body mass of hibernators did not differ significantly from that in daily heterotherms (Fig. 2, Table 3) and the slope and intercept of BMR of all mammalian heterotherms was indistinguishable from that of mammals in general (Hayssen and Lacy 1985). The BMR of avian heterotherms was significantly greater than that of mammalian heterotherms in slope and intercept (Table 3; $P<0.01$; t -test).

A substantial reduction in metabolism during torpor was observed in all species (Fig. 2, Table 4). A significant negative correlation between the mass-specific metabolic rate at $T_b=20^{\circ}$ C and body mass was observed in both hibernators and daily heterotherms. However, the metabolic rate at $T_b=20^{\circ}$ C was significantly higher ($P<0.001$; t -test) in daily heterotherms than in hibernators (Fig. 2, Table 4). The slopes relating body mass and \dot{V}_{O_2} at $T_b=20^{\circ}$ C in the two groups of heter-

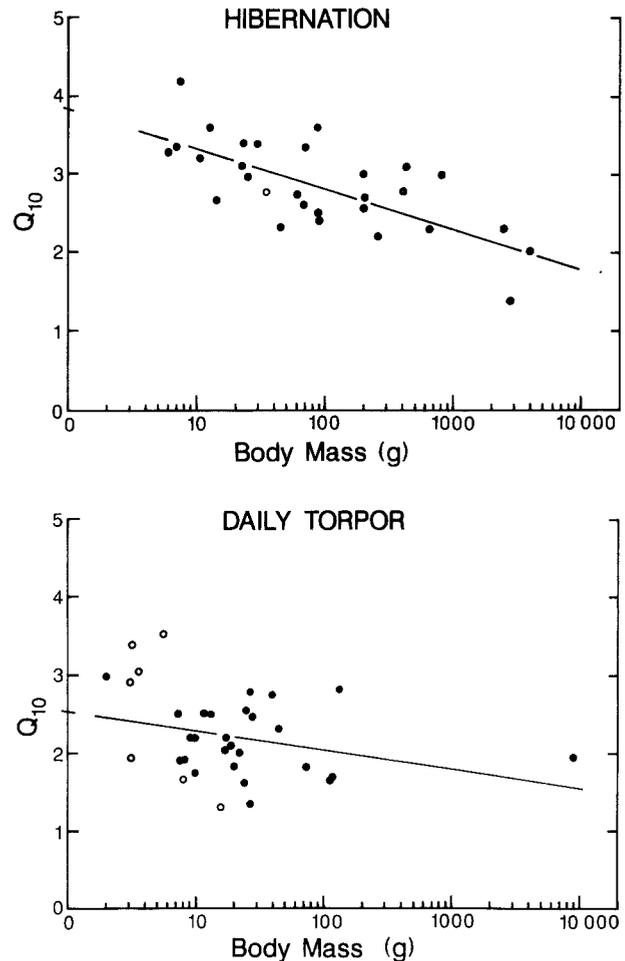


Fig. 1. The Q_{10} of energy metabolism (\dot{V}_{O_2}) between normothermia and torpor in hibernators at $T_b<10^{\circ}$ C and daily heterotherms. Each point represents the mean or a single determination of each species (\bullet mammals; \circ birds). Equations for the linear regressions are shown in Table 2

otherms were indistinguishable (Fig. 2; Table 4). The metabolic rate of hibernators at $T_b=5^{\circ}$ C did not show a significant relationship with body mass ($r^2=0.07$); the slope was almost zero and the mean oxygen consumption of all hibernators with a T_b of 5° C was 0.039 ± 0.016 ml O_2 /g h. In hibernators, the slope of the negative relationship between metabolic rate and body mass gradually decreased as T_b was lowered from normothermia (BMR) to 20° C and from 20° to 5° C ($P<0.01$; t -test). In diurnal heterotherms no significant differences between the slope in mass-specific increase in \dot{V}_{O_2} during normothermia (BMR) and torpor could be observed (Fig. 2; Table 4).

Discussion

The present study supports the view that metabolic inhibition during torpor is important for reduction

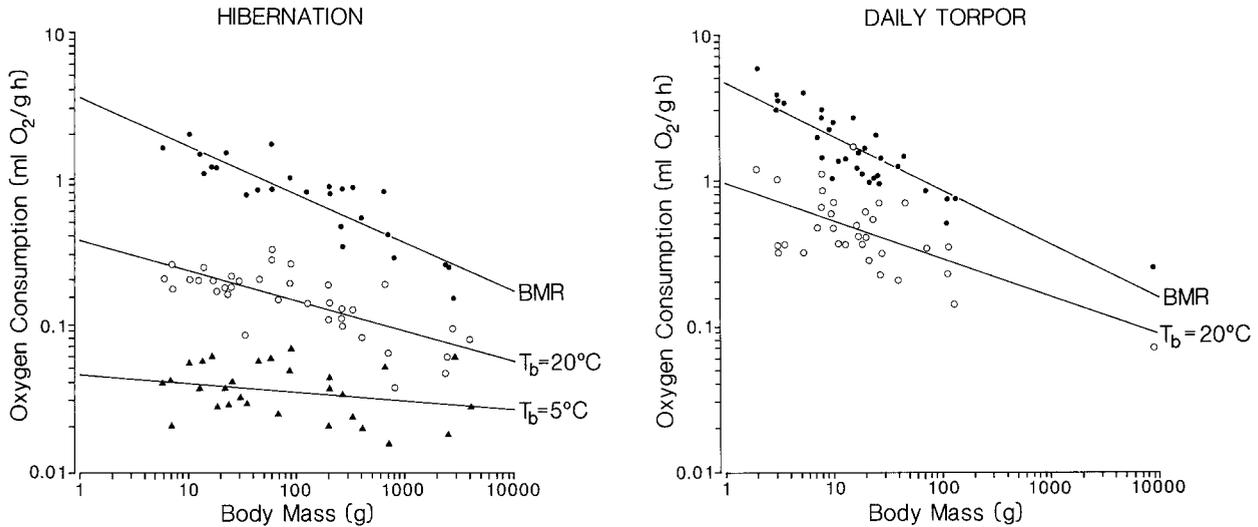


Fig. 2. The rate of oxygen consumption (\dot{V}_{O_2}) of hibernators and daily heterotherms during normothermia (BMR, ●), at $T_b = 20^\circ\text{C}$ (○), and at $T_b = 5^\circ\text{C}$ (▲) for hibernators only. Equations for the linear regressions are shown in Tables 3 and 4

Table 2. The relationship between body mass and the Q_{10} for the change of \dot{V}_{O_2} between normothermia and torpor

Group	T_b -range in torpor ($^\circ\text{C}$)	n	a	b	r^2	P
Hibernators	0.1–10	29	3.82 ± 0.19	-0.507 ± 0.096	0.51	<0.001
Daily heterotherms	10.1–30	33	2.53 ± 0.21	-0.248 ± 0.143	0.08	>0.07
Avian daily heterotherms	10.1–30	7	4.05 ± 0.84	-2.180 ± 1.132	0.42	>0.10
Mammalian daily heterotherms	10.1–30	26	2.27 ± 0.21	-0.093 ± 0.132	0.02	>0.10

Linear regressions were performed on log-transformed data and are described by the equation: $Q_{10} = a + b \log_{10} \text{Mass (g)}$; (a intercept \pm SE; b slope \pm SE). Slope and intercept for hibernators were significantly greater than in daily heterotherms ($P < 0.001$; t -test). Avian daily heterotherms may differ from the mammals because they show a steep increase in Q_{10} with decreasing mass, but not enough species were available to obtain a significant correlation. Data from Appendices 1 and 2. n = number of species

Table 3. Allometric relationship between basal metabolic rate (BMR) and body mass in heterothermic mammals and birds

Group	n	a	b	r^2	P
Hibernators	26	0.550 ± 0.081	-0.326 ± 0.036	0.77	<0.0001
Daily heterotherms	33	0.664 ± 0.052	-0.373 ± 0.036	0.77	<0.0001
Mammalian heterotherms	51	0.574 ± 0.045	-0.333 ± 0.024	0.80	<0.0001
Avian heterotherms	8	0.833 ± 0.111	-0.491 ± 0.127	0.71	<0.005
All heterotherms	59	0.635 ± 0.040	-0.359 ± 0.022	0.82	<0.0001

Only species in which BMR was measured (Appendices 1, 2) were included. Linear regressions were performed on log-transformed data and are described by the equation: $\log_{10} \text{BMR (ml O}_2\text{/g h)} = a + b \log_{10} \text{Mass (g)}$. Daily heterotherms did not differ significantly from hibernators in slope or intercept (t -test). Mammalian heterotherms had significantly smaller intercepts and slopes than avian heterotherms ($P < 0.01$; t -test). n = number of species; a = intercept \pm SE; b = slope \pm SE

of energy metabolism in many heterothermic endotherms. Because the Q_{10} for the change of \dot{V}_{O_2} between normothermia and torpor at high T_b 's is greater than 3 in hibernators it appears that temperature-induced reduction in the rate of biological reactions alone (Q_{10} 2–3) cannot explain the low metabolism. One likely explanation for these high Q_{10} 's is temperature-independent metabolic inhibition. Nevertheless, a reduction of metabolism

beyond temperature effects is not a general feature of torpor. The extent of metabolic reduction appears to depend on (i) pattern of torpor, (ii) body mass, and (iii) body temperature during torpor.

During deep hibernation ($T_b < 10^\circ\text{C}$), Q_{10} 's greater than 3 were only observed in small species. Thus, for small hibernators a further inhibition in \dot{V}_{O_2} beyond the reduction induced by temperature is apparently necessary, because they lack the large

Table 4. Allometric relationship between body mass and oxygen consumption during torpor in heterothermic mammals and birds

Group		<i>n</i>	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>P</i>
Daily heterotherms	<i>T</i> _b = 20 °C	33	-0.023 ± 0.085	-0.263 ± 0.059	0.39	< 0.0001
Hibernators	<i>T</i> _b = 20 °C	36	-0.428 ± 0.069	-0.206 ± 0.032	0.54	< 0.0001
Hibernators	<i>T</i> _b = 5 °C	29	-1.328 ± 0.086	-0.059 ± 0.042	0.068	> 0.1

Linear regressions were performed on log-transformed data and are described by the equation: $\log_{10} \dot{V}_{O_2}$ (ml O₂/g h) = *a* + *b* log₁₀ Mass (g). The \dot{V}_{O_2} 's were corrected to the *T*_b using the corresponding *Q*₁₀ values for each species and temperature. For correction of \dot{V}_{O_2} to *T*_b = 5 °C only species with *T*_b < 10 °C were included. For correction to *T*_b = 20 °C all species were included and the mean of several determinations was used for the regression. The \dot{V}_{O_2} during daily torpor was significantly higher than during hibernation at *T*_b = 20 °C (*P* < 0.001; *t*-test), the slopes were indistinguishable. *n* = number of species; *a* = intercept ± SE; *b* = slope ± SE

chemical energy stores in form of fat which are available to big hibernators. While chemical energy also can be stored by herbivores and granivores as food caches, this form of energy storage is not available to insectivorous species such as bats, which rely during hibernation solely on internal energy supplies. Small species that are unable to cache food must therefore reduce energy expenditure during winter by use of energy saving mechanisms during hibernation. Moreover, small species have higher BMR's than large species. If the reduction of metabolism during torpor would be the same in small and large species the mass-dependent difference in BMR should still be present in torpid animals. This means that if the thermal sensitivity of \dot{V}_{O_2} would not be a negative function of body mass, small species with their limited fat stores and high mass-specific metabolic rates would deplete energy reserves long before the end of the hibernating season.

In contrast to hibernators, daily heterotherms appear to be unable to reduce energy metabolism during torpor beyond the temperature-induced reductions of metabolic processes. *Q*₁₀ did not increase at small body mass and did not differ between high and low *T*_b's during torpor. However, birds that show daily torpor may differ from mammals in this respect because they show a relatively steep increase in *Q*₁₀ at small body masses (although the correlation was not significant because of small sample size. One must also consider difficulties in obtaining good BMR values in the very small hummingbirds which have extremely narrow thermo-neutral zones; high *Q*₁₀'s in the birds at very small masses may be artifacts of elevated BMR's). If metabolic inhibition is not available as an energy saving mechanism during daily torpor, small daily heterotherms also could achieve a decrease in daily energy expenditure by allowing *T*_b to fall to lower temperatures or to stay torpid for longer periods than larger species. The occurrence of daily torpor is more opportunistic than

seasonal hibernation and may happen at any time of the year during periods of food shortages and cold temperatures (Lynch et al. 1978; Geiser and Baudinette 1987). Because of the short torpor duration and the relatively long activity periods between successive torpor episodes, daily heterotherms, in contrast to hibernators, appear to rely largely on external energy sources even when they use torpor frequently.

The difference in energy metabolism between diurnal heterotherms and hibernators also becomes apparent when the metabolic rates at *T*_b = 20 °C are compared. Especially at small body mass the \dot{V}_{O_2} of the hibernators at *T*_b = 20 °C is only about half that of the diurnal heterotherms, whereas no significant difference in mass-specific BMR was observed. These results suggest that differences in energy metabolism at *T*_b = 20 °C in the two groups of heterotherms are due to differences in the reduction of metabolic processes during torpor. Because the correlation between body mass and \dot{V}_{O_2} during torpor at *T*_b = 20 °C is maintained in hibernators, but the slope is shallower than during normothermia, it appears that metabolic inhibition at high *T*_b in small species is more pronounced than in large hibernators. From *T*_b 20 to 5 °C, the slope relating \dot{V}_{O_2} and body mass is further decreased suggesting that over this range of temperatures large species rely on temperature effects; the utilization of additional metabolic inhibition at this temperature seems to be inversely related to body mass (Fig. 1).

The *Q*₁₀ for the change of \dot{V}_{O_2} over the temperature range between normothermia to torpor in the hibernators decreased with decreasing *T*_b in torpor. The *Q*₁₀ of oxygen consumption during torpor at different *T*_b's was smaller than the *Q*₁₀ between normothermia and torpor at all temperatures. This observation indicates that metabolic inhibition mainly occurs at high *T*_b's during entry into torpor, as previously suggested (Henshaw 1968). The *Q*₁₀ determined between normothermia

and torpor therefore does not represent a single slope but results from large Q_{10} 's at high T_b 's and small Q_{10} 's at low T_b 's.

Several studies report extremely high values of Q_{10} ($Q_{10} > 5$) during entry into torpor. These reports do not, however, take into account that entry into torpor usually occurs at low T_a and the metabolic rate of a normothermic animal may be many times larger than the BMR. If an animal enters torpor at low T_a it abandons the maintenance of a large ΔT between T_b and T_a (metabolic cost of thermoregulation) and the metabolic rate can fall to basal levels without lowering T_b . A further decrease in metabolism occurs with the passive cooling of the body. Therefore the high Q_{10} values during torpor entry at low T_a largely reflect the reduction in metabolism to BMR values rather than the reduction of \dot{V}_{O_2} by lowered T_b .

More direct evidence for metabolic inhibition than in endotherms is available for ectotherms. Dormant spadefoot toads (*Scaphiopus*) substantially reduce their metabolic rate when compared with awake individuals even under constant thermal conditions (Seymour 1973). Similarly, the oxygen consumption of the Australian arid zone crab *Holthuisana* was lowered when animals were transferred from hydrating to dehydrating conditions (MacMillen and Greenaway 1978). Thermally independent reduction in endotherms to this extent has not been observed to my knowledge.

The difference in metabolism during prolonged and daily torpor has some indirect implications. Duration of torpor is believed to be determined by production of metabolic wastes that cannot be excreted at low T_b 's or the depletion of nutrients that must be restored, and thus reflecting energy metabolism (Mrosovsky 1971; Lyman et al. 1982; French 1982). This view is supported by the increase in torpor duration that occurs when metabolic rate and T_b are decreased (Twente et al. 1977; Geiser 1986b; Geiser and Kenagy 1987). If the rate of energy metabolism determines torpor duration, the lack of metabolic inhibition in daily heterotherms and therefore high production of metabolites may partially explain the limitation to daily torpor. At T_b 's around 20 °C, i.e. those that are most frequent during daily torpor, torpor bouts in hibernators last only for 1–4 days in contrast to 1–2 weeks at T_b 's below 10 °C (Johansen and Krog 1959; Twente et al. 1977; French 1982; Geiser 1987). Because hibernators at that T_b expend only half the energy of diurnal heterotherms a great deal of the difference in torpor duration in the two groups may be due to differences in metabolism during torpor. However, the slightly in-

creasing mass-specific \dot{V}_{O_2} at low body masses at $T_b = 5$ °C in hibernators does not support the view that longer torpor duration in small hibernators, when compared with larger species, may reflect their smaller mass-specific energy metabolism during torpor (French 1985).

The increased Q_{10} of energy metabolism during entry into torpor raises the question about biochemical mechanisms that may explain the proposed metabolic inhibition. Malan (1986) hypothesized that the enhanced reduction in \dot{V}_{O_2} is due to the increase in CO_2 that is stored during entry into torpor (Snapp and Heller 1981) and the associated decrease in extracellular and intracellular pH at low T_b . This respiratory acidosis should inhibit glycolytic and respiratory enzyme activities and therefore whole animal energy metabolism. The release of CO_2 during arousals (Snapp and Heller 1981) further supports this hypothesis. However, Hand and Somero (1983) suggest that inhibition by low pH of glycolytic enzymes may not inhibit the whole animal energy production, but shift the fuel from glucose to lipids for energy substrates during torpor. Furthermore, the pH modulation of brown fat respiration at a high temperature (Malan 1986) is unlikely to be the only explanation for the distinct reduction of metabolism at the low T_b 's observed during torpor. While respiratory acidosis may contribute to reduction in metabolic activity, it is unlikely that changes in pH alone provide a satisfactory explanation for the extent of the metabolic reduction, and other short-term as well as long-term influences must be considered. For example, both glycolytic enzymes and mitochondrial respiratory enzymes have been shown to substantially increase Q_{10} during torpor as compared to active animals even under conditions of constant pH (Borgman and Moon 1976; Geiser and McMurchie 1984). Other possible mechanisms of energy savings are the increase in blood ketones during hibernation that may inhibit uptake of muscle glucose (Krilowicz 1985), or the low thyroid hormone concentrations during the hibernation season (Hulbert and Hudson 1976). The decrease in energy metabolism of hibernators that follows polyunsaturated dietary lipid treatment (Geiser and Kenagy 1987) is another example of metabolic reduction that is unlikely to be due to changes in cellular pH. These observations suggest that reduction of metabolism during hibernation is the result of a large number of factors which may operate on different time scales.

To my knowledge, the only example for a lack of exponential increase in mass-specific metabolism with body mass in animals is that of hiberna-

tors at low T_b . The metabolism of normothermic hibernators increased exponentially as expected. Because it is not known why BMR scales with mass to the 3/4 power in animals a final conclusion about the scaling of metabolism with mass to the almost 1 power in torpid hibernators is not possible.

Acknowledgements. I wish to thank B.M. Barnes, H.C. Heller, G.J. Kenagy, R.S. Seymour, J.S. Tsuji, and an anonymous referee for constructive criticisms on the manuscript. Supported by a Feodor Lynen Fellowship of the Alexander von Humboldt-Stiftung and a Flinders University Research Scholarship to the author, and by a NSF grant to G.J. Kenagy.

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Appendix 1. Body temperatures (T_b) and oxygen consumption (\dot{V}_{O_2}) of hibernators (species that enter prolonged torpor) during normothermia and torpor and the Q_{10} for \dot{V}_{O_2} between the two states

Group Species	T_{b1} (°C)	T_{b2} (°C)	BMR (ml O ₂ /g h)	\dot{V}_{O_2} torpor (ml O ₂ /g h)	Q_{10}	Mass (g)	Source
Monotremes							
<i>Tachyglossus aculeatus</i>	32.2	5.7	0.15	0.066	1.36	2800	Augee and Ealey (1968)
Marsupials							
<i>Cercartetus nanus</i>	34.9	11.6	0.86	0.19	1.92	@60	Bartholomew and Hudson (1962)
	34.9	20.1	0.86	0.21	2.6	@60	
	<i>Cercartetus concinnus</i>	34.4	6.6	1.20	0.034 (4)	3.6	18.6
34.4		13.2	1.20	0.058 (2)	4.17	18.6	
34.4		15.6	1.20	0.092 (3)	3.92	18.6	
<i>Cercartetus lepidus</i>	33.7	6.8	1.49	0.047 (2)	3.61	12.6	Present study; Geiser (1987)
	33.7	10.1	1.49	0.055 (3)	4.0	12.6	
	33.7	25.5	1.49	0.33 (2)	6.2	12.6	
<i>Burramys parvus</i>	36.1	6	0.83	0.063	2.35	44.3	Fleming (1985b)
<i>Acrobates pygmaeus</i>	34.9	7	1.08	0.07	2.66	14	Fleming (1985a)
Insectivores							
<i>Erinaceus europaeus</i>	35	5.2 ^a	0.433	0.016	3.0	@700	Thäti (1978)
	35	16 ^a	0.357	0.011	6.2	@700	
	35	7 ^a	0.47	0.022	2.98	@800	
<i>Tenrec ecaudatus</i>	33	16.5	0.27	0.025	4.2	1220	Kayser (1964); Hildwein (1970)
	33	16.9	0.31	0.02	5.5	360	
<i>Setifer setosus</i>	32	16.5	0.34	0.07	2.8	270	Kayser (1964); Hildwein (1972)
Bats							
<i>Myotis lucifugus</i>	37	2	2.0	0.022	3.6	5.2	Hock (1951)
	37	2	1.43	0.022	3.3	5.2	
	35	25	1.53	0.29	5.2	@6	
	35	5	1.53	0.06	2.94	@6	
<i>Myotis myotis</i>	37.5	4.5 ^a	1.45 ^b	0.04	2.96	25	Pohl (1961)
<i>Pipistrellus pipistrellus</i>	37	6 ^a	2.05 ^b	0.024	4.2	7.4	Kayser (1964)
<i>Nyctalus noctula</i>	37	5.3 ^a	1.47 ^b	0.03	3.4	23.8	Kayser (1964)
<i>Eptesicus fuscus</i>	36	10	2.0	0.1	3.2	10.4	Herreid and Schmidt-Nielsen (1966)

Appendix 1 (continued)

Group Species	T_{b1} (°C)	T_{b2} (°C)	BMR (ml O ₂ /g h)	\dot{V}_{O_2} torpor	Q ₁₀	Mass (g)	Source
<i>Tadarida brasiliensis</i>	36	10	1.2	0.1	2.6	16.9	Herreid and Schmidt-Nielsen (1966)
<i>Barbastella barbastellus</i>	37	4.5 ^a	2.08 ^b	0.04	3.37	7	Pohl (1961)
Rodents							
<i>Cricetus cricetus</i>	36.8	7.5 ^a	0.88	0.032	3.1	330	Kayser (1939, 1964)
<i>Mesocricetus auratus</i>	37	5	1.19 ^b	0.07	2.4	@90	Lyman (1948)
<i>Zapus princeps</i>	37.2	5.5	1.55 ^b	0.042	3.12	33.6	Cranford (1983)
	37.2	5.5	1.66 ^b	0.027	3.66	27.7	Cranford (1983)
<i>Zapus hudsonicus</i>	37.3	11 ^a	1.5	0.04	3.97	@25	Morrison and Ryser (1962);
	37.3	6 ^a	1.5	0.043	3.11	22.6	Muchalsky and Rybak (1978)
<i>Glis glis</i>	37.7	7 ^a	0.79	0.026	3.04	@200	Kayser (1939, 1961)
<i>Eliomys quercinus</i>	37	7.5 ^a	1.22 ^b	0.034	3.36	@70	Kayser (1964)
<i>Muscardinus avellanarius</i>	35.8	11 ^a	2.68	0.04	5.45	23.5	Kayser (1939, 1964)
	35.8	11 ^a	1.75 ^b	0.04	4.59	23.5	Kayser (1939, 1964)
<i>Marmota monax</i>	37	7 ^a	0.27 ^b	0.032	2.04	@4000	Lyman (1958)
<i>Marmota marmota</i>	37	10.5	0.26	0.018	2.74	2385	Kayser (1939, 1964)
<i>Marmota flaviventris</i>	36.6	7.5	0.25	0.022	2.3	@2500	Florant and Heller (1977)
<i>Spermophilus lateralis</i>	36.5	9.5	0.82	0.064	2.6	@200	Snapp and Heller (1981)
	37.2	10.9	0.629	0.068	2.3	@200	Snapp and Heller (1981)
	36.2	9.3	0.598	0.068	2.2	@200	Snapp and Heller (1981)
	37.4	13.9	0.867	0.084	2.7	@200	Snapp and Heller (1981)
	37.8	5.4	1.159	0.045	2.8	@200	Snapp and Heller (1981)
	37	9 ^a	0.85 ^b	0.03	3.2	@200	Steffen and Riedesel (1982)
<i>Spermophilus saturatus</i>	38	3.6	0.47 ^c	0.031 (7)	2.2	257	Present study; Kenagy and Vleck (1982)
	38	5.3	0.47 ^c	0.038 (7)	2.15	246	Present study; Kenagy and Vleck (1982)
	38	9.3	0.47 ^c	0.048 (7)	2.21	257	Present study; Kenagy and Vleck (1982)
<i>Spermophilus parryi</i>	37	7 ^a	0.8	0.063	2.3	650	Hock (1960)
<i>Spermophilus mohavensis</i>	35.8	21.3	0.85	0.15	3.3	260	Bartholomew and Hudson (1960)
<i>Spermophilus mexicanus</i>	36.2	8	0.85 ^b	0.06	2.56	@200	Newman and Cade (1964)
<i>Spermophilus tereticaudus</i>	35	11	0.72	0.048	3.09	@125	Bickler (1984)
	35	11	0.96	0.048	3.48	@125	Bickler (1984)
	36	26	0.78	0.23	3.42	@125	Bickler (1984)
<i>Spermophilus richardsonii</i>	37.1	5 ^a	0.53 ^c	0.02	2.78	@400	Wang (1978); Hudson and
	37.1	15 ^a	0.53 ^c	0.04	3.2	@400	Deavers (1973)
<i>Tamias striatus</i>	38.2	7.0	1.03	0.06	2.51	87	Wang and Hudson (1971)
<i>Eutamias amoenus</i>	38	1.2	1.69	0.042	2.72	60	Kenagy and Vleck (1982); Geiser and Kenagy (1987)
Birds							
<i>Phalaenoptilus nuttallii</i>	37	20	0.788	0.086	3.68	35	Withers (1977)
	37	10	0.788	0.05	2.77	35	Withers (1977)

Values in parentheses indicate the number of individuals used in that measurement of \dot{V}_{O_2} and T_b during torpor

T_{b1} = Body temperature during normothermia; T_{b2} = body temperature during torpor

^a Body temperature was calculated from given air temperatures + 1 °C

^b BMR was calculated from the equations of Hayssen and Lacy (1985) for the particular order or family

^c BMR was mass corrected using the equations of Hayssen and Lacy (1985) for the particular order or family

Appendix 2. Body temperatures (T_b) and oxygen consumption (\dot{V}_{O_2}) of daily heterotherms (species that enter daily torpor) during normothermia and torpor and the Q_{10} for \dot{V}_{O_2} between the two states

Group <i>Species</i>	T_{b1} (°C)	T_{b2} (°C)	BMR (ml O ₂ /g h)	\dot{V}_{O_2} torpor (ml O ₂ /g h)	Q_{10}	Mass (g)	Source
Marsupials							
<i>Marmosa</i> sp.	34.7	16	1.4	0.25	2.51	13	Morrison and McNab (1962)
<i>Sminthopsis crassicaudata</i>	34.1	16.5	1.22	0.40 (2)	1.88	17.3	Present study; Geiser and Baudinette (1987)
	34.3	18.3	1.20	0.27 (4)	2.54	17.7	Present study; Geiser and Baudinette (1987)
	34.1	25.8	1.22	0.81 (4)	1.64	17.3	Present study; Geiser and Baudinette (1987)
<i>Sminthopsis macroura</i>	33.9	17.4 ^d	1.02	0.57 (5)	1.42	22.0	Present study; Geiser and Baudinette (1987)
	34.0	12.7 ^d	1.03	0.29 (3)	1.81	26.9	Present study; Geiser and Baudinette (1987)
<i>Sminthopsis murina</i>	35	15	1.13	0.25	2.1	19	Geiser et al. (1984)
<i>Antechinomys laniger</i>	34.8	15.9	0.98	0.15 (2)	2.69	27.4	Present study; Geiser (1986b)
	34.8	25.8	0.98	0.38 (2)	2.86	27.4	Present study; Geiser (1986b)
<i>Dasyercus cristicauda</i>	35.5	23	0.5	0.27	1.63	113	Kennedy and McFarlane (1971)
<i>Dasyuroides byrnei</i>	34.3	24.4	0.74	0.44 (4)	1.68	116	Present study; Geiser et al. (1986)
	35.5	21.5	0.84	0.36 (2)	1.83	73	Present study; Geiser et al. (1986)
<i>Planigale gilesi</i>	32.6	17.5	1.43	0.54 (2)	1.91	8.3	Present study
<i>Planigale maculata</i>	34.2	19.6	1.01	0.45	1.74	10	Morton and Lee (1978)
<i>Ningau i yvonneae</i>	34.4	16.6	1.35	0.26 (3)	2.52	11.6	Present study
<i>Antechinus stuartii</i>	34.1	26.6	1.06	0.84 (4)	1.36	26.1	Present study
<i>Petaurus breviceps</i>	36.3	17	0.74	0.1	2.82	132	Fleming (1980)
Insectivores							
<i>Crocidura russula</i>	35.8	23	2.4	0.9	2.2	10	Nagel (1985)
<i>Suncus etruscus</i>	34.7	14	5.75	0.6	2.98	2	Frey (1979, 1980); Fons and Sicard (1976)
Bats							
<i>Nyctimene albiventer</i>	37	28.6	1.43	0.67	2.46	28	Bartholomew et al. (1970)
Rodents							
<i>Peromyscus leucopus</i>	36.7	17.6	1.66	0.53	1.82	20	Hill (1975); Deavers and Hudson (1981)
<i>Peromyscus eremicus</i>	37	16	1.56	0.3	2.2	17.4	MacMillen (1965)
<i>Phodopus sungorus</i>	37	20.7	2.06	1.0	1.55	25	Heldmaier and Steinlechner (1981 a, b)
<i>Perognathus hispidus</i>	38	17.1	1.25	0.15	2.75	40	Wang and Hudson (1970)
<i>Perognathus californicus</i>	38	15	0.97	0.20	2.0	22	Tucker (1965)
<i>Mus musculus</i>	37.4	19	1.47	0.65	2.3	45.5	Hudson and Scott (1979)
<i>Baiomys taylori</i>	35.5	22	1.95	0.55	2.5	7.3	Hudson (1965)
<i>Reithrodontomys megalotis longicaudatus</i>	37.5	12	2.63	0.5	1.9	7.9	Thompson (1985)
<i>Reithrodontomys megalotis rarus</i>	37.3	15	2.23	0.4	2.2	9.5	Thompson (1985)
Carnivores							
<i>Taxidea taxus</i>	37	28	0.26	0.13	2.15	9000	Harlow (1981)

Appendix 2 (continued)

Group Species	T_{b1} (°C)	T_{b2} (°C)	BMR (ml O ₂ /g h)	\dot{V}_{O_2} torpor	Q ₁₀	Mass (g)	Source
Birds							
<i>Eulampis jugularis</i>	40	18	3.0	1.0	1.65	8	Hainsworth and Wolf (1970)
<i>Archilochus alexandri</i>	40	23 ^a	3.5	0.45	3.3	3.2	Lasiewski (1963)
	40	17 ^a	3.5	0.20	3.47	3.2	Lasiewski (1963)
<i>Calypte costae</i>	40	21 ^a	3.0	0.39	2.9	3.1	Lasiewski (1963)
<i>Calypte anna</i>	40	24 ^a	3.85	0.54	3.4	5.4	Lasiewski (1963)
	40	16 ^a	3.85	0.17	3.66	5.4	Lasiewski (1963)
<i>Selasphorus rufus</i>	40	22.5 ^a	3.35	0.48	3.04	3.6	Lasiewski (1963)
<i>Selasphorus sasin</i>	40	23 ^a	3.8	1.24	1.93	3.1	Lasiewski (1963); Pearson (1950)
<i>Manacus vitellinus</i>	37.9	26.8	2.69	2.0	1.3	15.5	Bartholomew et al. (1983)

Values in parentheses indicate the number of individuals used in that measurement of \dot{V}_{O_2} and T_b during torpor

T_{b1} = Body temperature during normothermia; T_{b2} = body temperature during torpor

^a Body temperature was calculated from given air temperatures + 1 °C

^d Body temperature was estimated by extrapolating the \dot{V}_{O_2} below the minimum T_b to the abscissa assuming that $T_b = T_a$ when $\dot{V}_{O_2} = 0$

Appendix 3a. The Q₁₀ of oxygen consumption (\dot{V}_{O_2}) of hibernators between different body temperatures (T_b) during torpor

Group Species	T_b range (°C)	Q ₁₀	Mass (g)	Source
Marsupials				
<i>Cercartetus nanus</i>	11.6–20.1	1.01	60	Bartholomew and Hudson (1962)
<i>Cercartetus concinnus</i>	6.6–15.6	3.02	18.6	Present study; Geiser (1987)
<i>Cercartetus lepidus</i>	6.8–25.5	2.85	12.6	Present study; Geiser (1987)
Insectivores				
<i>Setifer setosus</i>	–	2.5	300	Hildwein (1970)
<i>Tenrec ecaudatus</i>	15.2–28	2.1	360	Kayser (1960)
Bats				
<i>Myotis lucifugus</i>	5 –25	2.1	5	Henshaw (1968)
Rodents				
<i>Spermophilus lateralis</i>	3 –13	2.39	200	Hammel et al. (1968)
	5.4– 9.5	2.36	200	Snapp and Heller (1981)
<i>Spermophilus saturatus</i>	3.6– 9.3	2.12	260	Present study
<i>Spermophilus tereticaudus</i>	11 –26	2.84	125	Bickler (1984)
<i>Spermophilus richardsonii</i>	2 –15	2.0	400	Wang (1978)
Birds				
<i>Phalaenoptilus nuttallii</i>	10 –20	2.77	35	Withers (1977)

Mean Q₁₀: 2.3 ± 0.6

Appendix 3b. The Q_{10} of oxygen consumption (\dot{V}_{O_2}) of daily heterotherms between different body temperatures (T_b) during torpor

Group <i>Species</i>	T_b range (°C)	Q_{10}	Mass (g)	Source
Marsupials				
<i>Sminthopsis crassicaudata</i>	16.5–25.8	2.14	17.3	Present study; Geiser and Baudinette (1987)
<i>Sminthopsis macroura</i>	15 –24	1.8	26.9	Present study; Geiser and Baudinette (1987)
<i>Antechinomys laniger</i>	15.9–25.8	2.55	27.8	Present study; Geiser (1986b)
<i>Antechinus stuartii</i>	–	2.7	25	Wallis (1976)
Rodents				
<i>Perognathus californicus</i>	15 –30	2.4	22	Tucker (1965)
<i>Baiomys tailori</i>	15 –30	2.1	6.4	Hudson (1965)
Insectivores				
<i>Suncus etruscus</i>	15 –21	1.6	2	Frey (1979, 1980)
Birds				
<i>Archilochus alexandri</i>	17 –23	3.86	3.2	Lasiewski (1963)
<i>Calypte anna</i>	16 –24	4.24	3.6	Lasiewski (1963)

Mean Q_{10} : 2.6 ± 0.9