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## Invited Perspectives in Physiological Zoology

### Hibernation versus Daily Torpor in Mammals and Birds: Physiological Variables and Classification of Torpor Patterns

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#### Abstract

*Hibernation and daily torpor are usually considered to be two distinct patterns of heterothermia. In the present comparison we evaluated (1) whether physiological variables of torpor from 104 avian and mammalian species warrant the distinction between hibernation and daily torpor as two different states of torpor and (2), if so, whether this distinction is best based on maximum torpor bout duration, minimum body temperature ( $T_b$ ), minimum metabolic rate during torpor, or the reduction of metabolic rate expressed as percentage of basal metabolism (BMR). Initially, animals were grouped into species displaying either daily torpor or prolonged torpor (hibernation) according to observations from original sources. Both cluster and discriminant analyses supported this division, and further analyses were therefore based on these two groups. Frequency distributions for all variables tested differed significantly ( $P < 0.001$ ) between daily torpor and hibernation. The average maximum torpor bout duration was 355.3 h in hibernators and 11.2 h in daily heterotherms. Mean minimum  $T_b$ 's were lower in hibernators than in daily heterotherms ( $5.8^\circ\text{C}$  vs.  $17.4^\circ\text{C}$ ) as were minimum metabolic rates measured as rate of oxygen consumption ( $\dot{V}O_2$ ;  $0.037$  vs.  $0.535\text{ mL O}_2\text{ g}^{-1}\text{h}^{-1}$ ), and the metabolic rate reduction expressed as percentage of BMR ( $5.1\%$  vs.  $29.5\%$ ). Furthermore, mean body weights were significantly higher in hibernators ( $2384\text{ g}$ ) than in daily heterotherms ( $253\text{ g}$ ;  $P < 0.001$ ). Thus, the comparisons of several physiological variables appear to justify a distinction between the two torpor patterns. However, of all variables tested, only the frequency distributions of maximum torpor bout duration ( $1.5\text{--}22\text{ h}$  for daily torpor;  $96\text{--}1,080\text{ h}$  for hibernation) showed a clear gap between daily heterotherms and hibernators.*

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*The minimum  $\dot{V}O_2$  also distinguished clearly between daily heterotherms and hibernators. All other variables, including minimum  $T_b$  during torpor, did not show a complete separation between the two patterns of heterothermia. We therefore suggest that classification of torpor patterns should be based on the duration of torpor bouts or the minimum  $\dot{V}O_2$  during torpor.*

## Introduction

Torpor in heterothermic mammals and birds is usually divided into two general categories. One of these is referred to as shallow, daily torpor with minimum body temperatures ( $T_b$ 's) between approximately 10°C and 25°C and torpor bouts of less than 24 h (Hudson 1973). The other category, hibernation, is usually characterized by  $T_b$ 's of less than 10°C and torpor bouts of several days or weeks (Hudson 1973; Dawson 1989; Wang 1989). Thus, classifications of species as either hibernators or daily heterotherms (those species exhibiting daily torpor) are typically based on two variables only: the minimum  $T_b$  during torpor and the duration of torpor bouts. Other variables, which may also differ between groups, such as the metabolic rate (MR), the degree of metabolic reduction expressed as percentage of basal metabolic rate (BMR), or body weight (BW) (Bartholomew 1982; Geiser 1988), are seldom applied.

The conventional classifications of heterothermic animals are often confounded by overlapping values. In several species that display daily torpor,  $T_b$ 's below 10°C have been reported (Dawson and Hudson 1970; Carpenter 1974; Reinertsen 1983; Withers, Richardson, and Wooller 1990), and some hibernators maintain  $T_b$ 's well above 10°C during torpor (Lachiver 1958; Scholl 1974; Watts et al. 1981; Fowler and Racey 1988). Furthermore, hibernators typically exhibit short bouts of torpor at the onset of the hibernation season and subsequently increase the duration of torpor bouts (see, e.g., French 1986; Fowler and Racey 1990). It is therefore questionable whether an arbitrary classification of heterothermic species relying only on  $T_b$  and the duration of torpor bouts is justified or whether other physiological variables would better characterize patterns of torpor.

In the present analyses we investigated (1) whether heterothermic endotherms do comprise two distinct groups and (2), if so, which physiological variables are most appropriate for classification of the groups. For these analyses we compared body weight, the minimum  $T_b$  that is metabolically defended during torpor, minimum MR ( $\dot{V}O_2$ ), reduction of minimum  $\dot{V}O_2$  expressed as percentage of BMR, and maximum duration of torpor bouts of

104 avian and mammalian heterothermic species exhibiting either daily torpor or hibernation.

## Data Selection and Statistics

Data on BW, minimum  $T_b$  during torpor, minimum  $\dot{V}O_2$  during torpor ( $\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ), degree of reduction of minimum  $\dot{V}O_2$  expressed as percentage of BMR, and the longest torpor bout from 20 birds and 83 mammals were collected from the literature; data for one mammal are unpublished observations of the authors (app. A, B). Only species in which the MR during torpor falls below the BMR were used in the comparison. Because hibernating species may display daily torpor at high ambient temperature ( $T_a$ ) or at the beginning of the hibernation season, only data on long torpor bouts at low  $T_a$ , MRs, and minimum  $T_b$ 's measured during prolonged periods of torpor were compared. If possible, mean values were used; individual determinations were used only when mean values were not available. Appendix B includes two large carnivores among the species exhibiting prolonged bouts of torpor. Although torpor in these species, particularly in the black bear *Ursus americanus*, is generally viewed as winter anorexia rather than hibernation, we still refer to the entire group, for reasons of simplicity, as hibernators. None of the statistical differences stated below or the conclusions drawn from the present analysis are affected by the inclusion of these carnivores. We considered avoiding the term "hibernation" for this analysis because of its seasonal connotation (Bartholomew 1982) and replacing it with "prolonged heterothermy," but in the end we decided to retain "hibernation" because it is a term that is widely used for describing prolonged torpor in any season, is deeply ingrained in the literature, is shorter, and sounds less awkward.

Data were analyzed in several steps. Initially, species were divided into two preliminary subgroups that comprised species exhibiting daily torpor (app. A) and species exhibiting prolonged torpor (app. B) according to the information provided in the original sources and as shown in the appendices. To test whether this classification is valid, combined data from both appendices were subjected to hierarchical cluster analysis with the average linkage between groups method. All variables listed in the appendices were transformed to  $z$  scores and entered in this procedure. Cluster analysis had to be restricted to those (58 species) for which complete sets of data were available. Therefore, we subsequently employed discriminant analysis, with overall variable means substituting for missing values, to further test the

classification of all (104) species. Variables that were not normally distributed were log transformed. All variables were entered simultaneously.

Since both cluster and discriminant analyses supported the preliminary grouping of species, appendices A and B remained unchanged. Because several variables such as  $T_b$  and MR were significantly correlated with each other, their separate contributions to the discriminant function could not be assessed from discriminant function variables alone. Therefore, frequency distributions of each variable were calculated separately for daily heterotherms and hibernators (classification according to app. A and B) and plotted on the same scale. To test for differences in frequency distribution between species showing daily and prolonged torpor, we used the Kolmogorov-Smirnov test. In addition, differences between physiological variables in both groups were tested by applying the Mann-Whitney  $U$ -test. We also determined the arithmetic mean, standard error of the mean (SE), median, range, and skewness of the distribution for all variables. To increase resolution of variation, frequency distributions were also presented on a logarithmic scale in most cases. Numerical values in the text are expressed as means  $\pm$  SE unless otherwise stated.

To test for possible correlations between body mass and minimum  $T_b$ , minimum  $\dot{V}O_2$  (mL O<sub>2</sub> g<sup>-1</sup>h<sup>-1</sup>), minimum  $\dot{V}O_2$  (percentage of BMR), and torpor bout duration, we calculated Spearman's rank-correlation coefficient ( $R$ ) for each variable versus BW. Significant correlations were fitted with reduced major axis linear regressions. Since many of the variables analyzed here were determined under different experimental conditions and in different individuals, we did not further interpret  $R$  for other interrelations between variables. Statistics were performed with the programs STATGRAF and SPSS.

## Analysis and Interpretation

Hierarchical cluster analysis of combined data from the appendices showed a sharp increase of the squared Euclidian distance after creation of three subgroups. One of the suggested subgroups consisted of a single avian species (*Manacus vitellinus*), which had the highest minimum  $\dot{V}O_2$  of the species for which all variables were available. Apart from this exception, the two other groups indicated by cluster analysis were completely identical to the preliminary classification in appendices A and B. Inclusion of a factor coding for phylogenetic groups led to a steady rise in distant coefficients, without the creation of any apparently meaningful clusters. It is important

that none of the agglomeration steps resulted in subgroups that showed considerable overlap with actual phylogenetic groups.

Similar to cluster analysis, discriminant analysis based on all physiological variables available supported the grouping in appendices A and B in 103 out of 104 species. The only suggested misclassification concerned the inclusion of *Perognathus longimembris* in the hibernators (app. B). In this species, classification was, however, based on only two out of five variables, namely, BW and minimum  $T_b$  during torpor.

Discriminant analysis showed a high association between discriminant scores and groups (canonical correlation = 0.92,  $P < 0.0001$ ). All variable means were significantly different between predicted groups ( $P < 0.0001$ , Wilks's lambda). Within-group correlations between physiological variables and discriminant functions were 0.90 for torpor bout duration,  $-0.60$  for minimum  $T_b$ ,  $-0.44$  for minimum  $\dot{V}O_2$ ,  $-0.39$  for minimum  $\dot{V}O_2$  expressed as percentage of BMR, and  $0.22$  for BW. Taken together, results from cluster and discriminant analyses clearly supported the classification of species into two distinct patterns of torpor, as presented in appendices A and B. None of the few classifications questioned by these procedures appeared to warrant the creation of additional groups or regrouping of species. However, discriminant analysis suggested a different contribution of the physiological variables to the separation of groups. Assessment of these contributions was confounded by between-variable correlations, in particular between minimum  $\dot{V}O_2$  and minimum  $\dot{V}O_2$  expressed as percentage of BMR ( $R = 0.67$ ) as well as between minimum  $\dot{V}O_2$  expressed as percentage of BMR and minimum  $T_b$  ( $R = 0.59$ ). Therefore, details on frequency distributions and statistical differences between the two groups of each variable are provided below.

### Body Weight

The mean BW was  $253 \pm 166$  g ( $n = 57$ ) in daily heterotherms and  $2,384 \pm 1,713$  g ( $n = 47$ ) in hibernators (table 1). Although BWs in both groups showed a very pronounced overlap (fig. 1), hibernators had significantly higher ( $P < 0.001$ ) BWs. Most daily heterotherms had a BW of less than 100 g, whereas most hibernators had BWs between 10 and 1,000 g. The mean BW of species was elevated in both groups by a few species (all carnivores) that weighed 1,000 g or more. However, BWs were still statistically different ( $P < 0.001$ ) when all carnivores were omitted. Avian daily heterotherms ( $22.4 \pm 5.5$  g) were lighter ( $U$ -test,  $P < 0.05$ ) than mammalian daily heterotherms. Frequency distributions in both hibernators and daily

TABLE 1

*Summary of Physiological Variables of Heterothermic Endotherms*

Variable	Hibernators	Daily Heterotherms
BW (g):		
<i>N</i> .....	47	57
Mean .....	2,384	253
Median .....	85	19
SE .....	1,713	166
Range .....	5.2–80,000	2–9,000
Minimum $T_b$ (°C):		
<i>N</i> .....	37	49
Mean .....	5.8	17.4
Median .....	4.7	16.7
SE .....	1.2	.8
Range .....	–2.9–32.3	5–29.6
Minimum $\dot{V}O_2$ (mL g <sup>–1</sup> h <sup>–1</sup> ):		
<i>N</i> .....	36	49
Mean .....	.037	.535
Median .....	.033	.45
SE .....	.003	.056
Range .....	.013–.07	.07–2.05
Minimum $\dot{V}O_2$ (percentage of BMR):		
<i>N</i> .....	36	44
Mean .....	5.1	29.5
Median .....	4.0	24.5
SE .....	.7	2.7
Range .....	1–20	4.4–67
Duration of torpor bouts (h):		
<i>N</i> .....	39	43
Mean .....	355	11.2
Median .....	280	10.5
SE .....	37.7	.7
Range .....	96–1,080	1.5–22

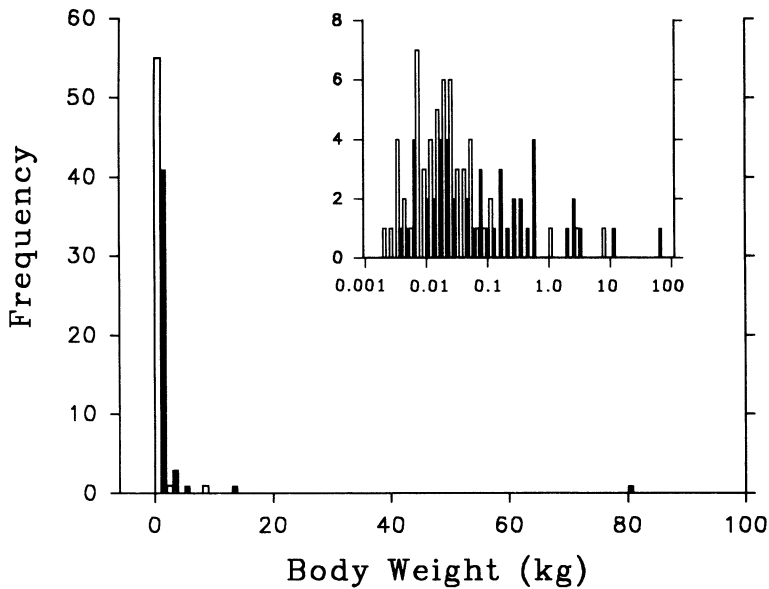


Fig. 1. Frequency distributions of BWs in hibernators (solid bars) and species exhibiting daily torpor (open bars). Body weights varied between 5.2 g and 80 kg in hibernators (median 85 g) and between 2 g and 9 kg in daily heterotherms (median 19 g). The inset graph shows the same distribution on a logarithmic scale. Body weights in hibernators were significantly ( $P < 0.001$ ) greater than in daily heterotherms.

heterotherms were skewed to the right (daily torpor, skewness 6.54; hibernation, skewness 6.56). In other words, in both groups most species were found toward the lower end of the BW scale.

Of all variables compared, BWs of hibernators and daily heterotherms showed the largest overlap. Apparently, neither BW nor weight-dependent metabolic characteristics of a species determine the use of a certain pattern of torpor. Nevertheless, the present analysis revealed a significant trend toward smaller BWs in species exhibiting daily torpor. Moreover, heterothermic birds, which all display daily torpor except for one species, were even smaller than mammalian daily heterotherms. A priori, the opposite relation might be expected; that is, small endotherms with relatively high energetic costs for thermoregulation during normothermia should display the most pronounced reduction of metabolism during torpor, namely, hibernation. The smaller BWs in species showing daily torpor may be related to the high frequency of arousals from torpor that is inherent in this pattern of heterothermia (Bartholomew 1982). Both energetic costs for heat pro-



duction and time spent for warm-up increase with body mass, which may act as a selective pressure against too-frequent alternations between torpor and normothermia in large animals. Moreover, it has been demonstrated that the relative amount of body fat reserves increases with BW (Morrison 1960). Therefore, as long as environmental conditions do not exclude such a strategy, the continuation of foraging activity and food uptake in combination with daily torpor should be particularly favorable for small animals with low internal energy stores. This need is easier to satisfy in small animals with lower absolute energy requirements than in large endotherms, for whom prolonged torpor, together with fat or food stores, appears to be more appropriate.

In both hibernators and daily heterotherms, body mass was skewed to the right. This supports the view that the use of torpor, daily or prolonged, is of particular importance for small endotherms, whereas most large species can survive adverse environmental conditions by employing other strategies.

#### *Minimum $T_b$ during Torpor*

The minimum  $T_b$  of daily heterotherms differed significantly from that of the hibernators ( $P < 0.001$ ; fig. 2). Most minimum  $T_b$ 's of daily heterotherms ranged between  $10^\circ$  and  $30^\circ\text{C}$ , with a mean of  $17.4^\circ \pm 0.8^\circ\text{C}$  ( $n = 49$ ; table 1), and minimum  $T_b$ 's of birds ( $18.6^\circ \pm 2.0^\circ\text{C}$ ;  $n = 13$ ) and mammals ( $17.0^\circ \pm 0.9^\circ\text{C}$ ;  $n = 36$ ) did not differ. Minimum  $T_b$ 's of most hibernators ranged from  $-3^\circ$  to  $16^\circ\text{C}$ , with a mean of  $5.8^\circ \pm 1.2^\circ\text{C}$  ( $n = 37$ ). The minimum  $T_b$  of the only known avian hibernator, the poorwill (*Phalaenoptilus nuttallii*), was  $6.0^\circ\text{C}$ , which is very similar to the group mean. There was some overlap between the distributions of hibernators and daily heterotherms, with minimum  $T_b$ 's during daily torpor falling as low as  $5^\circ\text{C}$  in honey possums (*Tarsipes rostratus*) and remaining as high as  $32.3^\circ\text{C}$  in hibernating black bears (*Ursus americanus*). The frequency distribution of minimum  $T_b$ 's during daily torpor was close to normal (skewness 0.35), whereas minimum  $T_b$ 's during hibernation were skewed to the right (skewness 2.44), mainly because of high minimum  $T_b$ 's in the European badger (*Meles meles*) and the black bear (*U. americanus*). The minimum  $T_b$  increased with BW in daily heterotherms ( $R = 0.31$ ,  $P < 0.05$ ; fig. 3), but this relationship was not significant in hibernators ( $R = 0.19$ , n.s.). Overlap of minimum  $T_b$ 's between daily heterotherms and hibernators occurred in very small and very large species (fig. 3).

Although frequently used in the past for classification of torpor patterns, the minimum  $T_b$  was not always a reliable marker for the distinction between

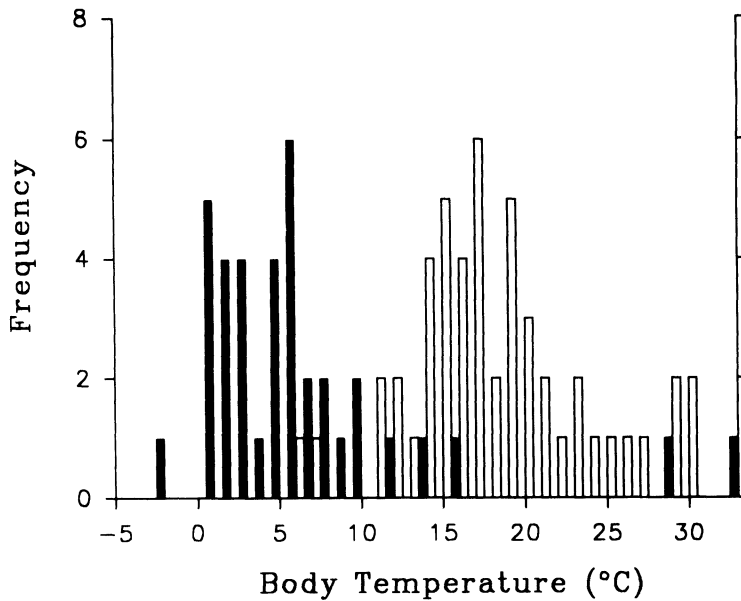


Fig. 2. Frequency distributions of minimum  $T_b$ 's in hibernators (solid bars) and daily heterotherms (open bars). Minimum  $T_b$ 's ranged from  $-2.9^\circ$  to  $32.3^\circ\text{C}$  (median  $4.7^\circ\text{C}$ ) in hibernators and from  $5^\circ$  to  $29.6^\circ\text{C}$  (median  $16.7^\circ\text{C}$ ) in daily heterotherms.

hibernation and daily torpor. Even when the data from exceptionally large animals (*M. meles*,  $28.3^\circ\text{C}$ ; *U. americanus*,  $32.3^\circ\text{C}$ ) were omitted, more than 25% of all hibernating species compared here had intermediate minimum  $T_b$ 's during torpor of between  $7^\circ$  and  $16^\circ\text{C}$  (see figs. 2, 3) and therefore could not be identified as hibernators or daily heterotherms on the basis of minimum  $T_b$  alone. This observation also emphasizes that the extremely low  $T_b$ 's found in some deep hibernators (Lyman 1948) are not a prerequisite for the occurrence of prolonged bouts of torpor.

The BWs were not randomly distributed in hibernators and daily heterotherms whose minimum  $T_b$ 's overlapped. All daily heterotherms with  $T_b$ 's below  $10^\circ\text{C}$  were among the animals with the lowest BWs ( $\leq 10$  g). On the other hand, all minimum  $T_b$ 's above  $10^\circ\text{C}$  in hibernators were observed in relatively large species ( $>80$  g; fig. 3). This observation is consistent with the argument above that energy and time constraints for arousal from torpor, which depend on BW as well as  $T_b$  during torpor (Hainsworth and Wolf 1970), may be selecting factors of torpor patterns in endotherms.

Purely physical constraints may also limit the lowering of  $T_b$  in very large species. The allometric decrease of thermal conductance with increasing

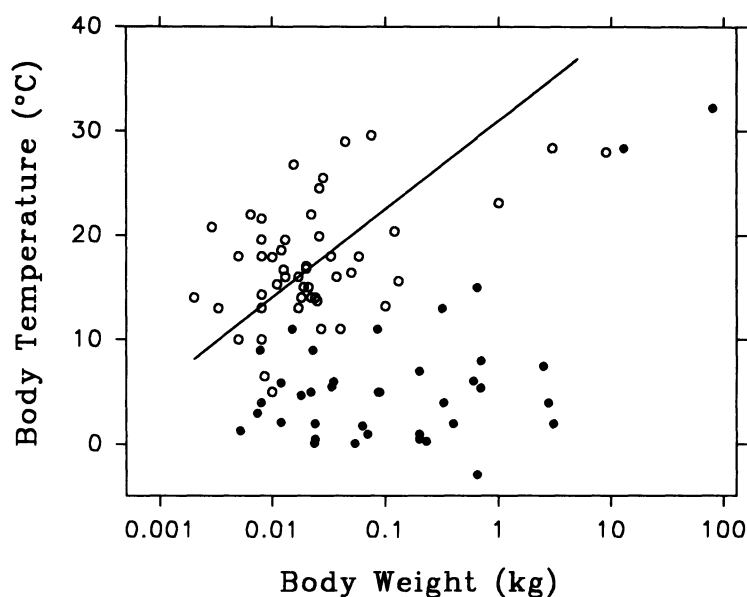


Fig. 3. The relationship between BW and minimum  $T_b$  of daily heterotherms (open circles) and hibernators (solid circles). The minimum  $T_b$  increased with BW in daily heterotherms ( $T_b = 5.57 + 8.49 \log_{10} BW$ ), but this relationship was not significant in hibernators.

BW (Herreid and Kessel 1967) would result in  $T_b$ 's during torpor that, in theory, range from as little as  $0.1^\circ\text{C}$  above  $T_a$  in a 5.2-g hibernator to  $10.8^\circ\text{C}$  above  $T_a$  in a 80-kg hibernator, even at a constant minimum  $\dot{V}\text{O}_2$  of  $0.037 \text{ mL O}_2 \text{ g}^{-1}\text{h}^{-1}$  during hibernation. These minimum gradients between  $T_b$  and  $T_a$  were calculated according to the Scholander-Irving model for thermoregulation, describing the relation between MR, thermal conductance ( $C$ ), and  $T_b - T_a$  gradients under steady state conditions by the formula  $\text{MR} = C(T_b - T_a)$  (Scholander et al. 1950). This relation should principally apply not only to normothermic but also to torpid animals at thermoequilibrium, that is, at constant  $T_a$ ,  $T_b$ , and MR. However, this makes no assumption as to the mechanism of how the MR is reduced during torpor. Metabolic rate was assumed to be  $0.037 \text{ mL O}_2 \text{ g}^{-1}\text{h}^{-1}$ , which is the mean minimum  $\dot{V}\text{O}_2$  of hibernators (table 1). Thermal conductance was estimated by the allometric relation for normothermic mammals (Hayssen and Lacy 1985) and yields  $0.00343 \text{ mL O}_2 \text{ g}^{-1}\text{h}^{-1} \text{ }^\circ\text{C}^{-1}$  in the case of the largest hibernator (*U. americanus*, 80 kg). The smallest theoretical thermal gradient calculated from  $T_b - T_a = \text{MR}/C$  is  $10.8^\circ\text{C}$  for this species. The gradient would be even more pronounced if a reduction of  $C$  during torpor were assumed. Data

from various hibernators support this prediction, as the minimum thermal gradient between body and environment increases with BW (Morrison 1960; Kayser 1964). However, the present comparison showed only weak correlations ( $R = 0.19\text{--}0.31$ ) between minimum  $T_b$  and BW in the two groups. This does not necessarily refute earlier studies because data compared here were determined under different environmental conditions. While BW may well determine how closely  $T_b$  can approach  $T_a$  during daily torpor or hibernation, BW alone does not explain the big differences in minimum  $T_b$ 's between species of similar BW.

The minimum  $T_b$ 's of most hibernators were close to  $0^\circ\text{C}$ , and the distribution was skewed to the right. This indicates that the minimum  $T_b$  of many hibernators is limited by the freezing point of body fluids, which prevents a further drop of  $T_b$ . The reason that more hibernators do not show high minimum  $T_b$ 's may be that they would frequently be required to defend  $T_b$  metabolically during torpor because the  $T_a$  in many hibernacula is around or slightly above  $0^\circ\text{C}$  (Wahlhovd 1976; Wang 1978; Arnold 1993).

In contrast to hibernators, daily heterotherms show a nearly normal distribution in their minimum  $T_b$ 's, perhaps because they defend their  $T_b$ 's well above  $0^\circ\text{C}$  and never reach the freezing point for body fluids. It is therefore likely that factors other than or additional to environmental temperature are important for selection of the minimum  $T_b$  in daily heterotherms.

#### *Minimum $\dot{V}O_2$ during Torpor and the Minimum $\dot{V}O_2$ Expressed as Percentage of BMR*

The mean minimum  $\dot{V}O_2$  in daily heterotherms ( $0.535 \pm 0.056 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ,  $n = 49$ ) was more than 10-fold that of hibernators ( $0.037 \pm 0.003 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ,  $n = 36$ ,  $P < 0.001$ ; table 1). The minimum  $\dot{V}O_2$  showed very little overlap between the two groups. Moreover, avian daily heterotherms had a higher minimum  $\dot{V}O_2$  ( $0.728 \pm 0.167 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ,  $n = 19$ ) than mammalian daily heterotherms ( $0.412 \pm 0.044 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ,  $n = 30$ ;  $U$ -test for difference between birds and mammals,  $P < 0.01$ ). The minimum  $\dot{V}O_2$  during daily torpor was spread over a wide range of values, whereas  $\dot{V}O_2$  during hibernation was narrowly clustered around the mean (fig. 4). In daily heterotherms, the frequency distribution of the minimum  $\dot{V}O_2$  was somewhat skewed to the right (skewness 1.98); hibernators showed a normal distribution (skewness 0.48). Metabolic rate during torpor was independent of BW in both groups (daily torpor,  $R = -0.11$ , n.s.; hibernation,  $R = -0.26$ , n.s.).

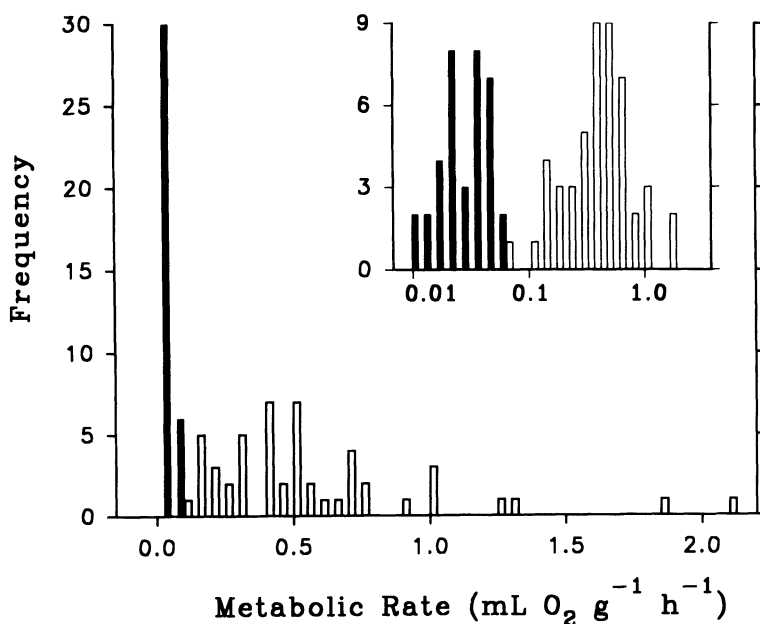


Fig. 4. Frequency distributions of MRs (minimum  $\dot{V}O_2$ ) in daily heterotherms (open bars) and during prolonged torpor bouts in hibernators (solid bars). The inset graph shows the same distribution on a logarithmic scale; hibernation, 0.013–0.07  $\text{mL O}_2 \text{g}^{-1} \text{h}^{-1}$  (median 0.033  $\text{mL O}_2 \text{g}^{-1} \text{h}^{-1}$ ); daily torpor, 0.07–2.05  $\text{mL O}_2 \text{g}^{-1} \text{h}^{-1}$  (median 0.45  $\text{mL O}_2 \text{g}^{-1} \text{h}^{-1}$ ).

The mean minimum  $\dot{V}O_2$ , expressed as a percentage of BMR, was  $29.5\% \pm 2.7\%$  ( $n = 44$ ) in daily heterotherms and thus was significantly larger ( $P < 0.001$ ) than in hibernators ( $5.1\% \pm 0.7\%$ ,  $n = 36$ ; table 1; fig. 5). Minimum  $\dot{V}O_2$  (percentage of BMR) during daily torpor was between 4% and 67% of BMR, was indistinguishable between birds and mammals, and showed a nearly normal distribution (skewness 0.68). Most minimum  $\dot{V}O_2$ 's during hibernation represented 1%–10% of BMR, with the exception of the echidna, *Tachyglossus aculeatus* (Monotremata), and the black bear *U. americanus* (Carnivora), in which the values were 20% and 19% of BMR, respectively (app. B). Values of the two groups showed considerable overlap (fig. 5). The metabolic reduction expressed as percentage of BMR was skewed to the right in hibernators (skewness 2.26), but log transformation normalized the distribution (fig. 5, inset graph). In contrast to minimum  $\dot{V}O_2$  per se, relative metabolic reduction increased as BW decreased in both daily heterotherms ( $R = 0.37$ ,  $P < 0.05$ ) and hibernators

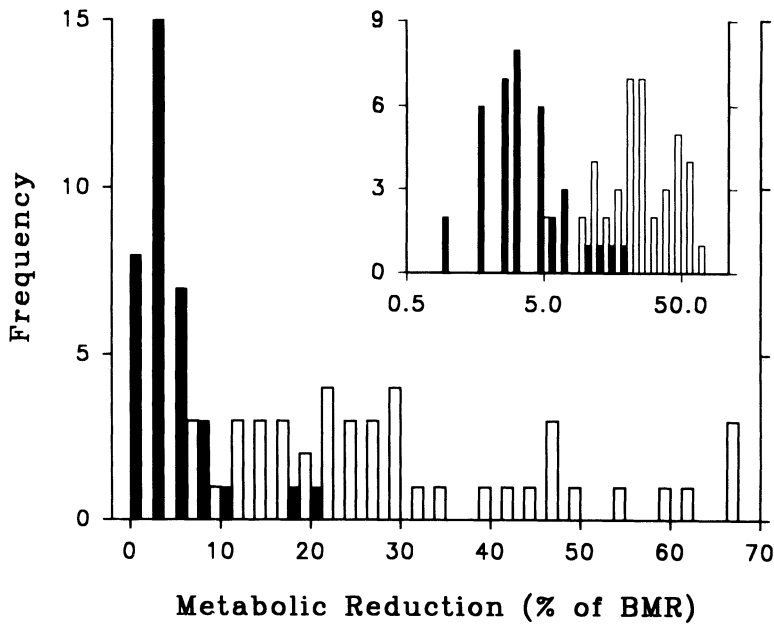


Fig. 5. Frequency distributions of MR reduction (minimum  $\dot{V}O_2$  as percentage of BMR) during hibernation (solid bars) and daily torpor (open bars). In hibernators,  $O_2$  consumption was reduced to 1%–20% of BMR (median, 4%), and in daily heterotherms to 4.4%–67% of BMR (median, 24.5%). The inset shows both distributions over a logarithmic scale of percentage of BMR.

( $R = 0.72$ ,  $P < 0.001$ ; fig. 6). The relative metabolic reduction was similar in small daily heterotherms and small hibernators but diverged with increasing BW (fig. 6).

Differences in minimum MRs between hibernation and daily torpor were more pronounced than differences between minimum  $T_b$ 's. This result supports the argument that minimum  $\dot{V}O_2$  better characterizes different states of torpor than minimum  $T_b$  (Watts et al. 1981). It also supports the view that low MRs are a prerequisite for prolonged torpor and that the duration of torpor bouts and MR during torpor are physiologically linked (French 1985; Geiser and Kenagy 1988).

In contrast to the minimum  $\dot{V}O_2$ , distributions of the degree of metabolic reduction (percentage of BMR) showed considerable overlap (fig. 5). This increased overlap is mainly due to the differences in BWs between hibernators and daily heterotherms. Since the minimum  $\dot{V}O_2$  during torpor is independent of body mass in both hibernators and daily heterotherms, the relative reduction of weight-specific metabolism is greater in small

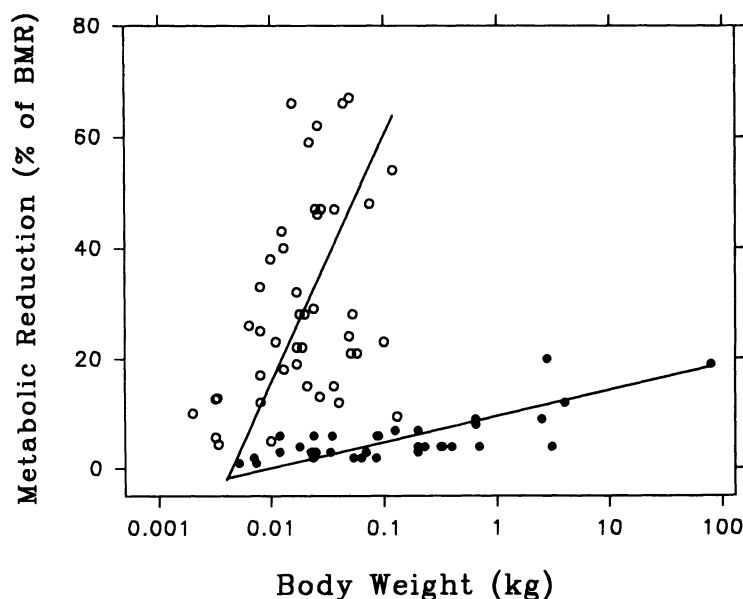


Fig. 6. The relationship between BW and MR reduction (minimum  $\dot{V}O_2$  as percentage of BMR) in daily heterotherms (open circles) and hibernators (solid circles). The MR reduction increased with BW in both daily heterotherms ( $\%BMR = -28.97 + 44.65 \log_{10}BW$ ) and hibernators ( $\%BMR = -4.67 + 4.71 \log_{10}BW$ ).

species (mainly daily heterotherms) with high BMRs than in large species (mainly hibernators) with low BMRs. The same argument can be applied to explain the significant correlation between BW and MR reduction (percentage of BMR), which was particularly pronounced among hibernating species ( $R = 0.72$ ; fig. 6). Metabolic rate reduction (percentage of BMR) in hibernators was related to BW, because BMR decreases with increasing BW, whereas the minimum  $\dot{V}O_2$  during torpor is independent of BW (Kayser 1964; Geiser 1988; Heldmaier and Ruf 1992; Nicol, Andersen, and Mesch 1992).

The absolute range of minimum  $\dot{V}O_2$ 's was more than 30 times greater in daily heterotherms than in hibernators. Some of this greater variability in species displaying daily torpor may be explained by the maintenance of large thermal gradients between  $T_b$  and  $T_a$  in some daily heterotherms, even at the species-specific minimum  $\dot{V}O_2$  during torpor, while, at least in small hibernators,  $T_b$  typically is very close to  $T_a$  (see, e.g., Geiser 1988; Heldmaier and Ruf 1992).

### *Duration of Torpor Bouts*

Duration of torpor bouts showed no overlap, and there was a clear gap of 74 h in bout length between hibernators and daily heterotherms (fig. 7). Torpor bouts lasted between 1.5 and 22 h in daily heterotherms ( $11.2 \pm 0.7$  h,  $n = 43$ ) and from 96 to 1,080 h in hibernators ( $355.3 \pm 37.7$  h,  $n = 39$ ) and differed significantly ( $P < 0.001$ ) between the two groups (table 1). Torpor bout duration of avian and mammalian daily heterotherms was indistinguishable. The frequency distribution was close to normal in daily heterotherms (skewness 0.31) but was skewed to the right in hibernators (skewness 1.44). Maximum torpor bout duration and BW showed no significant correlation in either group (daily torpor,  $R = 0.03$ , n.s.; hibernation,  $R = 0.04$ , n.s.).

Thus, the frequency distribution of torpor bout duration showed at least two interesting characteristics: (1) a clear gap of 74 h separating daily heterotherms from hibernators and (2) a high variability of maximum torpor

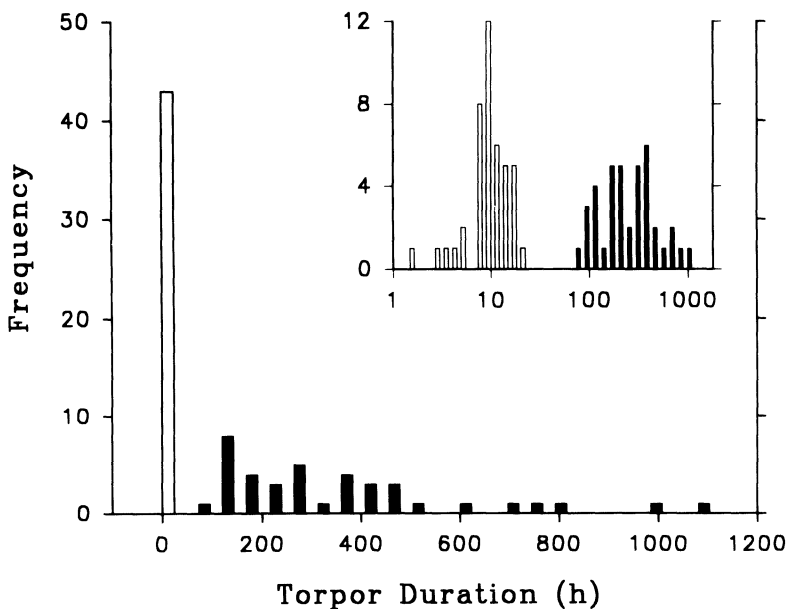


Fig. 7. Frequency distributions of maximum torpor bout duration in hibernators (solid bars) and daily heterotherms (open bars) on a linear scale (main graph) and a logarithmic scale (inset). Maximum torpor bout duration varied between 96 and 1,080 h in hibernating species (median 280 h) and between 1.5 and 22 h in daily heterotherms (median 10.5 h).



bout duration among hibernators, ranging from 4 to 45 d. The variation of duration of torpor bouts could not be explained by BW in either group. This is in contrast to earlier reports showing an increase of midwinter torpor bout duration with decreasing BW among certain hibernators (French 1985, 1986). The lack of such a correlation in the present study is probably due to the fact that we did not differentiate between hibernators that completely rely on body fat as the only energy source and those that hoard and consume food during the hibernation season (French 1986) because this information is not available for many species and may even differ within species (Michener 1993).

The lack of impact of BW on certain physiological variables was also not obscured by comparing data from different phylogenetic groups. When BW was regressed against the duration of torpor bouts of hibernators and daily heterotherms from birds and different mammalian orders (marsupials were treated as a single order because data on prolonged torpor were available only for the Diprotodontia), no significant correlation could be detected. Thus, our analysis provides no insight as to the cause and function of the more than 10-fold differences in maximum torpor bout duration among hibernators.

Nevertheless, the present study shows that maximum torpor bout duration is clearly the most distinctive variable separating hibernators from daily heterotherms. This result was not unexpected. First, duration of torpor bouts was the most important criterion underlying the classification in appendices A and B. Second, our focus on maximum torpor bout duration does not take into account the occurrence of both daily and prolonged torpor in certain hibernating species at different times of the year.

The clear gap of maximum duration of torpor bouts (between 22 h in daily heterotherms and 96 h in hibernators; table 1) raises the question of why there are no species with an intermediate duration of maximum torpor bouts. The answer to this question may lie in differences in activity patterns of daily heterotherms and hibernators. While typical hibernators retreat into secluded burrows for prolonged periods and rely on either internal or cached energy stores, daily heterotherms continue to be active and forage between torpor episodes. This alternation between torpor and activity in species showing daily torpor is governed by the circadian system, which ensures a proper timing of rewarming and return to the active state at the appropriate time of day (Lynch, Bunin, and Schneider 1980; Ruf, Steinlechner, and Heldmaier 1989; Kirsch, Ouarour, and Pevet 1991). Since daily heterotherms with an average torpor duration of 11 h always experience at least either dawn or dusk, this pattern also allows for the daily entrainment of the cir-

cadian system by light. In theory, however, an animal that would, for example, remain torpid for 60 h in a burrow and then emerge to forage on every third day would not be exposed to the entraining action of light for 3 consecutive days. Considering that the endogenous circadian period in daily heterotherms may deviate over 24 h by up to 1.5 h (Ruf et al. 1989), a free-running circadian system may amount to an "error" of 4.5 h over a 3-d interval. It is obvious that, in particular for strictly nocturnal or diurnal animals, such a deviation from synchronization with the natural light/dark cycle would be highly disadvantageous, even if it were of a much smaller magnitude. Hence, it seems that natural selection may disadvantage the intermediate pattern of torpor, that is, animals that continue regularly to forage but spend more than 24 h in the torpid state.

## Conclusion

Overall, in the present analysis the maximum torpor bout duration is the only variable that showed no overlap between daily heterotherms and hibernators and therefore is best suited for classifications of torpor patterns. However, the minimum MR during torpor was found to be almost equally distinctive. The clear difference of torpor bout duration together with the approximately 10-fold greater MR during daily torpor than during hibernation provide further support for the traditional classification into two distinct patterns of heterothermia. Other physiological variables, in particular the minimum  $T_b$ , are much less reliable markers for this distinction. We therefore conclude that "shallow" and "deep" are not appropriate single attributes for the characterization of daily torpor and hibernation. The emphasis should lie on daily versus prolonged torpor, because it is the temporal organization of heterothermia, more than any other factor, that separates daily heterotherms from hibernators.

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## Appendix A

TABLE A1  
Physiological Variables of Torpor in Daily Heterotherms (Species Exhibiting Daily Torpor)

Species	Body Mass (g)	Minimum $T_b$ (°C)	Minimum $\dot{V}O_2$ (mL g <sup>-1</sup> h <sup>-1</sup> )	Percentage of BMR	Longest Bout (h)	Source
<b>Marsupials:</b>						
<i>Marmosa</i> sp. ....	13	16	.25	18	6	Morrison and McNab 1962
<i>Dasyurus geoffroii</i> ....	1,000	23.1				Arnold 1976
<i>Dasyuroides byrnei</i> ....	120	20.4	.40	54	7.5	Geiser and Baudinette 1987
<i>Dasyercus cristicauda</i> ....	100	13.2	.12	23	10.5	MacMillen and Nelson 1969; Geiser and Masters 1994
<i>Antechinus flavipes</i> ....	26	24.5	.48	46	5.5	Geiser 1985a, 1985b, 1988
<i>Antechinus stuartii</i> ....	26	19.9	.66	62	9.0	Geiser 1985a, 1988
<i>Sminthopsis murina</i> ....	19	15.0	.25	22	8.0	Geiser et al. 1984
<i>Sminthopsis crassicaudata</i> ....	17	13.0	.27	22	19.5	Geiser and Baudinette 1987
<i>Sminthopsis macroura</i> ....	24	14.0	.30	29	17.9	Geiser and Baudinette 1987
<i>Ningau i yvonneae</i> ....	11	15.3	.30	23	12.3	Geiser and Baudinette 1988
<i>Antechinomys laniger</i> ....	27	11.0	.14	13	16.0	Geiser 1986
<i>Planigale maculata</i> ....	13	19.6	.40	40	1.5	Morton and Lee 1978
<i>Planigale gilesi</i> ....	8	14.3	.36	25	15.3	Geiser and Baudinette 1988
<i>Petaurus breviceps</i> ....	130	15.6	.07	9.5	15.5	Fleming 1980
<i>Tarsipes rostratus</i> ....	10	5.0	.15	5	14.4	Withers et al. 1990

Insectivores:						
<i>Suncus etruscus</i> . . . . .	2	14	.6	10	8	Fons and Sicard 1976; Frey 1979, 1980
<i>Crocodyra russula</i> . . . . .	10	17.9	.9	38	3	Nagel 1977, 1985
<i>Crocodyra leucodon</i> . . . . .	12	18.6				Nagel 1985
<i>Crocodyra suaveolens</i> . . . . .	8	21.6				Nagel 1985
Bats:						
<i>Nyctimene albiventer</i> . . . . .	28	25.5	.67	47		Bartholomew, Dawson, and Lasiewski 1970
Carnivores:						
<i>Mephitis mephitis</i> . . . . .	3,000	28.4			9	Mutch and Aleksiak 1977
<i>Taxidea taxus</i> . . . . .	9,000	28			22	Harlow 1981
Rodents:						
<i>Peromyscus leucopus</i> . . . . .	20	16.8	.47	28	13	Hill 1975; Deavers and Hudson 1981
<i>Peromyscus eremicus</i> . . . . .	17	16	.3	19	11.2	MacMillen 1965; Morhardt 1970
<i>Peromyscus boyleyi</i> . . . . .	33	18			8.8	Morhardt 1970
<i>Peromyscus crinitus</i> . . . . .	20	17			9.5	Morhardt 1970
<i>Peromyscus maniculatus</i> . . . . .	18	14	.55	28	10.8	McNab and Morrison 1963; Morhardt 1970; Geiser 1991
<i>Peromyscus gossypinus</i> . . . . .	22	14			4.9	Tannenbaum and Pivorum 1984
<i>Perognathus hispidus</i> . . . . .	40	11	.15	12	17	Wang and Hudson 1970
<i>Perognathus californicus</i> . . . . .	21	15	.15	15	9	Tucker 1965
<i>Mus musculus</i> . . . . .	37	16	.7	47	11	Hudson and Scott 1979
<i>Baiomys taylori</i> . . . . .	6.4	22	.5	26	20	Hudson 1965
<i>Reithrodontomys megalotis</i> . . . . .	8	13	.3	12	10	Thompson 1985

TABLE A1 (Continued)

Species	Body Mass (g)	Minimum $T_b$ (°C)	Minimum $\dot{V}O_2$ (mL g <sup>-1</sup> h <sup>-1</sup> )	Percentage of BMR	Longest Bout (h)	Source
<i>Gerbillus pusillus</i> .....	12.6	16.7	.38	43	20	Buffenstein 1985
<i>Phodopus sungorus</i> .....	25	12.3	.88	46	13.8	Ruf et al. 1993; T. Ruf, unpublished data
<i>Calomys musculus</i> .....	17		.52	32	16	Bozinovic and Rosenmann 1988
<i>Calomys venustus</i> .....	50	16.4	.96	67	8	Caviedes-Vidal et al. 1990
<i>Phyllotis darwini rupestris</i> .....	36		.19	15	12	Bozinovic and Marquet 1991
Birds:						
<i>Selasphorus rufus</i> .....	3.3	13	.43	12.8	10	Lasiewski 1963; Hiebert 1990
<i>Eulampis jugularis</i> .....	8	18	1.0	33		Hainsworth and Wolf 1970
<i>Archilochus alexandri</i> .....	3.2		.2	5.7		Lasiewski 1963
<i>Calypte anna</i> .....	3.4		.17	4.4		Lasiewski 1963
<i>Calypte costae</i> .....	3.2		.38	12.7		Lasiewski 1963
<i>Oreotrochilus estella</i> .....	8.5	6.5	.75		10	Carpenter 1974; Krüger, Prinzinger, and Schuchmann 1982

<i>Panterpe insignis</i> . . . . .	5	10	.5			Wolf and Hainsworth 1972
<i>Eugenes fulgens</i> . . . . .	8	10	.5			Wolf and Hainsworth 1972
<i>Lampornis clemenciae</i> . . . . .	8	19.6	.45	17		Krüger et al. 1982
<i>Ortoborhynchus cristatus</i> . . . . .	2.9	20.8	1.25			Krüger et al. 1982
<i>Chrysuronia oenone</i> . . . . .	5	18	2.05			Krüger et al. 1982
<i>Caprimulgus argus</i> . . . . .	75	29.6	.4	48		Dawson and Fisher 1969
<i>Delichon urbica</i> . . . . .	22	22	.75	59	12	Prinzinger and Siedle 1986, 1988
<i>Manacus vitellinus</i> . . . . .	15.5	26.8	1.8	66	3.5	Bartholomew, Vleck, and Bucher 1983
<i>Colius striatus</i> . . . . .	51		.39	21	10	Hoffmann and Prinzinger 1984
<i>Colius castaneus</i> . . . . .	58	18	.49	21	11	Prinzinger et al. 1981; Hoffmann and Prinzinger 1984
<i>Urocolius indicus</i> . . . . .	53		.68	28	10	Hoffmann and Prinzinger 1984
<i>Urocolius macrourus</i> . . . . .	49		.65	24	11	Hoffmann and Prinzinger 1984
<i>Scardafella inca</i> . . . . .	44	29	1.0	66	10	MacMillen and Trost 1967

Note. Percentage of BMR = minimum  $\dot{V}O_2$ /BMR  $\cdot$  100.

Appendix B

TABLE B1  
Physiological Variables of Torpor in Hibernators (Species Exhibiting Prolonged Torpor)

Species	Body Mass (g)	Minimum $T_b$ ( $^{\circ}\text{C}$ )	Minimum $\dot{V}\text{O}_2$ ( $\text{mL g}^{-1} \text{h}^{-1}$ )	Percentage of BMR	Longest Bout (h)	Source
Monotremes:						
<i>Tachyglossus aculeatus</i> . . . . .	2,800	4	.03	20	384	Augée and Ealey 1968; Grigg, Beard, and Augée 1989
Marsupials:						
<i>Cercartetus nanus</i> . . . . .	24	1.3	.018	2	552	Bartholomew and Hudson 1962; Geiser 1993
<i>Cecartetus concinnus</i> . . . . .	18	4.7	.046	4	264	Geiser 1987
<i>Cercartetus lepidus</i> . . . . .	12	5.9	.052	3	144	Geiser 1987
<i>Burrhamys parvus</i> . . . . .	63	1.8	.025	2	480	Geiser and Broome 1991
<i>Acrobates pygmaeus</i> . . . . .	12	2.1	.069	6	192	Fleming 1985; Jones and Geiser 1992
Insectivores:						
<i>Erinaceus europaeus</i> . . . . .	700	5.4	.016	4	231	Kristofferson and Soivio 1964; Thaeti 1978

<i>Setifer setosus</i> .....	320	13	.014	4	144	F. Lachiver (cited in Kayser [1961]); Kayser 1964; Hildwein 1970
<i>Tenrec ecaudatus</i> .....	650	15	.027	9	192	F. Lachiver (cited in Kayser [1961]); Kayser 1964; Hildwein 1970
<i>Echinops telfairi</i> .....	85	11	.026	2	120	Dryden, Gebczynski, and Douglas 1974; Scholl 1974
Bats:						
<i>Myotis myotis</i> .....	25		.04	3 <sup>a</sup>	989	Pohl 1961; Harmata 1987
<i>Myotis lucifugus</i> .....	5.2	1.3	.022	1	750	Hock 1951; French 1985
<i>Myotis adversus</i> .....	7.8	9			192	Kulzer et al. 1970
<i>Pipistrellus pipistrellus</i> .....	7.4	3	.024	1 <sup>a</sup>		Kayser 1964; Kulzer 1965
<i>Eptesicus fuscus</i> .....	22	5			600	Kulzer 1965; French 1985
<i>Nyctalus noctula</i> .....	23.8		.03	2		Kayser 1964
<i>Barbastella barbastellus</i> .....	7		.04	2 <sup>a</sup>		Pohl 1961
<i>Miniopterus schreibersii</i> .....	15				288	Hall 1982
<i>Rhinolophus hipposideros</i> .....	6				427	Harmata 1987
<i>Rhinolophus ferrum equinum</i> ..	23	9			240	Kulzer 1965; Ransome 1990
Carnivores:						
<i>Meles meles</i> .....	13,000	28.4			1,080	Fowler and Racey 1988
<i>Ursus americanus</i> .....	80,000	32.3	.042	19		Watts et al. 1981
Rodents:						
<i>Cricetus cricetus</i> .....	330	4	.032	4		Eisentraut 1933; Kayser 1939, 1964



TABLE B1 (Continued)

Species	Body Mass (g)	Minimum $T_b$ (°C)	Minimum $\dot{V}O_2$ (mL g <sup>-1</sup> h <sup>-1</sup> )	Percentage of BMR	Longest Bout (h)	Source
<i>Mesocricetus auratus</i> . . . . .	90	5	.07	6 <sup>a</sup>	264	Lyman 1948; Pohl 1961
<i>Mesocricetus brandti</i> . . . . .	140				130	Pohl 1987
<i>Zapus princeps</i> . . . . .	33.6	5.5	.042	3 <sup>a</sup>	504	Cranford 1983
<i>Zapus hudsonicus</i> . . . . .	22.6		.043	3	451	Muchlinski and Rybak 1978
<i>Perognathus parvus</i> . . . . .	24	2	.05	3	192	MacMillen 1983
<i>Perognathus longimembris</i> . . . . .	8	4				Bartholomew and Cade 1957
<i>Glis glis</i> . . . . .	200	1	.026	3	792	Wyss 1932; Kayser 1939, 1961; Pengelley and Fisher 1961
<i>Eliomys quercinus</i> . . . . .	70	1	.034	3	384	Kayser 1964; Pajunen 1983
<i>Muscardinus avellanarius</i> . . . . .	23.5	0	.04	2 <sup>a</sup>	384	Kayser 1939, 1964; Eisentraut 1956; Walhovd 1976
<i>Marmota marmota</i> . . . . .	3,100	2	.013	4	344	Arnold 1988, 1993; Ortman 1989; Arnold et al. 1991
<i>Marmota monax</i> . . . . .	4,000		.032	12		Lyman 1958
<i>Marmota flaviventris</i> . . . . .	2,500	7.5	.022	9	430	Florant and Heller 1977; French 1985

<i>Spermophilus lateralis</i> . . . . .	200	.5	.045	4	384	Heller and Colliver 1974; Snapp and Heller 1981; Barnes et al. 1986
<i>Spermophilus saturatus</i> . . . . .	230	.3	.017	4 <sup>a</sup>	264	Geiser, Hiebert, and Kenagy 1990
<i>Spermophilus beldingi</i> . . . . .	400				280	French 1982
<i>Spermophilus beecheyi</i> . . . . .	600	6.1			120	Strumwasser 1960; Pengelley and Kelly 1966
<i>Spermophilus variegatus</i> . . . . .	700	8.0			144	Pengelley 1964; Pengelley and Kelly 1966
<i>Spermophilus parryii</i> . . . . .	650	-2.9	.063	8	480	Hock 1960; Barnes 1989
<i>Spermophilus mexicanus</i> . . . . .	200	7	.06	7 <sup>a</sup>		Neumann and Cade 1965
<i>Spermophilus tereticaudus</i> . . . . .	125		.048	7	120	Pengelley and Kelly 1966; Bickler 1984
<i>Spermophilus richardsonii</i> . . . . .	400	2	.02	4	456	Hudson and Deavers 1973; Wang 1978
<i>Tamias striatus</i> . . . . .	87	5	.06	6	150	Wang and Hudson 1971; Pivorun 1976
<i>Eutamias amoenus</i> . . . . .	54	.1	.026	2	220	Kenagy and Vleck 1982; Geiser et al. 1990
Birds:						
<i>Phalaenoptilus nuttallii</i> . . . . .	35	6	.05	6	96	Marshall 1955; Ligon 1970; Withers 1977

Note. Percentage of BMR = minimum  $\dot{V}O_2$ /BMR  $\cdot$  100.  
<sup>a</sup> BMR was calculated from the equations of Hayssen and Lacy (1985) for the particular order or family.

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