
Invited Perspectives in Physiological Zoology

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

Fritz Geiser^{1,*}

Thomas Ruf^{2,†}

¹Department of Zoology, University of New England, Armidale, New South Wales 2351, Australia; ²Department of Biological Sciences, Kent State University, Kent, Ohio 44242

Accepted 4/4/95

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°C vs. 17.4°C) as were minimum metabolic rates measured as rate of oxygen consumption ($\dot{V}O_2$; 0.037 vs. 0.535 mL O_2 $g^{-1}h^{-1}$), 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 g) than in daily heterotherms (253 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 (1.5–22 h for daily torpor; 96–1,080 h for hibernation) showed a clear gap between daily heterotherms and hibernators.

* To whom correspondence should be addressed.

† Present address: Fachbereich Biologie, Philipps Universität, 35032 Marburg, Germany.

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_2 $g^{-1}h^{-1}$), 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 ± 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 ± 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 ⁻¹ h ⁻¹):		
<i>N</i>	36	49
Mean037	.535
Median033	.45
SE003	.056
Range013–.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
SE7	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

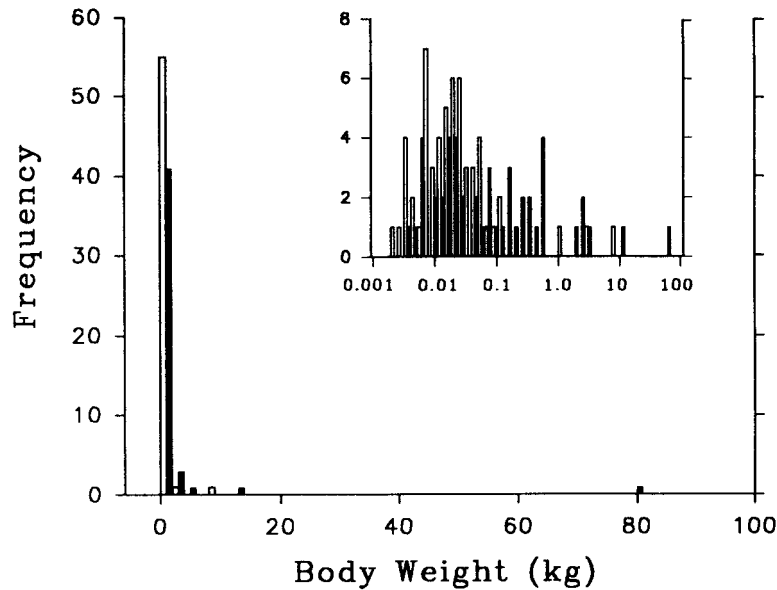


Fig. 1. Frequency distributions of BWs in hibernators (solid bars) and species exhibiting daily torpor (open bars). Body weights varied between 5.2 g and 80 kg in hibernators (median 85 g) and between 2 g and 9 kg in daily heterotherms (median 19 g). The inset graph shows the same distribution on a logarithmic 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° and 30°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° to 16°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 (*Pbalaenoptilus nuttallii*), was 6.0°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°C in honey possums (*Tarsipes rostratus*) and remaining as high as 32.3°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

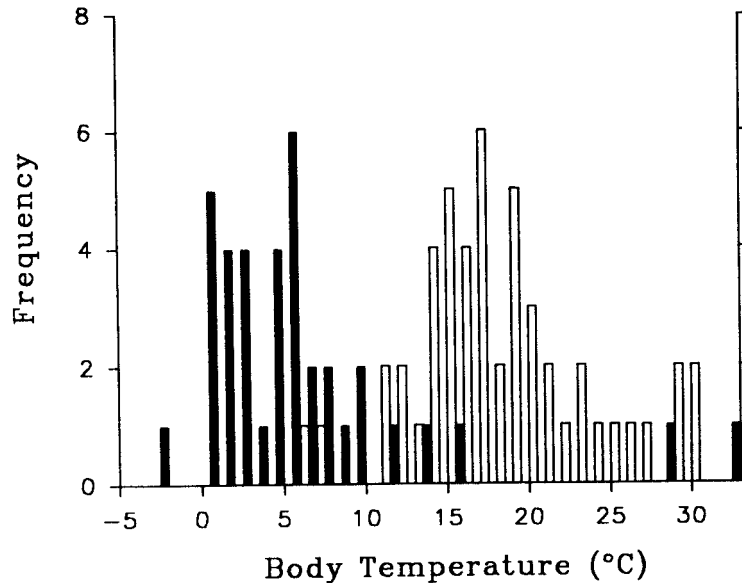


Fig. 2. Frequency distributions of minimum T_b 's in hibernators (solid bars) and daily heterotherms (open bars). Minimum T_b 's ranged from -2.9° to 32.3°C (median 4.7°C) in hibernators and from 5° to 29.6°C (median 16.7°C) in daily heterotherms.

hibernation and daily torpor. Even when the data from exceptionally large animals (*M. meles*, 28.3°C ; *U. americanus*, 32.3°C) were omitted, more than 25% of all hibernating species compared here had intermediate minimum T_b 's during torpor of between 7° and 16°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°C were among the animals with the lowest BWs (≤ 10 g). On the other hand, all minimum T_b 's above 10°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

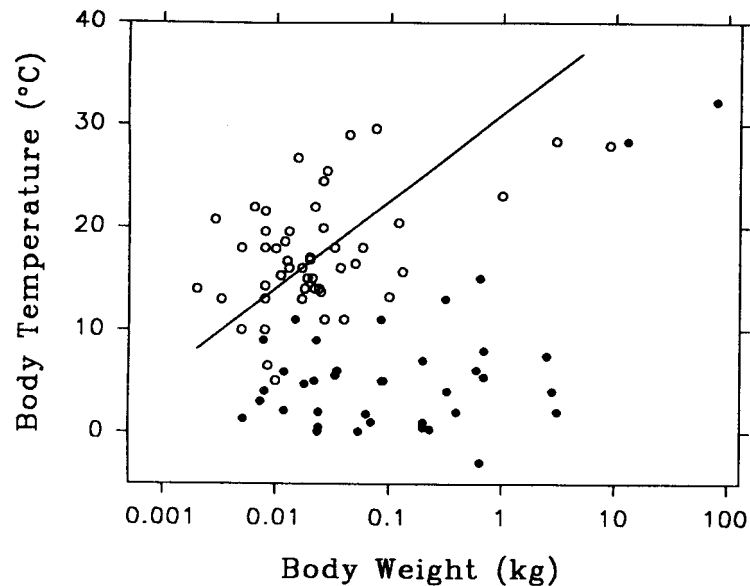


Fig. 3. The relationship between BW and minimum T_b of daily heterotherms (open circles) and hibernators (solid circles). The minimum T_b increased with BW in daily heterotherms ($T_b = 5.57 + 8.49 \log_{10} BW$), but this relationship was not significant in hibernators.

BW (Herreid and Kessel 1967) would result in T_b 's during torpor that, in theory, range from as little as 0.1°C above T_a in a 5.2-g hibernator to 10.8°C above T_a in a 80-kg hibernator, even at a constant minimum $\dot{V}O_2$ 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 $MR = C(T_b - T_a)$ (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 $\dot{V}O_2$ 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 $T_b - T_a = MR/C$ is 10.8°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°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°C (Wahlhøvd 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°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.).

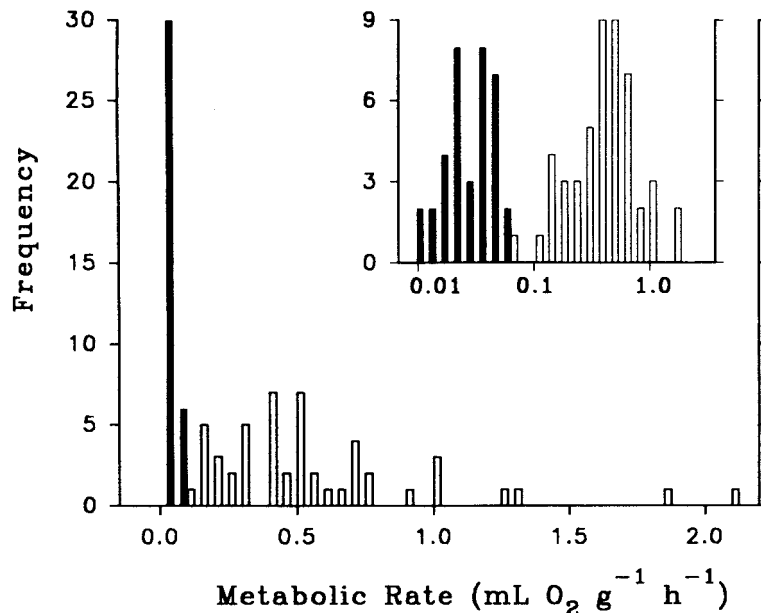


Fig. 4. Frequency distributions of MRs (minimum $\dot{V}O_2$) in daily heterotherms (open bars) and during prolonged torpor bouts in hibernators (solid bars). The inset graph shows the same distribution on a logarithmic scale; hibernation, 0.013–0.07 mL O₂ g⁻¹ h⁻¹ (median 0.033 mL O₂ g⁻¹ h⁻¹); daily torpor, 0.07–2.05 mL O₂ g⁻¹ h⁻¹ (median 0.45 mL O₂ g⁻¹ 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

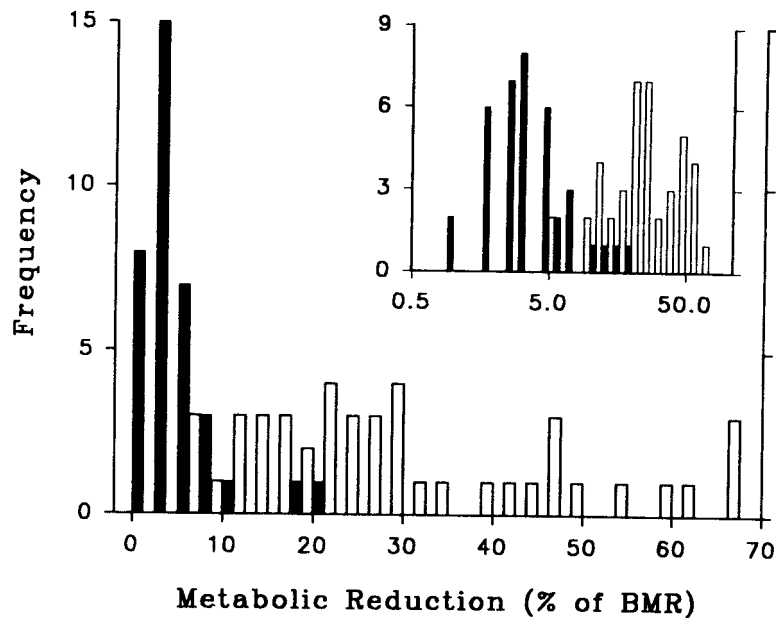


Fig. 5. Frequency distributions of MR reduction (minimum $\dot{V}O_2$ as percentage of BMR) during hibernation (solid bars) and daily torpor (open bars). In hibernators, O_2 consumption was reduced to 1%–20% of BMR (median, 4%), and in daily heterotherms to 4.4%–67% of BMR (median, 24.5%). The inset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

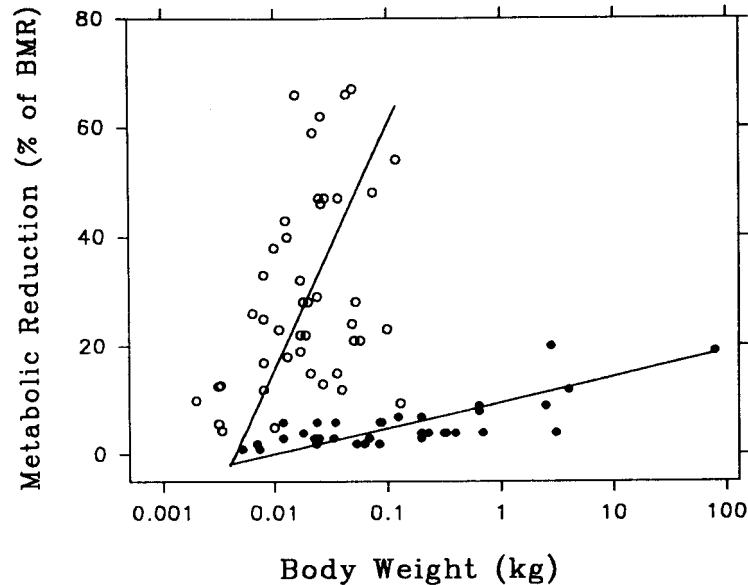


Fig. 6. The relationship between BW and MR reduction (minimum $\dot{V}O_2$ as percentage of BMR) in daily heterotherms (open circles) and hibernators (solid circles). The MR reduction increased with BW in both daily heterotherms ($\%BMR = -28.97 + 44.65 \log_{10}BW$) and hibernators ($\%BMR = -4.67 +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

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 ± 0.7 h, $n = 43$) and from 96 to 1,080 h in hibernators (355.3 ± 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

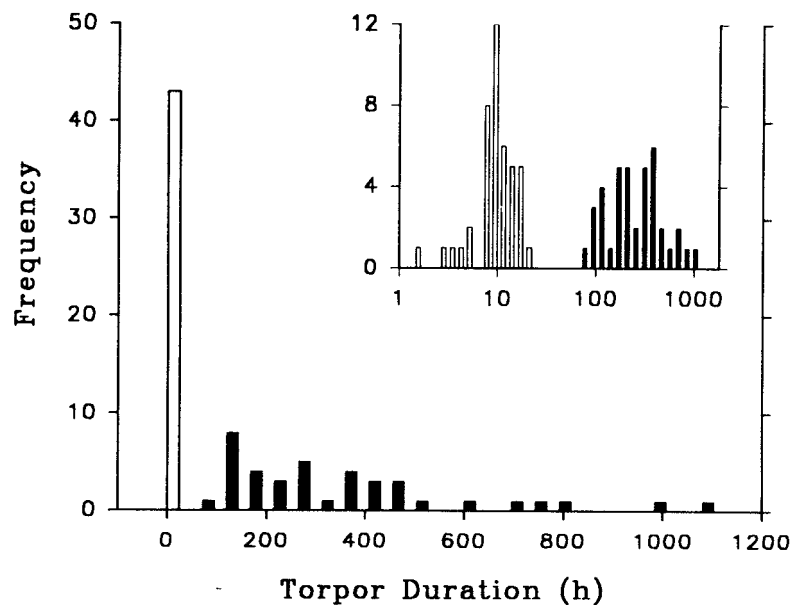


Fig. 7. Frequency distributions of maximum torpor bout duration in hibernators (solid bars) and daily heterotherms (open bars) on a linear scale (main graph) and a logarithmic scale (inset). Maximum torpor bout duration varied between 96 and 1,080 h in hibernating species (median 280 h) and between 1.5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

adian 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.

Acknowledgments

This work was supported by grants from the Australian Research Council to F.G. and a Feodor Lynen Fellowship of the Alexander von Humboldt-Stiftung to T.R. We would like to thank Bronwyn McAllan and two referees for critical comments on the manuscript.

Appendix A

TABLE A1

Physiological Variables of Torpor in Daily Heterotherms (Species Exhibiting Daily 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
Marsupials:						
<i>Marmosa</i> sp.	13	16	.25	18	6	Morrison and McNab 1962
<i>Dasyurus geoffroi</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>Smintbopsis murina</i>	19	15.0	.25	22	8.0	Geiser et al. 1984
<i>Smintbopsis crassicaudata</i>	17	13.0	.27	22	19.5	Geiser and Baudinette 1987
<i>Smintbopsis macroura</i>	24	14.0	.30	29	17.9	Geiser and Baudinette 1987
<i>Ningau 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>Crocidura rissula</i>	10	17.9	.9	38	3	Nagel 1977, 1985
<i>Crocidura leucodon</i>	12	18.6				Nagel 1985
<i>Crocidura 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 Aleksziuk 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 boylei</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>Batomys 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 ($^{\circ}\text{C}$)	Minimum \dot{V}_{O_2} ($\text{mL g}^{-1} \text{h}^{-1}$)	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, Prinzing, and Schuchmann 1982

<i>Pantherpe 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>Orthorhynchus 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 castanotus</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 · 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}_{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	Augee and Ealey 1968; Grigg, Beard, and Augee 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>Burramys 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 ^a	989	Pohl 1961; Harmata 1987
<i>Myotis lucifugus</i>	5.2	1.3	.022	1	750	Hock 1951; French 1985
<i>Myotis aduersus</i>	7.8	9			192	Kulzer et al. 1970
<i>Pipistrellus pipistrellus</i>	7.4	3	.024	1 ^a		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 ^a		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 ($^{\circ}\text{C}$)	Minimum \dot{V}_{O_2} ($\text{mL g}^{-1} \text{h}^{-1}$)	Percentage of BMR	Longest Bout (h)	Source
<i>Mesocricetus auratus</i>	90	5	.07	6 ^a	264	Lyman 1948; Pohl 1961
<i>Mesocricetus brandti</i>	140				130	Pohl 1987
<i>Zapus princeps</i>	33.6	5.5	.042	3 ^a	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>Eltomys quercinus</i>	70	1	.034	3	384	Kayser 1964; Pajunen 1983
<i>Muscardinus avellanarius</i>	23.5	0	.04	2 ^a	384	Kayser 1939, 1964; Eisentraut 1956; Walhovd 1976
<i>Marmota marmota</i>	3,100	2	.013	4	344	Arnold 1988, 1993; Ortmann 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 ^a	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 parryi</i>	650	-2.9	.063	8	480	Hock 1960; Barnes 1989
<i>Spermophilus mexicanus</i>	200	7	.06	7 ^a	120	Neumann and Cade 1965
<i>Spermophilus tereticaudus</i>	125		.048	7		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 · 100.

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

Literature Cited

- ARNOLD, J. M. 1976. Growth and bioenergetics of the Chuditch, *Dasyurus geoffroii*. Ph.D. thesis. University of Western Australia, Perth.
- ARNOLD, W. 1988. Social thermoregulation during hibernation in alpine marmots. *J. Comp. Physiol.* 158B:151–156.
- . 1993. Energetics of social hibernation. Pages 65–80 in C. CAREY, G. L. FLORANT, B. A. WUNDER, and B. HORWITZ, eds. *Life in the cold: ecological, physiological and molecular mechanisms*. Westview, Boulder, Colo.
- ARNOLD, W., G. HELDMAIER, S. ORTMANN, H. POHL, T. RUF, and S. STEINLECHNER. 1991. Ambient temperatures in hibernacula and their energetic consequences for alpine marmots (*Marmota marmota*). *J. Therm. Biol.* 16:223–226.
- AUGEE, M. L., and E. H. M. EALEY. 1968. Torpor in the echidna, *Tachyglossus aculeatus*. *J. Mammal.* 49:446–454.
- BARNES, B. 1989. Freeze avoidance in a mammal: body temperatures below 0°C in an Arctic hibernator. *Science* 244:1593–1595.
- BARNES, B. M., M. KRETZMANN, P. LICHT, and I. ZUCKER. 1986. The influence of hibernation on testes growth and spermatogenesis in the golden-mantled ground squirrel, *Spermophilus lateralis*. *Biol. Reprod.* 35:1289–1297.
- BARTHOLOMEW, G. A. 1982. Body temperature and energy metabolism. Pages 333–406 in M. S. GORDON, ed. *Animal physiology: principles and adaptations*. Macmillan, New York.
- BARTHOLOMEW, G. A., and T. J. CADE. 1957. Temperature regulation, hibernation and aestivation in the little pocket mouse, *Perognathus longimembris*. *J. Mammal.* 38:60–72.
- BARTHOLOMEW, G. A., W. R. DAWSON, and R. C. LASIEWSKI. 1970. Thermoregulation and heterothermy in some of the smaller flying foxes (Megachiroptera) of New Guinea. *Z. Vergleichende Physiol.* 70:196–209.
- BARTHOLOMEW, G. A., and J. W. HUDSON. 1962. Hibernation, estivation, temperature regulation, evaporative water loss, and heart rate of the pygmy possum *Cercoartus nanus*. *Physiol. Zool.* 35:94–107.
- BARTHOLOMEW, G. A., C. M. VLECK, and T. L. BUCHER. 1983. Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. *Physiol. Zool.* 56:370–379.
- BICKLER, P. E. 1984. CO₂ balance of a heterothermic rodent: comparison of sleep, torpor, and awake states. *Am. J. Physiol.* 246:R49–R55.
- BOZINOVIC, F., and P. A. MARQUET. 1991. Energetics and torpor in the Atacama Desert-dwelling rodent *Phyllotis darwini rupestris*. *J. Mammal.* 72:734–738.
- BOZINOVIC, F., and M. ROSENMAN. 1988. Daily torpor in *Calomys musculinus*, a South American rodent. *J. Mammal.* 69:150–152.
- BUFFENSTEIN, R. 1985. The effect of starvation, food restriction, and water deprivation on thermoregulation and average daily metabolic rates in *Gerbillus pusillus*. *Physiol. Zool.* 58:320–328.
- CARPENTER, F. L. 1974. Torpor in an Andean hummingbird: its ecological significance. *Science* 183:545–547.

- CAVIEDES-VIDAL, E., E. C. CODELIA, V. ROIG, and R. DOÑA. 1990. Facultative torpor in the South American rodent *Calomys venustus* (Rodentia: Cricetidae). *J. Mammal.* 71:72–75.
- CRANFORD, J. A. 1983. Body temperature, heart rate and oxygen consumption of normothermic and heterothermic western jumping mice (*Zapus princeps*). *Comp. Biochem. Physiol.* 74A:595–599.
- DAWSON, T. J. 1989. Responses to cold of monotremes and marsupials. Pages 255–288 in L. C. H. WANG, ed. *Advances in comparative and environmental physiology*. Vol. 4. Springer, Berlin and Heidelberg.
- DAWSON, W. R., and C. D. FISHER. 1969. Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). *Condor* 71:49–53.
- DAWSON, W. R., and J. W. HUDSON. 1970. Birds. Pages 223–293 in G. C. WHITTOW, ed. *Comparative physiology of thermoregulation*. Academic Press, New York.
- DEAVERS, D. R., and J. W. HUDSON. 1981. Temperature regulation in two rodents (*Clethrionomys gapperi* and *Peromyscus leucopus*) and a shrew (*Blarina brevicaudata*) inhabiting the same environment. *Physiol. Zool.* 54:94–108.
- DRYDEN, G. L., M. GEBZYNSKI, and E. L. DOUGLAS. 1974. Oxygen consumption by nursing and adult musk shrews. *Acta Theriol.* 19:453–461.
- EISENTRAU, M. 1933. Winterstarre, Winterschlaf und Winterruhe. *Mitt. Zool. Museum Berlin* 19:48–63.
- . 1956. *Der Winterschlaf mit seinen ökologischen und physiologischen Begleiterscheinungen*. Fischer, Jena.
- FLEMING, M. R. 1980. Thermoregulation and torpor in the sugar glider, *Petaurus breviceps* (Marsupialia: Petauridae). *Aust. J. Zool.* 28:521–534.
- . 1985. The thermal physiology of the feathertail glider, *Acrobates pygmaeus* (Marsupialia: Burramyidae). *Aust. J. Zool.* 33:667–681.
- FLORENT, G. L., and H. C. HELLER. 1977. CNS regulation of body temperature in euthermic and hibernating marmots (*Marmota flaviventris*). *Am. J. Physiol.* 232:R203–R208.
- FONS, R., and R. SICARD. 1976. Contribution à la connaissance du métabolisme énergétique chez deux crocidurinae: *Suncus etruscus* (Savi, 1882) et *Crocidura russula* (Hermann, 1780) (Insectivora, Soricidae). *Mammalia* 40:299–311.
- FOWLER, P. A., and P. A. RACEY. 1988. Overwintering strategies of the badger, *Meles meles*, at 57°N. *J. Zool. Lond.* 214:635–651.
- . 1990. Daily and seasonal cycles of body temperature in the hedgehog *Eri-naceus europaeus*. *J. Comp. Physiol.* 160B:299–307.
- FRENCH, A. R. 1982. Intraspecific differences in the pattern of hibernation in the ground squirrel *Spermophilus beldingi*. *J. Comp. Physiol.* 148B:83–91.
- . 1985. Allometries of the duration of torpid and euthermic intervals during mammalian hibernation: a test of the theory of metabolic control of the timing of changes in body temperature. *J. Comp. Physiol.* 156B:13–19.
- . 1986. The patterns of thermoregulation during mammalian hibernation. Pages 393–402 in H. C. HELLER, X. J. MUSACCHIA, and L. C. H. WANG, eds. *Living in the cold: physiological and biochemical adaptations*. Elsevier, New York.
- FREY, H. 1979. La température corporelle de *Suncus etruscus* (Soricidae, Insectivora) au cours de l'activité, du repos normothermique et du la torpeur. *Rev. Suisse Zool.* 86:653–662.

- . 1980. Le métabolisme énergétique de *Suncus etruscus* (Soricidae, Insectivora) en torpeur. *Rev. Suisse Zool.* 87:739–748.
- GEISER, F. 1985a. Physiological and biochemical aspects of torpor in Australian marsupials. Ph.D. thesis. Flinders University, Adelaide.
- . 1985b. Tagesschlafethargie bei der gelbfüssigen Breitfussbeutelspitzmaus, *Antechinus flavipes* (Marsupialia: Dasyuridae). *Z. Säugetierkunde* 50:125–127.
- . 1986. Thermoregulation and torpor in the kultarr, *Antechinomys laniger* (Marsupialia: Dasyuridae). *J. Comp. Physiol.* 156B:751–757.
- . 1987. Hibernation and daily torpor in two pygmy possums (*Cercartetus* spp., Marsupialia). *Physiol. Zool.* 60:93–102.
- . 1988. Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition? *J. Comp. Physiol.* 158B:25–37.
- . 1991. The effect of unsaturated and saturated dietary lipids on the pattern of daily torpor and the fatty acid composition of tissues and membranes of the deer mouse *Peromyscus maniculatus*. *J. Comp. Physiol.* 161B:590–597.
- . 1993. Hibernation in the eastern pygmy possum, *Cercartetus nanus* (Marsupialia: Burramyidae). *Aust. J. Zool.* 41:67–75.
- GEISER, F., M. L. AUGEE, H. C. K. MCCARRON, and J. K. RAISON. 1984. Correlates of torpor in the insectivorous dasyurid marsupial *Sminthopsis murina*. *Aust. Mammal.* 7:185–191.
- GEISER, F., and R. V. BAUDINETTE. 1987. Seasonality of torpor and thermoregulation in three dasyurid marsupials. *J. Comp. Physiol.* 157B:335–344.
- . 1988. Daily torpor and thermoregulation in the small dasyurid marsupials *Planigale gilesi* and *Ningauai yvonneae*. *Aust. J. Zool.* 36:473–481.
- GEISER, F., and L. S. BROOME. 1991. Hibernation in the mountain pygmy possum *Burramys parvus* (Marsupialia). *J. Zool. Lond.* 223:593–602.
- GEISER, F., S. HIEBERT, and G. J. KENAGY. 1990. Torpor bout duration during the hibernation season of two sciurid rodents: interrelations with temperature and metabolism. *Physiol. Zool.* 63:489–503.
- GEISER, F., and G. J. KENAGY. 1988. Torpor duration in relation to temperature and metabolism in hibernating ground squirrels. *Physiol. Zool.* 61:442–449.
- GEISER, F., and P. MASTERS. 1994. Torpor in relation to reproduction in the mulgara, *Dasyercus cristicauda* (Dasyuridae: Marsupialia). *J. Therm. Biol.* 19:33–40.
- GRIGG, G. C., L. A. BEARD, and M. L. AUGEE. 1989. Hibernation in a monotreme, the echidna (*Tachyglossus aculeatus*). *Comp. Biochem. Physiol.* 92A:609–612.
- HAINSWORTH, F. R., and L. L. WOLF. 1970. Regulation of oxygen consumption and body temperature during torpor in a hummingbird, *Eulampis jugularis*. *Science* 168:368–369.
- HALL, L. S. 1982. The effect of cave microclimate on winter roosting behaviour in the bat, *Miniopterus schreibersii blepotis*. *Aust. J. Ecol.* 7:129–136.
- HARLOW, H. J. 1981. Torpor and other physiological adaptations of the badger (*Taxidea taxus*) to cold environment. *Physiol. Zool.* 54:267–275.
- HARMATA, W. 1987. The frequency of winter sleep interruptions in two species of bats hibernating in limestone tunnels. *Acta Theriol.* 32:331–332.

- HAYSSEN, V., and R. C. LACY. 1985. Basal metabolic rates in mammals: taxonomic differences and the allometry of BMR and body mass. *Comp. Biochem. Physiol.* 81A:741-754.
- HELDMAIER, G., and T. RUF. 1992. Body temperature and metabolic rate during natural hypothermia in endotherms. *J. Comp. Physiol.* 162B:696-706.
- HELLER, H. C., and G. W. COLLIVER. 1974. CNS regulation of body temperature during hibernation. *Am. J. Physiol.* 227:583-589.
- HERREID, C. F., II, and B. KESSEL. 1967. Thermal conductance in birds and mammals. *Comp. Biochem. Physiol.* 21:405-414.
- HIEBERT, S. M. 1990. Energy costs and temporal organization of torpor in the rufous hummingbird (*Selasphorus rufus*). *Physiol. Zool.* 63:1082-1097.
- HILDWEIN, G. 1970. Capacités thermorégulatrices d'un mammifère insectivore primitive, le tenrec; leurs variations saisonnières. *Arch. Sci. Physiol.* 24:55-71.
- HILL, R. W. 1975. Daily torpor in *Peromyscus leucopus* on an adequate diet. *Comp. Biochem. Physiol.* 51A:413-423.
- HOCK, R. J. 1951. The metabolic rates and body temperatures of hibernating bats. *Biol. Bull.* 101:289-299.
- . 1960. Seasonal variations in physiologic functions of Arctic ground squirrels and black bears. *Bull. Museum Comp. Zool.* 124:155-171.
- HOFFMANN, R., and R. PRINZINGER. 1984. Torpor und Nahrungsausnutzung bei 4 Mausvogelarten (Coliiformes). *J. Ornithol.* 125:225-237.
- HUDSON, J. W. 1965. Temperature regulation and torpidity in the pygmy mouse, *Baiomys taylori*. *Physiol. Zool.* 38:243-254.
- . 1973. Torpidity in mammals. Pages 97-165 in G. C. WHITTOW, ed. *Comparative physiology of thermoregulation*. Academic Press, New York.
- HUDSON, J. W., and D. R. DEEVERS. 1973. Thermoregulation at high ambient temperatures of six species of ground squirrels (*Spermophilus* spp.) from different habitats. *Physiol. Zool.* 46:95-109.
- HUDSON, J. W., and I. M. SCOTT. 1979. Daily torpor in the laboratory mouse, *Mus musculus* var. albino. *Physiol. Zool.* 52:205-218.
- JONES, C. J., and F. GEISER. 1992. Prolonged and daily torpor in the feathertail glider, *Acrobates pygmaeus* (Marsupialia: Acrobatidae). *J. Zool. Lond.* 227:101-108.
- KAYSER, C. 1939. Exchanges respiratoires des hibernants réveillés. *Ann. Physiol. Physicochim. Biol.* 15:1087-1219.
- . 1961. *The physiology of natural hibernation*. Pergamon, Oxford.
- . 1964. La dépense d'énergie des mammifères en hibernation. *Arch. Sci. Physiol.* 18:137-150.
- KENAGY, G. J., and D. VLECK. 1982. Daily temporal organisation of metabolism in small mammals: adaptation and diversity. Pages 322-337 in J. ASCHOFF, S. DAAN, and G. GROOS, eds. *Vertebrate circadian systems*. Springer, Berlin and Heidelberg.
- KIRSCH, R., A. OUAROUR, P. PEVET. 1991. Daily torpor in the Djungarian hamster (*Phodopus sungorus*): photoperiodic regulation, characteristics and circadian organization. *J. Comp. Physiol.* 168A:121-128.
- KRISTOFFERSSON, R., and A. SOIVIO. 1964. Hibernation of the hedgehog (*Erinaceus europaeus* L.). The periodicity of hibernation of undisturbed animals during the winter in a constant ambient temperature. *Ann. Acad. Sci. Fenn., A IV, Biol.* 80: 1-22.

- KRÜGER, K. R., R. PRINZINGER, and K.-L. SCHUCHMANN. 1982. Torpor and metabolism in hummingbirds. *Comp. Biochem. Physiol.* 73A:679–689.
- KULZER, E. 1965. Temperaturregulation bei Fledermäusen (Chiroptera) aus verschiedenen Klimazonen. *Z. Vergleichende Physiol.* 50:1–34.
- KULZER, E., J. E. NELSON, J. L. MCKEAN, and P. F. MÖHRES. 1970. Untersuchungen über die Temperaturregulation australischer Fledermäuse. *Z. Vergleichende Physiol.* 69:426–451.
- LASIEWSKI, R. C. 1963. Oxygen consumption of torpid, resting, active and flying hummingbirds. *Physiol. Zool.* 36:122–140.
- LIGON, J. D. 1970. Still more responses of the poor-will to low temperatures. *Condor* 72:496–498.
- LYMAN, C. P. 1948. The oxygen consumption and temperature regulation in hibernating hamsters. *J. Exp. Zool.* 109:55–78.
- . 1958. Oxygen consumption, body temperature and heart rate of woodchucks entering hibernation. *Am. J. Physiol.* 194:83–91.
- LYNCH, G. R., J. BUNIN, and J. E. SCHNEIDER. 1980. The effect of constant light and dark on the circadian nature of daily torpor in *Peromyscus leucopus*. *Int. J. Biometeorol.* 24:49–55.
- MACMILLEN, R. E. 1965. Aestivation in the cactus mouse *Peromyscus eremicus*. *Comp. Biochem. Physiol.* 16:227–247.
- . 1983. Adaptive physiology of heteromyid rodents. *Great Basin Nat. Memoirs* 7:65–76.
- MACMILLEN, R. E., and J. E. NELSON. 1969. Bioenergetics and body size in dasyurid marsupials. *Am. J. Physiol.* 217:1246–1251.
- MACMILLEN, R. E., and C. H. TROST. 1967. Nocturnal hypothermia in the Inca dove, *Scardafella inca*. *Comp. Biochem. Physiol.* 23:243–253.
- MARSHALL, J. T. 1955. Hibernation in captive goatsuckers. *Condor* 57:129–134.
- M McNAB, B. K., and P. R. MORRISON. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. *Ecol. Monogr.* 33:63–82.
- MICHENER, G. R. 1993. Sexual differences in hibernaculum content of Richardson's ground squirrels: males store food. Pages 109–118 in C. CAREY, G. L. FLORANT, B. A. WUNDER, and B. HORWITZ, eds. *Life in the cold: ecological, physiological and molecular mechanisms*. Westview, Boulder, Colo.
- MORHARDT, J. E. 1970. Body temperatures of white-footed mice (*Peromyscus* sp.) during daily torpor. *Comp. Biochem. Physiol.* 33:423–439.
- MORRISON, P. R. 1960. Some interrelations between weight and hibernation function. *Bull. Museum Comp. Zool.* 124:75–91.
- MORRISON, P. R., and B. K. McNAB. 1962. Daily torpor in a Brazilian murine opossum (*Marmosa*). *Comp. Biochem. Physiol.* 6:57–68.
- MORTON, S. R., and A. K. LEE. 1978. Thermoregulation and metabolism in *Planigale maculata* (Marsupialia: Dasyuridae). *J. Therm. Biol.* 3:117–120.
- MUCHLINSKI, A. E., and E. N. RYBAK. 1978. Energy consumption of resting and hibernating meadow jumping mice. *J. Mammal.* 59:435–437.
- MUTCH, G. P., and M. ALEKSIUK. 1977. Ecological aspects of winter dormancy in the striped skunk (*Mephitis mephitis*). *Can. J. Zool.* 55:607–615.

- NAGEL, A. 1977. Torpor in the European white-toothed shrews. *Experientia* 33:1454–1456.
- . 1985. Sauerstoffverbrauch, Temperaturregulation und Herzfrequenz bei europäischen Spitzmäusen (Soricidae). *Z. Säugetierkunde* 50:249–266.
- NEUMANN, R. L., and T. J. CADE. 1965. Torpidity in the Mexican ground squirrel, *Citellus mexicanus parvidens* (Mears). *Can. J. Zool.* 43:133–140.
- NICOL, S., N. A. ANDERSEN, and U. MESCH. 1992. Metabolic rate and ventilatory pattern in the echidna during hibernation and arousal. Pages 150–159 in M. L. AUGEE, ed. *Platypus and echidnas*. Royal Zoological Society of New South Wales, Sydney.
- ORTMANN S. 1989. Jahreszeitliche Anpassung der Stoffwechselrate beim Alpenmurmeltier *Marmota marmota* (Linne): Winterschlaf und Normothermie. Ph.D. thesis. Philipps University, Marburg.
- PAJUNEN, I. 1983. Ambient temperature dependence of the body temperature and of the duration of hibernation periods in the garden dormouse, *Eliomys quercinus* L. *Cryobiology* 20:690–697.
- PENGELLEY, E. T. 1964. Responses of a new hibernator (*Citellus variegatus*) to controlled environments. *Nature* 203:892.
- PENGELLEY, E. T., and K. C. FISHER. 1961. Rhythmical arousal from hibernation in the golden-mantled ground squirrel, *Citellus lateralis tescorum*. *Can. J. Zool.* 39:105–120.
- PENGELLEY, E. T., and K. H. KELLY. 1966. A “circannian” rhythm in hibernating species of the genus *Citellus* with observations on the physiological evolution. *Comp. Biochem. Physiol.* 19:603–617.
- PIVORUN, E.B. 1976. A biotelemetry study of the thermoregulatory patterns of *Tamias striatus* and *Eutamias minimus* during hibernation. *Comp. Biochem. Physiol.* 53A:265–271.
- POHL, H. 1961. Temperaturregulation und Tagesperiodik des Stoffwechsels bei Winterschläfern. *Z. Vergleichende Physiol.* 45:109–153.
- . 1987. Circadian pacemaker does not arrest in deep hibernation: evidence for desynchronisation from light cycle. *Experientia* 43:293–294.
- PRINZINGER, R., R. GÖPPEL, A. LORENZ, and E. KULZER. 1981. Body temperature and metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. *Comp. Biochem. Physiol.* 69A:689–692.
- PRINZINGER, R., and K. SIEDLE. 1986. Experimenteller Nachweis von Torpor bei jungen Mehlschwalben. *J. Ornithol.* 127:95–96.
- . 1988. Ontogeny of metabolism, thermoregulation and torpor in the house martin *Delichon u. urbica* (L.) and its ecological significance. *Oecologia* 76:307–312.
- RANSOME, R. 1990. *The natural history of hibernating bats*. Helm, London.
- REINERTSEN, R. E. 1983. Nocturnal hypothermia and its energetic significance for small birds living in the arctic and subarctic regions: a review. *Polar Res.* 1:269–284.
- RUF, T., S. STEINLECHNER, and G. HELDMAIER. 1989. Rhythmicity of body temperature and torpor in the Djungarian hamster, *Phodopus sungorus*. Pages 53–62 in A. MALAN and B. CANGUILHEM, eds. *Living in the cold*. Libbey, London.

- RUF, T., A. STIEGLITZ, S. STEINLECHNER, J. L. BLANK, and G. HELDMAIER. 1993. Cold exposure and food restriction facilitate physiological responses to short photoperiod in Djungarian hamsters (*Phodopus sungorus*). *J. Exp. Zool.* 276:104–112.
- SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, and L. IRVING. 1950. Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.* 99:237–258.
- SCHOLL, P. 1974. Temperaturregulation beim madegassischen Igeltenrek *Echinops telfairi* (Martin 1838). *J. Comp. Physiol.* 89:175–195.
- SNAPP, B. D., and H. C. HELLER. 1981. Suppression of metabolism during hibernation in ground squirrels (*Citellus lateralis*). *Physiol. Zool.* 54:297–307.
- STRUMWASSER, F. 1960. Some physiological principles governing hibernation in *Citellus beecheyi*. *Bull. Museum Comp. Zool.* 124:282–318.
- TANNENBAUM, M., and E. PIVORUN. 1984. Differences in daily torpor patterns among three southeastern species of *Peromyscus*. *J. Comp. Physiol.* 154B:233–236.
- THAETI, H. 1978. Seasonal differences in O₂ consumption and respiratory quotient in a hibernator (*Erinaceus europaeus*). *Ann. Zool. Fenn.* 15:69–7.
- THOMPSON, S. D. 1985. Subspecific differences in metabolism, thermoregulation, and torpor in the western harvest mouse *Reithrodontomys megalotis*. *Physiol. Zool.* 58:430–444.
- TUCKER, V. A. 1965. Oxygen consumption, thermal conductance, and torpor in the Californian pocket mouse *Perognathus californicus*. *J. Cell. Comp. Physiol.* 65:393–404.
- WALHOVD, H. 1976. Partial arousal from hibernation in a pair of common dormice, *Muscardinus avellanarius* (Rodentia, Gliridae), in their natural hibernaculum. *Oecologia* 25:321–330.
- WANG, L. C. H. 1978. Energetics and field aspects of mammalian torpor: the Richardson's ground squirrel. Pages 109–145 in L. C. H. WANG and J. W. HUDSON, eds. *Strategies in cold*. Academic Press, New York.
- . 1989. Ecological, physiological, and biochemical aspects of torpor in mammals and birds. Pages 361–401 in L. C. H. WANG, ed. *Advances in comparative and environmental physiology*. Springer, Berlin and Heidelberg.
- WANG, L. C. H., and J. W. HUDSON. 1970. Some physiological aspects of temperature regulation in normothermic and torpid hispid pocket mouse, *Perognathus hispidus*. *Comp. Biochem. Physiol.* 32:275–293.
- . 1971. Temperature regulation in normothermic and hibernating eastern chipmunk, *Tamias striatus*. *Comp. Biochem. Physiol.* 38A:59–90.
- WATTS, P. D., N. A. ØRITSLAND, C. JONKEL, and K. RONALD. 1981. Mammalian hibernation and the oxygen consumption of a denning black bear (*Ursus americanus*). *Comp. Biochem. Physiol.* 69A:121–123.
- WITHERS, P. C. 1977. Respiration, metabolism, and heat exchange of euthermic and torpid poorwills and hummingbirds. *Physiol. Zool.* 50:43–52.
- WITHERS, P. C., K. C. RICHARDSON, and R. D. WOOLLER. 1990. Metabolic physiology of euthermic and torpid honey possums, *Tarsipes rostratus*. *Aust. J. Zool.* 37:685–693.
- WOLF, L. W., and F. R. HAINSWORTH. 1972. Environmental influence on regulated body temperature in torpid hummingbirds. *Comp. Biochem. Physiol.* 41A:167–173.
- WYSS, O. A. M. 1932. Winterschlaf und Wärmehaushalt, untersucht am Siebenschläfer (*Myoxus glis*). *Pflügers Arch.* 229:599–635.