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# Allometries of the durations of torpid and euthermic intervals during mammalian hibernation: A test of the theory of metabolic control of the timing of changes in body temperature

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**Summary.** The durations of the intervals of torpor and euthermia during mammalian hibernation were found to be dependent on body mass. These relationships support the concept that the timing of body temperature changes is controlled by some metabolic process. Data were obtained from species spanning nearly three orders of magnitude in size, that were able to hibernate for over six months without food at 5 °C. The timing of body temperature changes was determined from the records of copper-constantan thermocouples placed directly underneath each animal. Because all species underwent seasonal changes in their patterns of hibernation, animals were compared in midwinter when the duration of euthermic intervals was short and relatively constant and when the duration of torpid intervals was at its longest. Large hibernators remained euthermic longer than small hibernators (Fig. 2). This was true among and within species. The duration of euthermic intervals increased with mass at the same rate ($\text{mass}^{0.38}$) that mass-specific rates of euthermic metabolism decrease, suggesting that hibernators remain at high body temperatures until a fixed amount of metabolism has been completed. These data are consistent with the theory that each interval of euthermia is necessary to restore some metabolic imbalance that developed during the previous bout of torpor. In addition, small species remained torpid for longer intervals than large species (Fig. 3). The absolute differences between different-sized species were large, but, on a proportional basis, they were comparatively slight. Mass-specific rates of metabolism during torpor also appear to be much less dependent on body mass than those during euthermia, but the precision of these metabolic measurements is insufficient for them to provide a conclusive test of the metabolic theory. Finally, small species with high mass-specific rates of euthermic metabolism are under tighter energetic constraints during dormancy than large species. The data presented here show that, in midwinter, small species compensate both by spending less time at high body temperatures following each arousal episode and by arousing less frequently, although the former is far more important energetically than the latter.

## Introduction

The large and repetitive changes in body temperature that mammalian hibernators exhibit throughout dormancy are enigmatic from both adaptive and mechanistic points of view. Low body temperatures are associated with low rates of energy expenditure, and as such are essential for small mammals that must survive for many months on limited stores of energy. However, all hibernators periodically arouse and then briefly thermoregulate at euthermic levels despite the considerable energetic costs involved. From an energetic perspective the arousals appear counterproductive, and thus it is generally assumed that they have some, as yet unknown, physiological function.

An oft-cited theory suggests that arousals may be triggered by, and the subsequent euthermic intervals necessary for the elimination of, some chemical imbalance that builds up while mammals metabolize at low body temperatures (Fisher 1964). Although direct evidence of such a metabolic imbalance is lacking, links among rates of metabolism and the durations of both euthermic and torpid intervals in midwinter are apparent. The

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concept that arousals are initiated when some imbalance reaches a critical level is supported by the observations that within a species: (1) arousal frequency in midwinter and metabolic rates during deep torpor scale similarly ($Q_{10} \approx 2.4$ for ground squirrels) with respect to temperature (Twente and Twente 1965; Hammel et al. 1968); (2) arousal frequency increases when body temperature is actively regulated at a gradient above ambient during torpor (Pengelley and Kelley 1966; Lachiver and Boulouard 1967; Soivio et al. 1968); and (3) individuals become more irritable and likely to arouse prematurely in response to environmental disturbances as each bout of torpor progresses (Twente and Twente 1968). Similarly, the idea that hibernators in midwinter remain euthermic only long enough to restore metabolic homeostasis is consistent with the findings that: 1) the euthermic intervals of an individual are shorter than normal following bouts of torpor that are terminated prematurely by environmental disturbances (French 1982a); and 2) within a species, the durations of euthermic intervals following undisturbed torpors are inversely related to rates of euthermic metabolism (French 1982a).

If the mechanism that triggers arousals from and re-entries into torpor is similar among different species of hibernators, then the above metabolic theory would predict that the durations of euthermic and torpid intervals in midwinter should each scale with body size in a relationship inverse to that of mass-specific rates of metabolism during euthermia and torpor respectively. The present investigation tests these predictions using data collected from a series of long-term hibernators that span nearly three orders of magnitude in size.

## Materials and methods

The bats (*Myotis lucifigus, Pipistrellus subflavus, Eptesicus fuscus*) and rodents (*Zapus princeps, Spermophilus beldingi, S. lateralis, Marmota flaviventris*) used in this study were chosen to minimize the possibility that differences in hibernation performance were due to factors other than those related directly to body size. These hibernators are similar in that they store energy in the form of body fat, can survive a hibernation season lasting over six months without eating, and do not regulate body temperature at a large gradient above a 5 °C ambient during torpor in midwinter. All species except *Pipistrellus* coexist in restricted areas of the eastern Sierra Nevada of California and thus can be exposed to similar macroenvironmental conditions in nature.

All species of rodents were captured during 1977–1981 in Mono and Nevada Counties, CA, and additional *Zapus* were collected in Wasatch County, Utah in 1982. Except in the case of an adult male marmot that was in captivity for two years, patterns of hibernation were monitored in the winter following each animal's capture. Prior to experimentation, the rodents were maintained at 22–25 °C on a diet of sunflower seeds, Purina laboratory chow, a variety of fresh fruits and vegetables, and water ad libitum. When each animal became lethargic or reached its seasonal peak in body weight, food was removed and it was placed in a constant-temperature (±0.5 °C) environmental room held at 5 °C with constant dim (less than 0.05 watts/m$^2$) illumination. Most animals began hibernating within a couple of days. Bats were collected from caves in northern Illinois at the start of the 1981 hibernation season. They were immediately transported by air to Riverside, and resumed hibernation when placed into the 5 °C environmental rooms. Rodents were caged individually and each hibernated inside a nest box containing cotton. Bats were kept singly in small plastic tubes suspended above water in an insulated ice chest. Each bat hung from a strip of hardware cloth that was positioned in the tube such that the distance the animal could move was no more than one body length.

The timing of entrances into and arousals from hibernation was determined from the records of copper-constantan thermocouples attached to the hardware cloth in each bat's plastic tube or to the floor of each rodent's nest box. The thermocouples were connected to 24-channel Honeywell recording potentiometers, and the temperature directly underneath each animal was recorded at 3–6 minute intervals. A euthermic animal produced a temperature record several degrees above room temperature. A slow decline in temperature, the rate of which varied with body size, occurred when an animal entered hibernation, and this was easily distinguished from the abrupt drop in temperature that occurred each time an active rodent momentarily left its nest box.

An episode of torpor was taken to include both the entry interval when body temperature declined and the interval of deep torpor when body temperature approximated ambient. It was calculated from the start of the slow decline in the temperature record to the first evidence of an increase in temperature at the start of the succeeding arousal. The duration of a euthermic interval was defined as the time between the end of the arousal (warming) process and the start of the entry into the next bout of torpor. This was calculated from the cessation of the temperature rise associated with an arousal to the start of the gradual decline in temperature back towards ambient. All times were rounded off to the nearest 10 min. The accuracy of this method was estimated in animals not used in the long-term experiments by comparing its results with those obtained simultaneously from direct measurements of body temperature using either radiotelemetry (*Spermophilus beldingi*) or rectal thermocouple probes (*Myotis, Zapus, Marmota*). As size increased, the rates of changes in body temperature slowed and the accuracy of the indirect measurements decreased. However, when expressed as a percentage, errors in the duration of the euthermic intervals were independent of body size and rarely exceeded 5%. Errors in the durations of the long torpors never exceeded 0.5% and were judged to be inconsequential.

## Results

The durations of bouts of torpor changed seasonally with general patterns that were independent of body size (Fig. 1). These changes made it necessary to compare individuals at equivalent points in their hibernation seasons, and I chose data, usually from midwinter, that represented the maximum hibernating ability for each animal. Previous studies (Twente and Twente 1965; Twente et al.

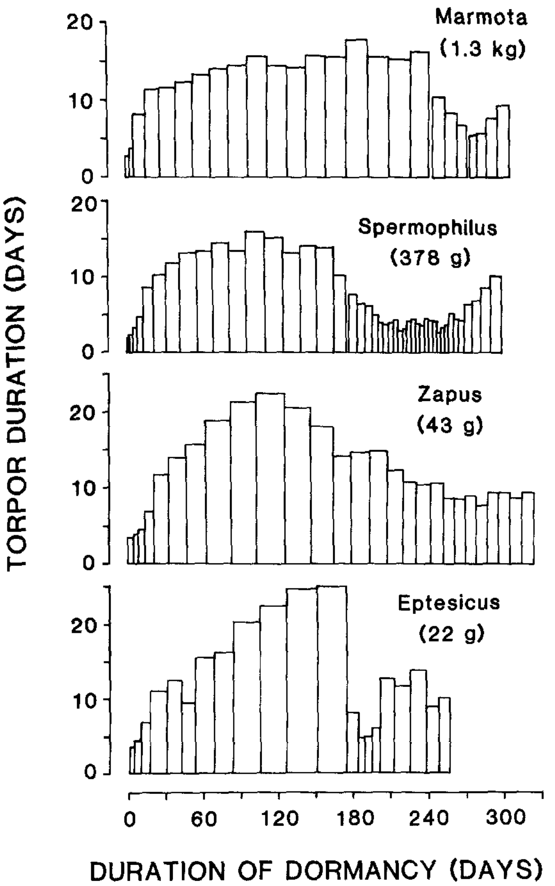

**Fig. 1.** Seasonal changes in the duration of sequential intervals of torpor in representative females of different-sized species kept at 5 °C without food. All are adults except *Marmota*. Note that all animals, regardless of size, showed an increase in duration of sequential torpors followed by a springtime decrease, and all survived for $8^1/_2$–10 months before their fat reserves were depleted. Adult *Marmota*, adult male *Spermophilus beldingi*, and a few large male *S. lateralis* spontaneously terminated hibernation after about 6 months in the cold and thus did not exhibit the springtime pattern of short torpors

1977; French 1982b) have divided the hibernation season into autumn, winter, and spring phases based on the duration of torpor bouts. However these are arbitrary distinctions and are especially subjective when applied to species that show continuous changes in the duration of sequential torpors throughout the winter. To standardize the analysis, animals were compared on the basis of their longest and the average of their five longest bouts of torpor. In contrast, the durations of euthermic intervals reported here represent minimal values and are averages of those intervals that occurred during the period when an individual's torpor bouts were longer than 50% of maximum. Euthermic intervals that followed arousals induced prematurely by environmental disturbances were excluded from the analysis. Many *Myotis* and *Pipistrellus* had unexpectedly-short torpors and died after only two to four months in the cold. I felt that the conditions in captivity were probably inappropriate because these bats normally have much longer hibernation seasons in nature, and thus torpors from individuals that did not hibernate for over six months were also excluded. There did not appear to be a systematic variation in the fraction of mass lost by the time torpor duration reached a maximum, and thus prehibernation mass was used as an estimate of body size.

The amount of time hibernators spent at high body temperatures following periodic arousals was a positive function of their size (Fig. 2). Data were fitted best by power functions where the duration of euthermic intervals was proportional to mass$^{0.38}$ (all species) or mass$^{0.32}$ (rodents only). This general relationship appears to hold for intraspecific comparisons as well as interspecific ones. Two species in which juveniles do not grow to adult size prior to their first hibernation exhibited large variations in body mass. Size differences were most pronounced in *Marmota flaviventris*, and the intraspecific scaling of the duration of euthermic intervals is obvious from the data in Fig. 2. *Spermophilus beldingi* showed less variation in size, but large individuals also remained euthermic longer than small ones. This is true not only at 5 °C, but at 10 °C and 15 °C as well (French 1982a).

In contrast to the trend in euthermic intervals, the maximum duration of torpor bouts was inversely related to body mass (Fig. 3). There was approximately a 400-hour difference in duration of the longest torpor between bats and marmots. However, large species tended to have numerous long torpors of relatively constant duration in midwinter whereas small species were more likely to display progressive changes in the duration of sequential torpors (Fig. 1). Thus, when the five longest bouts of torpor were averaged, the magnitude of the size dependency was reduced (Fig. 3). Although these absolute values were large, the proportional differences between individuals were comparatively slight. Across the entire range of hibernators, there was only a two-fold difference in the duration of the longest torpors as compared to an order of magnitude difference in the duration of euthermic intervals.

## Discussion

The relationship between the duration of euthermic intervals and body mass supports the idea that some metabolic process controls the timing of body temperature changes during mammalian hi-

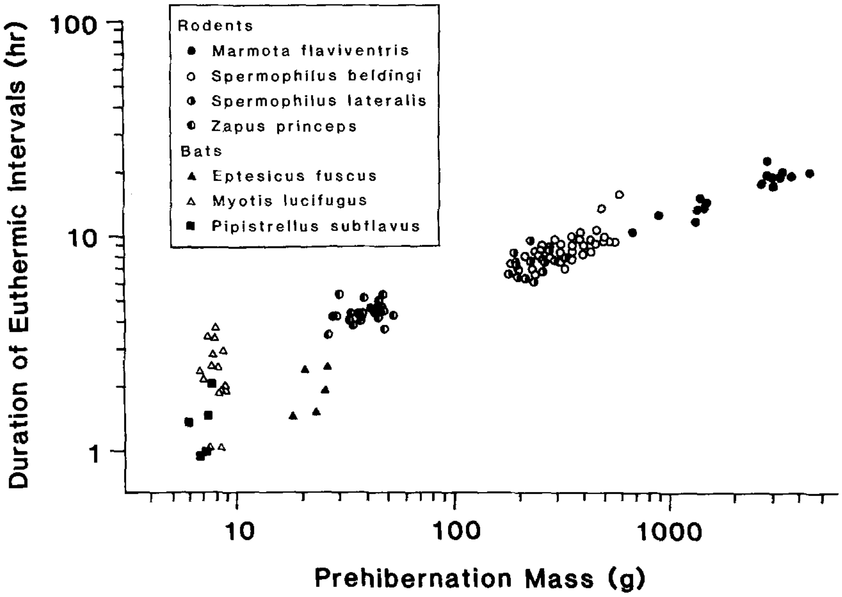

**Fig. 2.** The duration of the euthermic portions of arousal episodes as a function of body mass for mammals that hibernated undisturbed in 5 °C cold rooms without food. Each point represents the average of all the euthermic intervals (6–18) following torpors that were greater than 50% of maximum for one animal. Data are described best ($r^2=0.89$) by the equation $D_e=0.98\ M^{0.38}$ where $D_e$ is the duration of euthermic intervals in hours and $M$ is prehibernation mass in grams. When bats, that lacked cotton insulation and that showed large intraindividual variation, are excluded, the equation becomes $D_e=1.44\ M^{0.32}$ ($r^2=0.92$). The 95% confidence limit for both exponents is 0.02. Data for *S. lateralis* and *Z. princeps* fall within the range of values reported previously for those species (Torke and Twente 1977; Cranford 1983)

bernation. If a metabolic imbalance develops during torpor and is somehow eliminated during the subsequent euthermic interval, then the lower the rate of elimination, the longer the animal must remain euthermic prior to the next torpor bout. Kleiber (1975) has pointed out that the rate at which a given concentration of a substance is cleared from (or added to) the body is a function of mass-specific rates of metabolism. For euthermic hibernators, mass-specific rates of basal metabolism are proportional to mass$^{-0.38}$ (Kayser 1950), a value similar to those obtained from other subsets of small mammals (Withers et al. 1979; Vleck and Kenagy 1982). Thus, as body size increases, the duration of euthermic intervals increases (Fig. 2) at the same rate that mass-specific rates of basal metabolism decrease. This implies that hibernators remain euthermic until they have completed a fixed amount of metabolism; precisely what would be expected if they were restoring a metabolic imbalance, the magnitude of which was similar among species. The positive correlation between ambient temperature and duration of euthermic episodes in ground squirrels (French 1982a) suggests that the allometry of total, rather than basal, metabolic rates should be used in the above comparison of animals kept at 5 °C. This was not done because (1) such an allometric relationship has not yet been constructed (although those specific metabolic rates should also decrease with increasing body size), and (2) a similar influence of ambient temperature on the duration of euthermic intervals in *Zapus princeps* was not obvious (unpublished data).

The allometry of torpor duration (Fig. 3) is suggestive of a metabolic influence, but it provides a less-useful test of that concept because the precise relationship between metabolic rates during torpor and body mass is not known. If the metabolic theory is correct, then the data from Fig. 3 suggest that, at a constant ambient temperature, mass-specific rates of metabolism while torpid in midwinter should scale approximately with mass$^{0.1}$. At first glance this appears contrary to expectations based upon an extrapolation from the allometry of euthermic metabolic rates. In other words, it might be expected that mass-specific rates of torpor metabolism should scale with mass in a similar fashion to basal rates of euthermic metabolism (i.e. mass$^{-0.38}$) provided that the rate of change of metabolism with changes in body temperature is the same for all hibernators. However, this extrapolation may not be valid for two reasons. First, the rate at which metabolism changes with body temperature as the hibernator goes from a euthermic to a torpid state appears to be inversely related to mass (Kayser 1950; Morrison 1960; Morrison and Ryser 1962). $Q_{10}$ values for metabolism, calculated between basal rates during euthermia ($T_b>$ 35 °C) and minimal rates during deep torpor, lie between 3.4 and 4.2 in small bats (Kayser 1940; Hock 1951; Herreid 1963; Henshaw 1968) and jumping mice (Morrison and Ryser 1962), whereas they usually range between 2.0 and 2.5 in larger ground squirrels (Snapp and Heller 1981), and marmots (Kayser 1950; Florant and Heller 1977). The difference in these $Q_{10}$'s cannot be satisfactorily explained by the erroneous use of euthermic

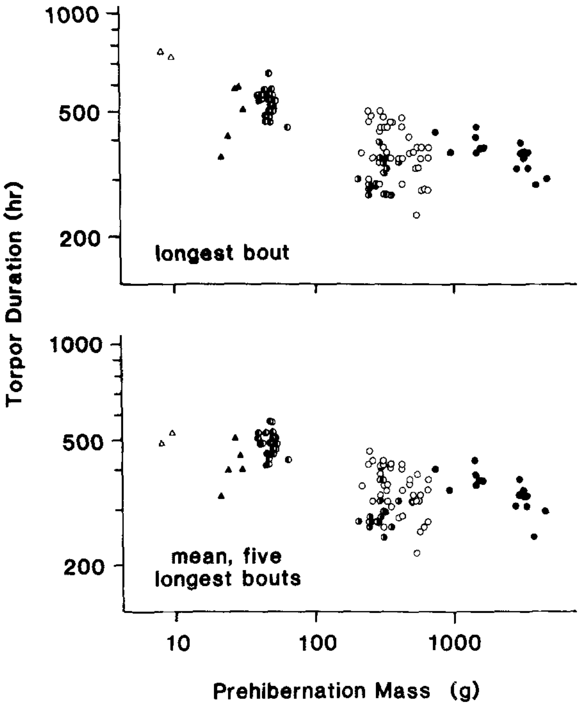

**Fig. 3.** The maximum length of time mammals remained continuously torpid as a function of body mass for individuals that survived for over 6 months in 5 °C cold rooms without food. Symbols are as in Fig. 2. Data on the longest and the average of the five longest bouts of torpor are described by the equations $D_t = 6.65\,M^{-0.11}$ ($r^2 = 0.42$) and $D_t = 6.46\,M^{-0.09}$ ($r^2 = 0.38$) respectively, where $D_t$ is torpor duration in hours and $M$ is prehibernation mass in grams. The exponents of these equations are significantly different from zero ($P < 0.001$) but are not different from each other ($P = 0.82$)

rates elevated by activity or thermoregulatory thermogenesis, and at the moment the basis for them is unknown. Second, the minimum gradient between body and ambient temperatures during torpor is a positive function of mass (Morrison 1960; Kayser 1963, 1964). Thus at any ambient temperature, small species may undergo a greater decrease in metabolic rate per degree reduction in body temperature, and also attain lower body temperatures during torpor than large species. Both these factors act to disproportionately reduce the metabolic rate of small hibernators and thereby negate the presumed "metabolic advantage" of large body size.

At present, the empirical basis for constructing an appropriate allometry of metabolism during torpor is lacking. Kayser (1950) initially reported that the minimum mass-specific metabolism of torpid hibernators scaled with mass$^{-0.08}$, but, with the addition of more data, he later revised that to mass$^{-0.02}$ (Kayser 1964). Certainly 0.02 is not too dissimilar from an exponent of $-0.1$ predicted from Fig. 3. However, Kayser's calculations were based on data from animals at a variety of ambient and body temperatures. The few measurements made at an ambient of 5 ± 1 °C also show no obvious trend with size (Table 1), but these data are either quite variable or are averages computed from a variety of experimental conditions and their accuracy is insufficient to provide an unequivocal test of the metabolic theory. Such a test requires not only that the metabolic measurements be precise but also that they coincide with measurements of torpor duration. Thus in the present case, metabolic measurements during the longest bouts of torpor are needed. The necessity of this is obvious from an inspection of data collected by Cranford (1983) on *Zapus princeps*. The metabolic rate of mice torpid at an ambient temperature of 5 °C averaged 0.042 $mlO_2/g\cdot h$ at the beginning of the season when torpors averaged only 8.3 days in duration, but later decreased to an average of 0.024 $mlO_2/g\cdot h$ at a time when torpor duration had increased to an average of 21 days. Similar seasonal changes in torpid metabolism have been documented for hedgehogs (Tähti 1978). These changes in metabolism are likely associated with slight changes in the level at which body temperature is regulated during torpor. The metabolic

**Table 1.** Minimum rates of metabolism measured during torpor at an ambient temperature of 5 ± 1 °C

| Species | Mass(g) | MR (ml $O_2$/g·h) | Citation |
|---|---|---|---|
| *Pipistrellus pipistrellus* | 7 | 0.022 | Kayser (1940) |
| *Nyctalus noctula* | 24 | 0.022 | Kayser (1940) |
| *Zapus princeps* | 28[a] | 0.024[a] | Cranford (1983) |
| *Eliomys quercinus* | 37–88 | 0.029–0.039 | Kayser (1959) |
| *Spermophilus (Citellus) citellus* | 100–170 | 0.015–0.022 | Kayser (1950) |
| *Glis glis* | 165 | 0.016 | Kayser (1940) |
| *Spermophilus lateralis* | ~200 | 0.03 | Hammell et al. (1968) |
| *Cricetus cricetus* | 300[a] | 0.032 | Kayser (1959) |
| *Erinaceus europaeus* | 320–600 | 0.016–0.021 | Kayser (1950) |
|  | 272–890 | 0.011 | Tähti (1978) |
| *Spermophilus undulatus* | ~650 | 0.03 | Hock (1960) |
| *Erinaceus europaeus* | 1,073 | 0.028 | Kayser (1950) |
| *Marmota flaviventris* | ~2,500 | 0.018[b] | Florant and Heller (1977) |

[a] Average value

[b] Converted from Watts to ml $O_2$ assuming 4.184 J/cal and 4.7 cal/ml$O_2$

theory would also provide an explanation for the changes in duration of sequential torpors if such changes in metabolism occur gradually throughout the hibernation season.

If one assumes that mass-specific rates of metabolism during torpor are in fact independent of size, then the inverse relationship between the maximum duration of torpor and body mass (Fig. 3) could still be reconciled with the metabolic theory by hypothesizing that large species are slightly less tolerant of the proposed metabolic imbalance than small species. Although not as simple and therefore less appealing, this interpretation does little to alter the arguments based upon the allometry of euthermic intervals. If the trend in Fig. 3 reflects solely a differential tolerance to some metabolic imbalance, then the magnitude of that imbalance would be approximately proportional to $\text{mass}^{-0.09}$. If the rate that imbalance is restored during euthermia is proportional to $\text{mass}^{-0.38}$, then the time required for restoration would be proportional to $\text{mass}^{-0.09}/\text{mass}^{-0.38} = \text{mass}^{0.29}$; a value not significantly different from that obtained from the tight relationship between the duration of euthermic intervals and body mass in rodents (Fig. 2), or other measurements of physiological time in general (Lindstedt and Calder 1981).

Regardless of the physiological mechanisms involved, the allometric relationships reported here are interesting from the perspective of energy balance during hibernation. Over 70% of the energy used during the dormant season is consumed during the periodic arousals and subsequent intervals of euthermia (Wang 1979). Morrison (1960) has pointed out that, as size increases, the maximum amount of fat that is naturally stored by hibernators increases faster than absolute rates of euthermic metabolism (proportional to $\text{mass}^1$ vs $\text{mass}^{2/3}$). Thus, small hibernators that subsist solely on body fat are more constrained energetically than large ones. Since the duration of the hibernation season, although variable, is independent of size (Fig. 1), it follows that, in general, small species spend a smaller proportion of their time at high body temperatures than large species. The data presented here (Figs. 2, 3) show that, at least in midwinter, small hibernators compensate energetically both by arousing less frequently and by spending less time at high body temperatures following each arousal than large hibernators. However, the latter adaptation is by far the most important from an energetic standpoint.

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