Torpor Bout Duration during the Hibernation Season of Two Sciurid Rodents: Interrelations with Temperature and Metabolism

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Abstract

Torpor bouts of mammalian hibernators are generally shorter at the beginning and end and are consistently longer during the main part of the hibernation season. Because it is not known why the duration of torpor bouts changes at the beginning and end of the hibernation season, we studied this phenomenon in two sciurid rodents: Spermophilus saturatus *(200–300 g) and* Eutamias amoenus *(45–60 g). We examined the seasonal change in torpor bout duration during hibernation at a constant air temperature (T_a) of 2° C in relation to (1) the minimum body temperature (minimum T_b) to which the animals could be experimentally cooled before they maintained a constant T_b or began to arouse, (2) T_a at the time of minimum T_b (minimum T_a), and (3) oxygen consumption ($\dot{V}O_2$) of torpid individuals at T_a 2° C. Average duration of torpor bouts during the main part of the hibernation season was about 11 d in* S. saturatus *and 8–9 d in* E. amoenus*; in response to experimental cooling, minimum T_b of both species declined as low as −0.2° C. In early and late hibernation, when torpor bouts were short, minimum T_b, minimum T_a, and $\dot{V}O_2$ during torpor were higher than in the main part of the hibernation season. Regression analyses suggest that minimum T_b and minimum T_a are more strongly correlated with torpor bout duration than $\dot{V}O_2$ in both species.*

Introduction

Hibernating mammals rewarm spontaneously from torpor throughout the hibernating season at intervals of several days to several weeks (Pengelley and Fisher 1961; Pohl 1961). The duration of these torpor bouts differs not only among species, but also throughout the hibernation season. Torpor

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bouts are short at the beginning of hibernation and increase to a longer, more or less stable duration for most of the hibernation season until they shorten again toward the end (Wang 1978; French 1986).

Although seasonal differences in the duration of torpor bouts have been observed in many hibernating species, the physiological basis for this consistent pattern of change is not currently understood, nor is it known why the energetically expensive arousals from torpor occur at all (Lyman et al. 1982). However, body temperature (T_b) and oxygen consumption ($\dot{V}O_2$) of hibernators that are torpid at different air temperatures (T_a) are inversely related to the duration of torpor bouts (Twente and Twente 1965; Geiser and Kenagy 1988). This supports the view that the duration of torpor bouts may be determined by the body temperature and $\dot{V}O_2$ of the torpid animal.

We investigated whether seasonal changes in duration of torpor bouts are also related to changes in $\dot{V}O_2$. Furthermore, we determined whether the species-specific minimum T_b and T_a, at which T_b is regulated during torpor (Heller and Hammel 1972), are correlated with the seasonal changes in the duration of torpor bouts. We studied two members of the squirrel family (Sciuridae) that differ in both size and length of hibernation season. The golden-mantled ground squirrel, *Spermophilus saturatus* (200–300 g), hibernates in nature for about 7 mo, and the yellow pine chipmunk, *Eutamias amoenus* (45–60 g), hibernates for about 4–5 mo (Kenagy and Barnes 1988).

Material and Methods

Fourteen *Spermophilus saturatus* (five males and nine females) and six *Eutamias amoenus* (three males and three females) were captured near Fish Lake, Chelan County, Washington, transported to the University of Washington, and kept individually in cages provided with wood shavings. Purina Rodent Laboratory Chow and water were freely available throughout the experiment. From September 1, *S. saturatus* were exposed to an air temperature (T_a) of 12° ± 1°C and a photoperiod of 8L:16D (lights on 0800–1600 hours PST) in a walk-in controlled-temperature room. On September 30 the *E. amoenus* were transferred into the same room and T_a was lowered to 6° ± 1°C. The T_a was further decreased to 2° ± 1°C on October 17 and held at this temperature throughout the rest of the experiment. This temperature change corresponds to the autumnal decline in soil temperatures below 50 cm, a typical hibernaculum depth in the area from which the two species were captured (Kenagy, Sharbaugh, and Nagy 1989).

We determined duration of torpor bouts by observing the animals daily at 1000 hours for displacement of the sawdust that we placed on each animal's back on the day it was first observed torpid. Sawdust is displaced only when the animal has aroused during the previous 24 h. The $\dot{V}O_2$ of torpid animals at T_a 2°C was determined after we transferred them from their cages in the walk-in holding chamber to a 2-L respirometry vessel in a small temperature-controlled (±0.2°C) cabinet. Flow rates were 200 mL/min for *S. saturatus* and 80 mL/min for *E. amoenus*. After $\dot{V}O_2$ at T_a 2°C had stabilized for at least 30 min, we slowly cooled the respirometer (<0.02°C/min) until the animal increased its $\dot{V}O_2$, either to regulate T_b and avoid a further decline in T_b or to initiate arousal. When an animal began to increase its $\dot{V}O_2$, it was immediately removed from the respirometer and T_b was measured by 3-cm rectal insertion of a thermocouple probe. This temperature was designated as minimum T_b; the T_a at which the increase in $\dot{V}O_2$ occurred was called minimum T_a (Geiser and Kenagy 1987). To ascertain that the determination of the minimum T_b was reproducible, we measured five *E. amoenus* twice in November. The minimum T_b's of the two determinations, which were made within 8 d, were 1.88° ± 1.01°C and 1.70° ± 0.97°C, respectively, and the means were indistinguishable ($P > 0.5$; *t*-test). To maximize heat exchange with the air during cooling experiments, we suspended animals in a plastic mesh hammock in the respirometer (fig. 1). Because the sensitivity to disturbance increases toward the end of a torpor bout, cooling experiments were performed between days 2 and 4 of a bout and never later than what would have been the middle of a torpor bout, as determined from the length of undisturbed bouts at that time of the year. Duration of the hibernation season was also determined. However, since some individuals still showed short bouts of torpor at the end of the experiments, these values represent underestimations.

The $\dot{V}O_2$ was monitored continuously, after removal of H_2O and CO_2 from the airstream, with an Applied Electrochemistry S-3A oxygen analyzer and calculated according to Withers (1977). Flow rates were measured and controlled with a Brooks thermal mass flow controller. The T_a was measured continuously in the respirometer by thermocouple and recorded along with oxygen concentration on a Leeds and Northrup Speedomax 250 chart recorder. Point readings of T_a were taken using a Sensortek digital thermocouple thermometer, calibrated to the nearest 0.1°C with a mercury Bureau of Standards thermometer.

Numeric values are presented as means ± 1 SD.

Results

Hibernation of *Spermophilus saturatus* and *Eutamias amoenus* in the laboratory was strongly seasonal and similar in duration to the hibernation sea-

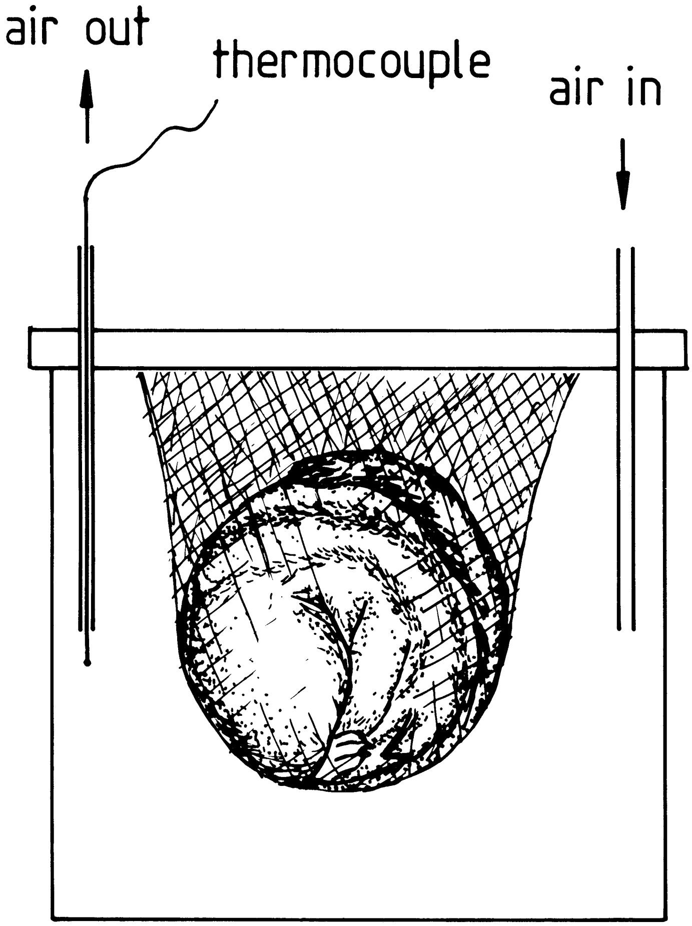

Fig. 1. Experimental setup for cooling experiments. Animals were suspended in a plastic mesh hammock in the respirometer to maximize heat exchange with surrounding air.

son in nature. *Spermophilus saturatus* hibernated for a mean of 7.4 ± 0.3 mo, which was longer than 5.6 ± 0.4 mo in *E. amoenus* ($P < 0.0001$; *t*-test).

The duration of torpor bouts in individuals of each species was short in the beginning of the hibernation season, increased to a more or less stable value during the main part of hibernation, and shortened again toward the end (fig. 2). In *S. saturatus* the increase and decrease of torpor bout duration at beginning and end of the hibernation season were gradual. In contrast, short bouts of about 4 d in *E. amoenus* at the beginning of hibernation season changed abruptly to long bouts that were about twice as long. At the end of hibernation some *E. amoenus* showed only two or three short bouts before becoming continuously homeothermic. The cooling experiments,

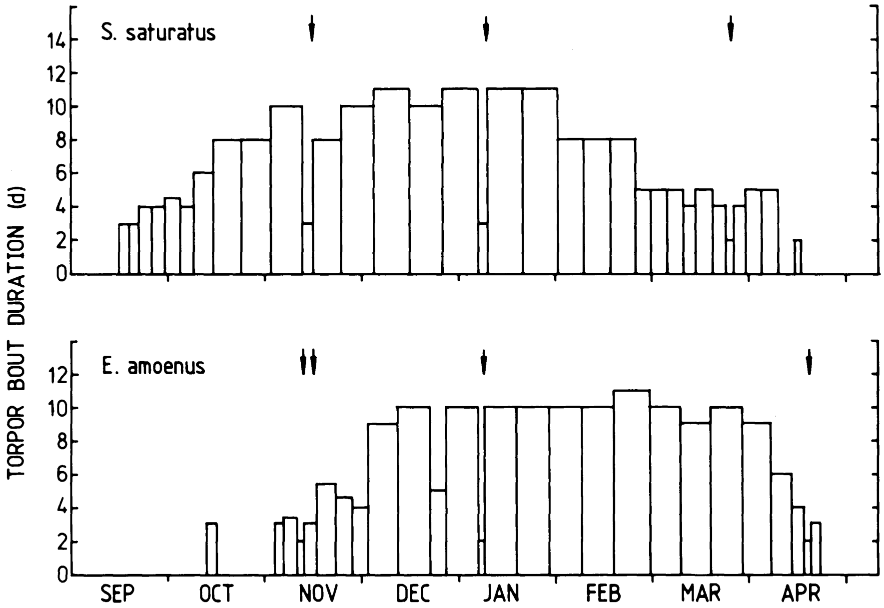

Fig. 2. Duration of torpor bouts and hibernation season in an individual Spermophilus saturatus *(upper) and* Eutamias amoenus *(lower). Each column represents one torpor bout. Arrows indicate time of cooling experiments, which disrupted torpor bouts.* T_a *was 2° C from October 17 to end of experiment.*

performed at three times during the hibernation season, interrupted the usual pattern by inducing premature arousal, but this did not appear to influence the length of subsequent bouts (fig. 2).

The average duration of torpor bouts at T_a 2°C in both *S. saturatus* and *E. amoenus* changed significantly with season (figs. 3 and 4). Torpor bout duration in *S. saturatus* increased from a mean of about 8 d in October/November to about 10–11 d from December to March. Shorter bouts of about 7 d were observed in April (fig. 3). *Eutamias amoenus* showed a similar pattern of torpor bout duration (fig. 4). Bouts of only 3–5 d were observed in October/November and in April, but the duration of torpor bouts was stable at a mean of about 8–9 d between December and March (fig. 4). Body masses of both species decreased steadily throughout the hibernation season (figs. 3 and 4).

The $\dot{V}O_2$, minimum T_b, and minimum T_a of both species also changed significantly with season: they were high during times of short torpor bouts and low during times of long torpor bouts (figs. 3 and 4). The minimum T_b in *S. saturatus* fell from a mean of 1.1° ± 0.4°C in November to 0.3° ± 0.3°C in January and rose again to 1.3° ± 1.3°C in April (fig. 3). In January, one

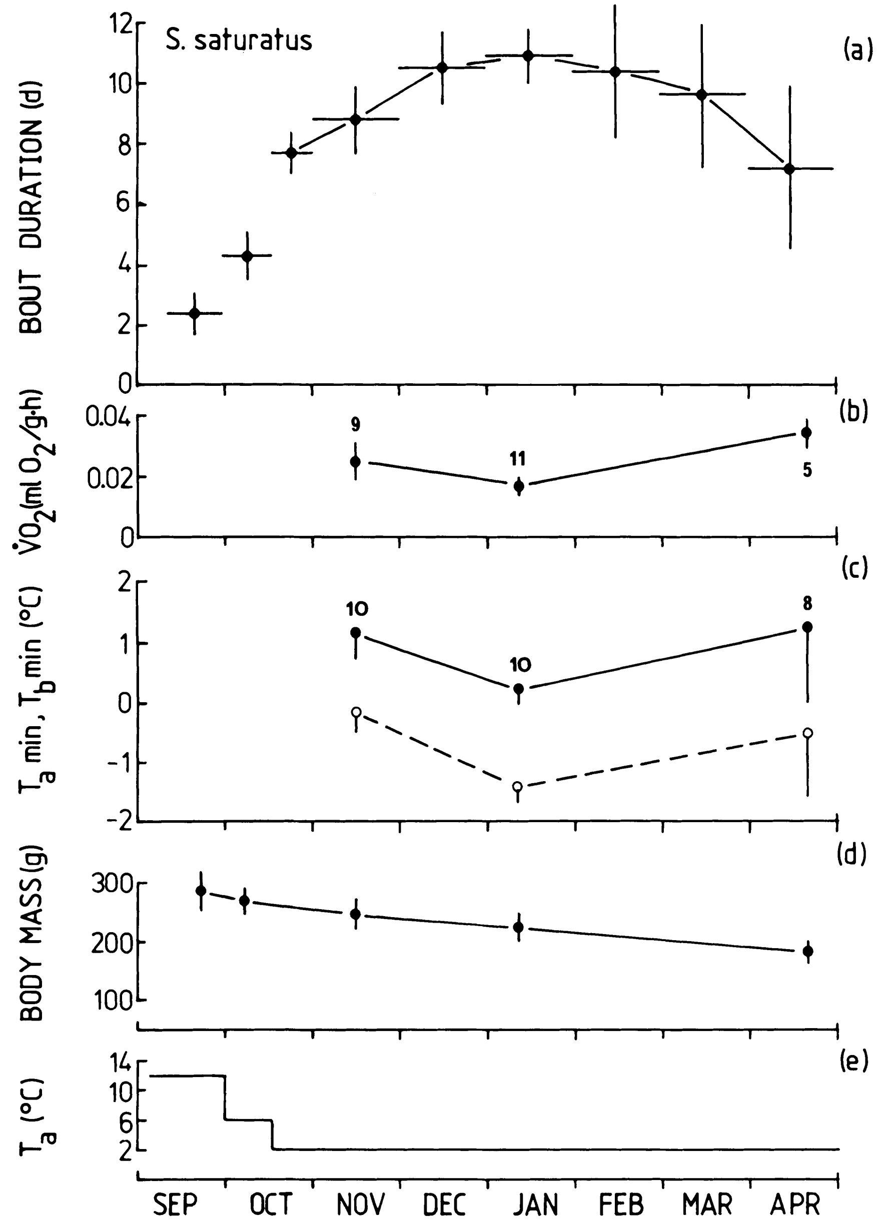

Fig. 3. Seasonal patterns, for Spermophilus saturatus, *of* (a) *duration of torpor bouts over the periods indicated by horizontal bars,* (b) *mass-specific* $\dot{V}O_2$ during torpor at T_a *2° C,* (c) *minimum* T_b *and* T_a (T_b *min,* T_a *min) of torpid animals experimentally cooled below* T_a *2° C,* (d) *body mass, and* (e) T_a *at which the animals were maintained and torpor durations determined. When torpor bouts extended over 2 calendar mo, the torpor bout was included in the month in which the longer part of the bout occurred. Values are means with SD. Duration of torpor bouts and body mass* (a, d) *were determined on 14 individuals from September to February and on 13*

individual showed a minimum T_b of −0.2°C. In *E. amoenus* the seasonal change was more pronounced; the mean minimum T_b was 1.8° ± 0.9°C in November, 0.1° ± 0.2°C in January, and 1.5° ± 1.0°C in April. In January, three of the six *E. amoenus* showed a minimum T_b that was 0.0°C or less, and the lowest value was −0.2°C. The minimum T_a of both species was about 1.5°C lower than the minimum T_b throughout our measurements (figs. 3 and 4). In January, the $\dot{V}\text{O}_2$ of *S. saturatus* was significantly lower than that of *E. amoenus* ($P < 0.001$; *t*-test), whereas the minimum T_b of the two species were indistinguishable ($P > 0.1$; *t*-test).

Because the seasonal changes in $\dot{V}\text{O}_2$, minimum T_b, and minimum T_a of torpid *S. saturatus* and *E. amoenus* all showed the same inverse relationship to torpor bout duration, we tested the amount of variation that can be explained by each of these variables. Linear regression analyses with torpor bout duration as dependent variable and minimum T_b, minimum T_a, and $\dot{V}\text{O}_2$ as independent variables suggest that torpor bout duration is negatively related to minimum T_b and minimum T_a (torpor bout duration vs. minimum T_b, *S. saturatus:* $r^2 = 0.47$, $P < 0.0001$, $n = 24$; *E. amoenus:* $r^2 = 0.53$, $P < 0.001$, $n = 14$; torpor bout duration vs. minimum T_a, *S. saturatus:* $r^2 = 0.48$, $P < 0.0001$, $n = 24$; *E. amoenus:* $r^2 = 0.55$, $P < 0.001$, $n = 14$). The $\dot{V}\text{O}_2$ was not as strongly correlated with torpor bout duration in both species (*S. saturatus:* $r^2 = 0.33$, $P < 0.0005$, $n = 24$; *E. amoenus;* $r^2 = 0.36$, $P < 0.01$, $n = 14$). When the minimum T_b or T_a were considered together with $\dot{V}\text{O}_2$ in multiple linear regression analyses, only slightly more of the variation of torpor bout duration could be explained than by either of the variables alone (torpor duration vs. minimum T_b and $\dot{V}\text{O}_2$, *S. saturatus:* $r^2 = 0.51$, $P < 0.0002$, $n = 24$; *E. amoenus:* $r^2 = 0.57$, $P < 0.01$, $n = 14$; torpor duration vs. minimum T_a and $\dot{V}\text{O}_2$, *S. saturatus:* $r^2 = 0.51$, $P < 0.002$, $n = 24$; *E. amoenus:* $r^2 = 0.57$, $P < 0.01$, $n = 14$).

Discussion

Comparative Seasonal Torpor Patterns

Under constant environmental conditions, both *Spermophilus saturatus* and *Eutamias amoenus* showed significant seasonal changes in torpor bout

individuals in March and April. Sample sizes for b *and* c *are shown in the figure. One-way ANOVA revealed significant seasonal changes in all the variables: duration of torpor bouts at* T_a *2° C (*F = *9.0; df = 6,89;* $P < 0.0001$*),* $\dot{V}\text{O}_2$ *(*F = *21.1; df = 2,22;* $P < 0.0001$*), minimum* T_b *(*F = *4.8; df = 2,25;* $P < 0.02$*), minimum* T_a *(*F = *10.1; df = 2,25;* $P < 0.001$*).*

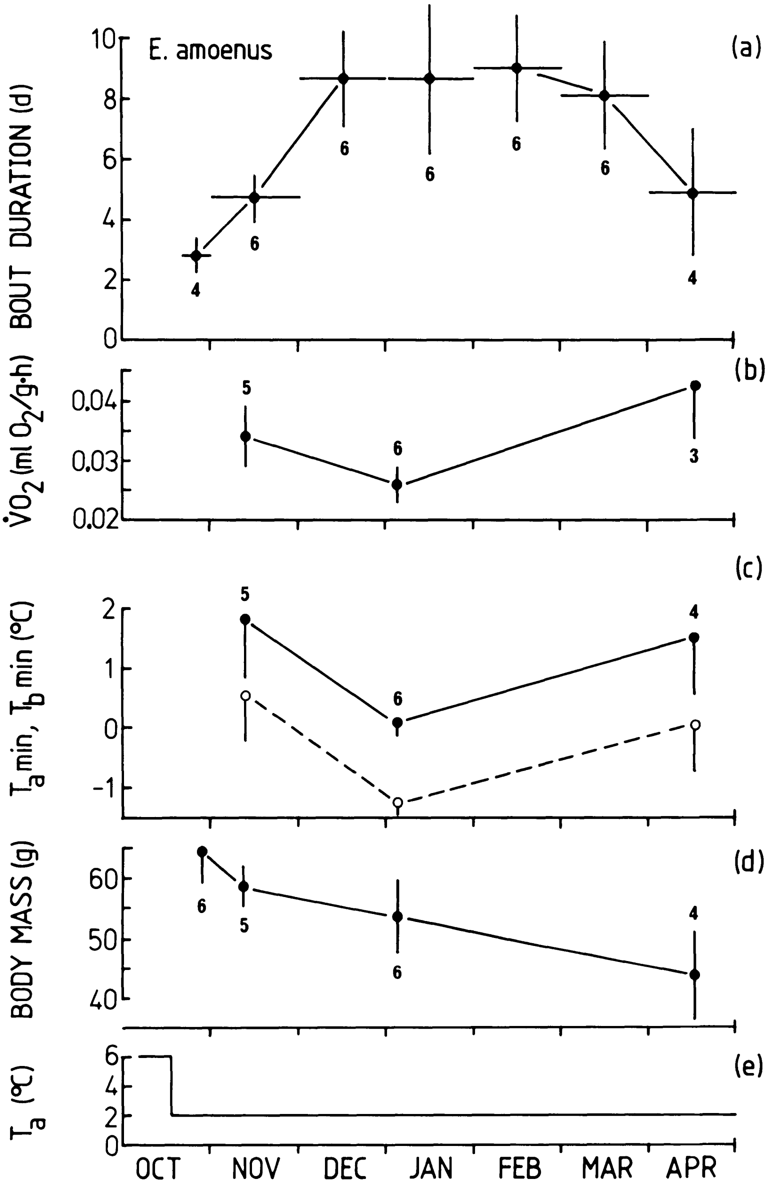

Fig. 4. Seasonal patterns, for Eutamias amoenus, *of* (a) *duration of torpor bouts over the periods indicated by horizontal bars,* (b) *mass-specific* $\dot{V}O_2$ *during torpor at* T_a *2° C.* (c) *minimum* T_b *and* T_a *of torpid animals experimentally cooled below* T_a *2° C,* (d) *body mass, and* (e) T_a *at which the animals were maintained and torpor durations determined. When torpor bouts extended over 2 calendar mo the torpor bout was included in the month in which the longer part of the bout occurred. Values are means with SD and numbers of individuals shown. One-way ANOVA revealed significant seasonal changes in all the variables: duration of torpor bouts at* T_a *2° C* (F = *10.4; df = 6,31;* $P < 0.0001$), $\dot{V}O_2$ (F = *10.7; df = 2,11;* $P < 0.005$), *minimum* T_b (F = *8.5; df = 2,12;* $P < 0.005$), *minimum* T_a (F = *11.7; df = 2,12;* $P < 0.002$).

duration—short at the beginning and end and long during the main part of hibernation. However, the larger species, *S. saturatus,* hibernated longer than the smaller species, *E. amoenus.* These interspecific differences in length of the hibernation season in the laboratory are similar to those observed in nature (Kenagy and Barnes 1988). The shorter surface activity season of *S. saturatus* may be associated with the diet of the species, which, early in the season, consists mainly of green herbaceous foods and later, after the greens dry up, hypogeous fungi. Flowering and fruiting plant parts and conifer seeds that become available later in the season are consumed only in very small amounts by *S. saturatus* (Kenagy et al. 1989). In contrast, *E. amoenus* eat parts of flowers and fruits, as well as seeds, that are available over a longer season (Broadbooks 1958; Trombulak 1985; Kenagy et al. 1989). As consumers of perishable foods, *S. saturatus* fatten extensively in preparation for hibernation, whereas *E. amoenus* fatten only slightly (Kenagy and Barnes 1988) and accumulate extensive food caches in their winter burrows (Broadbooks 1958).

Torpor bout duration in *S. saturatus* (200–300 g) was also longer than in *E. amoenus* (45–60 g). This appears in contrast to recent analyses that suggest that torpor bout duration is inversely related to body mass in heterothermic mammals (French 1985; Geiser 1988*a*). However, the relationship with mass holds only for hibernators that store fat and have hibernation seasons of similar durations. *Spermophilus saturatus,* which rely heavily on fat, may need to be more conservative with energy reserves than *E. amoenus,* which can build up substantial cached food stores for their shorter hibernation period. Furthermore, periodic rewarming from torpor in the large *S. saturatus* should take much longer than in the smaller species *E. amoenus* (Heinrich and Bartholomew 1971) and therefore should be more costly. These findings suggest that the large species, *S. saturatus,* which utilizes fat stores for its long hibernation season, maximizes energy savings by employing long torpor bouts.

The $\dot{V}O_2$, minimum T_b, and minimum T_a changed with season and the minimum temperatures of the two species were similar. The minimum T_b of both species dropped as low as −0.2°C in some individuals and apparently cannot not be lowered much further because body fluids probably would freeze (Barnes 1989). Thus both species approach their physical limits during lowering of T_b. Much further exploitation of the effect of lowering T_b on reduction of metabolism is therefore not possible.

Because it is not possible to lower T_b much more, the smaller species, *E. amoenus,* must use other avenues if further reduction of energy expenditure during torpor is required. Despite the differences in the body mass of the two species, which result in a higher (3.6-fold) mass-specific basal meta-

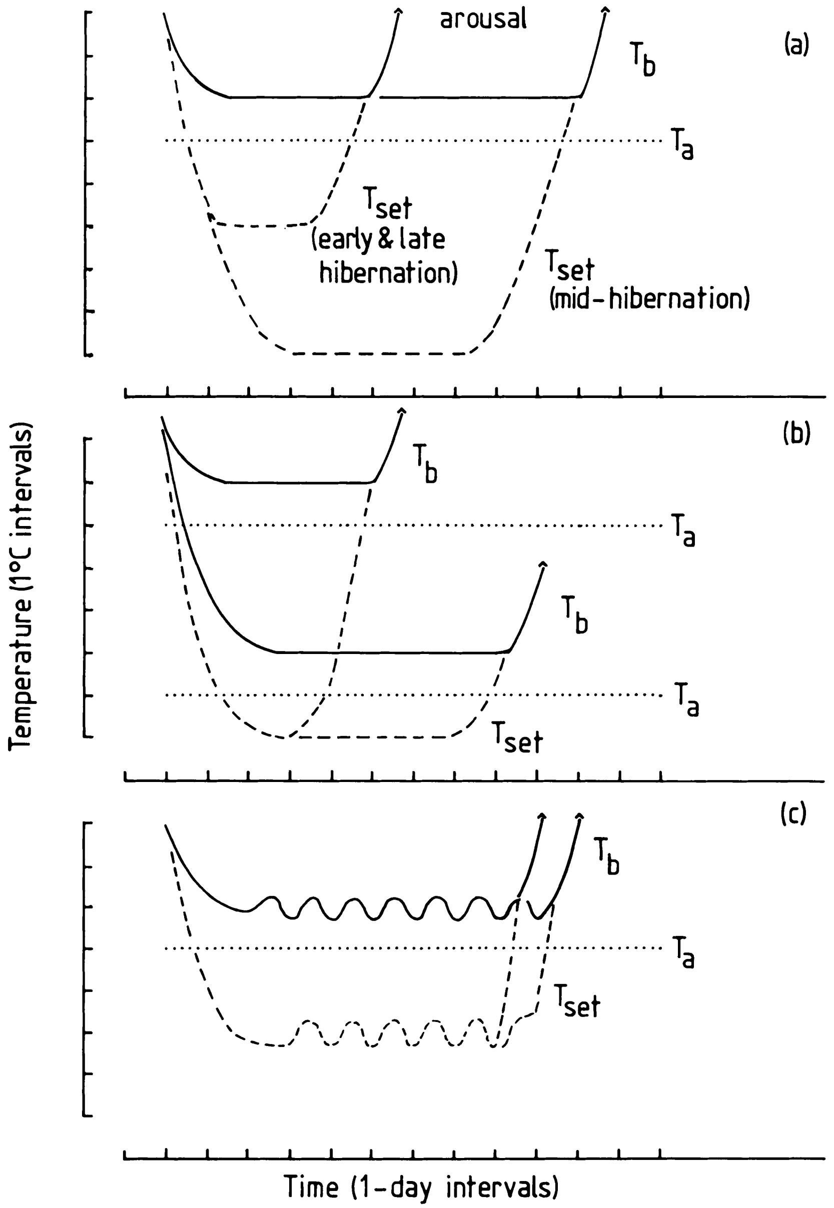

*Fig. 5. Theoretical model for (*a*) influence of season on hypothalamic* T_{set}*, which is reflected in the minimum* T_b *during early and late hibernation, and during the main season of hibernation (midhibernation). Arousal occurs when* T_{set} *rises above* T_b *of the torpid animal (arrows). (*b*) Seasonal alterations of the duration of torpor bouts are influenced by* T_a*, which influences the* $\dot{V}O_2$ and T_b*, and thereby the time of increase in* T_{set} *of torpid animals. The effect of a change in* T_a *on torpor bout duration is indicated by the two patterns of increase in* T_{set}*. (*c*) Daily fluctuations of* T_b*,* $\dot{V}O_2$ *(not shown), and* T_{set} *increase the probability of arousal at certain times of day.*

bolic rate in *E. amoenus* than in *S. saturatus* (Geiser 1988*b*), metabolic rates of torpid *E. amoenus* were only 1.5-fold greater than in *S. saturatus* at the same T_b and T_a. The Q_{10} for $\dot{V}O_2$ between normothermia and torpor was in the normal range of biological reactions in *S. saturatus* (Q_{10} = 2.5), whereas it was greater than expected in *E. amoenus* (Q_{10} = 3.2). Therefore, the effect of reduction in T_b on $\dot{V}O_2$ must differ between the two species. It has been suggested earlier that small hibernating species such as *E. amoenus* may employ metabolic inhibition in addition to the physical effect of low T_b on metabolic rate, whereas larger species such as *S. saturatus* rely predominately on the effect of temperature (Geiser 1988*b*).

It appears that the two species have two different modes of hibernation that reflect their body size, energy supply, and energy storage. The *S. saturatus* predominately employ longer torpor bouts for reducing energy expenditure during torpor because fat may be limited and arousals are so energetically costly. The *E. amoenus* can afford to arouse more frequently because rewarming takes less time (Heinrich and Bartholomew 1971) and should require less energy, which can be replenished from food stores. Rather than extending the duration of a torpor bout, *E. amoenus* seems to lower its metabolic rate beyond what is expected from the reduction of T_b alone. This allows the animal to reduce energy loss within a torpor bout and therefore overall energy cost of hibernation.

A Model for Determination of Torpor Bout Duration

In both *S. saturatus* and *E. amoenus*, the seasonal change of $\dot{V}O_2$, minimum T_b, and minimum T_a of torpid individuals showed a significant inverse relationship to the duration of torpor bouts. The seasonal change of the minimum T_b, determined in the central part of a torpor bout, suggests that the temperature to which the set point for control of T_b (T_{set}) falls during a torpor bout changed with season. The T_{set} is generally specified as the set point temperature of the hypothalamus itself, but since hypothalamic and rectal temperatures are essentially identical in hibernating golden-mantled ground squirrels in the T_a range of −2° to 2°C (Heller and Colliver 1974),

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A delay of increase in T_{set} *by half a day should result in a 1-d delay of arousal if the onset of increase in* T_{set} *falls within the time of increase in* T_b *and* $\dot{V}O_2$ *in the former, but within the time of decrease in* T_b *and* $\dot{V}O_2$ *in the latter.*

the minimum rectal temperatures measured in the present study should be close to T_{set}.

One of the hypotheses that have been proposed to explain the predictable occurrence of bouts of torpor is that arousals are triggered by gradual, hourglass-like processes, such as accumulation of metabolic waste products that cannot be excreted at low T_b or by depletion of energy reserves (Mrosovsky 1971; Galster and Morrison 1975). This idea is based largely on the observation that metabolic rate and torpor bout duration are inversely related (Soivio, Tähti, and Kristoffersson 1968; Geiser 1986; Geiser and Kenagy 1987). However, metabolic rate only partially accounts for changes in torpor bout length that occur at different T_a's, and T_b is a better predictor of torpor bout length than $\dot{V}O_2$ (Geiser and Kenagy 1988). This suggests that both T_b and $\dot{V}O_2$ are involved in determining arousal. A reduction in neural sensitivity to buildup of metabolites or depletion of nutrients at low T_b could be responsible for later arousals. An inadequacy of this hypothesis is that seasonal changes in torpor bout duration occur at a constant T_a, at which T_b also should be stable because the difference between T_b and T_a of torpid sciurids does not change during most of the hibernation season (Barnes et al. 1986; present study).

We therefore wish to propose a new model to explain changes of torpor bout duration (fig. 5). We incorporated findings of the present study with those on observations on the thermal response of torpor bout duration (Geiser and Kenagy 1988). We also incorporated the observations of an increase in hypothalamic T_{set} toward the end of a torpor bout (Florant and Heller 1977) into our model. We propose that the seasonal change in torpor bout duration is determined by gradual seasonal changes of the minimum T_b, which corresponds to a change in T_{set} (fig. 5*a*). Arousal is initiated when T_{set} reaches T_b of the torpid animal. Because T_{set} falls to low temperatures in midhibernation, the rise in T_{set} should reach T_b later than when T_{set} remains relatively high in early and late hibernation. The increase in T_{set} is initiated by accumulation of metabolites or depletion of fuels that are related to the metabolic rate. The low rate of metabolism in midhibernation in comparison to early and late hibernation could result in a later increase in T_{set} and prolonged torpor bouts.

Experimental results show that change in T_a is correlated with a change in torpor bout duration, which appears to be due to changes of T_b and $\dot{V}O_2$ of hibernating animals (Geiser and Kenagy 1988). We therefore propose that the time of increase in T_{set} is influenced by T_b and $\dot{V}O_2$, which depend on the prevailing T_a. Our model shows how a drop of T_a above T_{set} would decrease T_b (and $\dot{V}O_2$, not shown) and result in a later rise of T_{set} and a longer torpor bout (fig. 5*b*). A drop of T_a below T_{set} would require an increase in

$\dot{V}O_2$ for thermoregulation, and arousal would occur earlier (not shown) than in our example of low T_a.

Our model could also explain why the probability of arousals is high at certain times of the day (Twente and Twente 1987). In hibernating individuals T_b and $\dot{V}O_2$ fluctuate in a predictable daily rhythm in phase with the T_b and $\dot{V}O_2$ fluctuations in normothermic animals (Menaker 1959; Pohl 1961). Thus T_b and $\dot{V}O_2$ are highest in torpid individuals during the active period of normothermic animals. If we assume that T_{set} also fluctuates in phase with T_b, and the rise of T_{set} is accelerated during times of rise in $\dot{V}O_2$ and T_b, then arousals will tend to occur during the active period of normothermic animals (fig. 5*c*). However, figure 5*c* will no longer be valid if the recent suggestion is verified that bouts of torpor are extensions of circadian cycles due to the slowing effect of low temperature (Heller, Krilowicz, and Kilduff 1989).

Our model may explain some of the seasonal and thermal variations of the duration of torpor bouts. It does not explain why this seasonal change of the minimum T_b has evolved. However, the seasonal change of soil temperature at 50 cm depth at a hibernaculum site (Kenagy et al. 1989) is similar to that of the minimum T_b and may explain its seasonal fluctuations. It appears that throughout the hibernation season the minimum T_b of both species remains 1.7° to 3.7°C below the soil temperature, thus avoiding thermoregulation during torpor and the associated loss of energy.

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