

TORPOR DURATION IN RELATION TO TEMPERATURE AND METABOLISM IN HIBERNATING GROUND SQUIRRELS¹

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To understand the basis of the thermally sensitive physiological processes that govern the duration of individual bouts of torpor, we determined torpor bout duration in relation to air temperature (T_a), body temperature (T_b), and oxygen consumption ($\dot{V}O_2$) in hibernating golden-mantled ground squirrels, *Spermophilus saturatus*, during the midst of the hibernation season when bout length was stable. Over the range of T_a from 8 down to 2 C, length of torpor bouts increased as T_b and $\dot{V}O_2$ decreased, and the difference between T_b and T_a (ΔT) remained about 1.5 C. However, when T_a was lowered from 2 C to -2 C, the trend reversed and torpor duration and T_b decreased, whereas $\dot{V}O_2$ and ΔT increased. This response is due to an increase in heat production that keeps T_b from declining below about 1 C. We examined our data in terms of the hypothesis that arousal is determined by accumulation of metabolites during torpor; if this is true, then the arousal frequency should be directly proportional to energy metabolism ($\dot{V}O_2$). Using linear and multiple regression, we found that T_b and T_a are better predictors of torpor duration than $\dot{V}O_2$. The best relationship was, however, achieved by regression of T_b and $\dot{V}O_2$. We conclude that T_b per se also contributes, along with metabolism, to determining the length of torpor bouts.

INTRODUCTION

During hibernation in small mammals, torpid individuals arouse spontaneously at periodic intervals of several days to about 2 wk (Pengelley and Fisher 1961; Pohl 1961). The duration of these torpor bouts increases following onset of hibernation and stabilizes by early winter (Kristoffer-son and Soivio 1964; Wang 1978; Pajunen 1983; Barnes et al. 1986; French 1986). The bouts are shortened again at the end of the hibernation season. Arousals from torpor are energetically expensive, amounting to most of the energy used during hibernation (Kayser 1953; Wang 1978), yet the functional significance of arousal is not understood. Two hypotheses

attempt to explain the regular occurrence of arousals during hibernation. The first states that torpor bouts represent a prolongation of the sleep cycle or rest phase at low temperature (Folk 1957; Strumwasser 1959; Pohl 1961; Lyman et al. 1982). The second hypothesis proposes that depletion of energy reserves and accumulation of metabolic wastes triggers arousals (Dubois 1896; Hock 1958; Mrosovsky 1971; Lyman et al. 1982).

The duration of torpor bouts is sensitive to environmental temperature. Experimental decrease in air temperature (T_a), which reduces body temperature (T_b), results in an increase in torpor bout duration (Twente and Twente 1965; French 1982). At low T_b both the rates of energy-substrate oxidation and the accumulation of waste metabolites are reduced. Because T_b is still regulated during torpor, although at a lower "set point" than during normothermia (Heller and Hammel 1972), and because T_b must be maintained at or above a specific minimum temperature ($T_{b\text{minimum}}$) even when T_a decreases below $T_{b\text{minimum}}$, it is necessary for the torpid animal to increase heat production when $T_a < T_{b\text{minimum}}$ to avoid a lethal decline in T_b . This suggests that if torpor duration is inversely related to the rate of metabolism, a

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reversal of the relationship between T_a and torpor duration should occur when T_a falls below the $T_{b\text{minimum}}$, i.e., length of torpor bouts should decrease. Such a reduction of torpor duration has been observed in species that show prolonged torpor (Pengelley and Kelly 1966; Soivio, Tähti, and Kristofferson 1968; Pajunen 1983; Geiser and Kenagy 1987) and in those that show shallow, daily torpor (Geiser 1986a). However, no attempt has been made to analyze systematically how torpor duration is interrelated with both T_b and metabolic rate at T_a 's above and below the $T_{b\text{minimum}}$.

In the present study we determined the duration of torpor bouts of captive golden-mantled ground squirrels, *Spermophilus saturatus*, as a function of T_a during hibernation. *Spermophilus saturatus* weighs 200–300 g and hibernates in nature from August or September to early April (Kenagy and Barnes 1988). We analyzed the relationship of torpor duration to energy metabolism (measured as oxygen consumption) and T_b in terms of the hypothe-

sis that arousal is determined by accumulation of metabolites during torpor.

MATERIAL AND METHODS

Seventeen *Spermophilus saturatus* were caught in August 1984 in the Cascade Mountains, Chelan County, Washington, transported to the University of Washington, and kept individually in cages provided with hard wood shavings. Rodent laboratory chow and water were freely available throughout the experiment. The animals hibernated over winter 1984–1985 under an artificial photoperiod that followed the natural change in daylength and with temperatures that cycled seasonally between 4 C in winter and 20 C in summer. Beginning in November 1985 the animals were exposed to T_a 4 ± 1 C and a constant photoperiod of 8L:16D (lights on 0800–1600 hours PST). We measured the duration of torpor beginning in early December, about 1 mo after the onset of hibernation. Torpor duration was determined by observing the animals daily

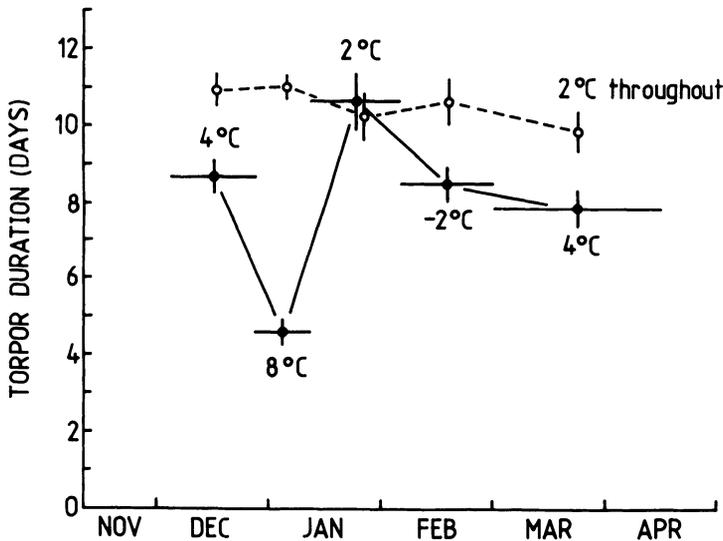


FIG. 1.—The duration of torpor (mean \pm SE) in 17 *Spermophilus saturatus* hibernating between December and April that were exposed to four different air temperatures (\bullet) over the range of dates indicated by the horizontal line through each mean and in 12 *S. saturatus* that were exposed to constant 2 C over the same seasonal period (\circ). At 2 C torpor duration of the 12 individuals did not change significantly over season (one-way ANOVA: $F = 0.98$; $df = 4, 59$; $P > .4$). Torpor duration of the 17 individuals exposed to change in temperature differed significantly at the various temperatures (one-way ANOVA: $F = 20.81$; $df = 4, 84$; $P < .0001$). Because the two determinations at T_a 4 C at the beginning and the end of the hibernation period were not significantly different (Student-Newman-Keuls test; $P > .05$), and because the duration of torpor was constant at 2 C, it was concluded that spontaneous seasonal changes in torpor duration were negligible and that any significant deviation from the mean duration at T_a 4 C was due to the effect of temperature.

at 1000 hours for the displacement of fine sand from an animal's back that occurred when it had aroused during the previous 24 h. These measurements were made successively at T_a 4 C (December 3–December 26); T_a 8 C (December 27–January 11); T_a 2 C (January 12–February 4); T_a -2 C (February 5–February 28); and 4 C (March 1–April 15) (fig. 1). When a rapid decline in torpor bout duration occurred spontaneously in April, and some animals remained normothermic for more than 1 day, measurements were discontinued and the shortened bouts at the end of the hibernation season excluded from the analysis. A second group of 12 individuals was caught in spring 1986. During their nonhibernation period they were exposed to an artificial photoperiod of natural daylength and to temperature fluctuation as were the other individuals. Beginning in late October 1986 until April 1987 these animals were exposed to T_a 2 C and a constant photoperiod of 8L:16D. Torpor duration was determined over the same time intervals as for the other individuals.

Oxygen consumption of torpid animals was determined after transferring them from their cages in the walk-in holding chamber to a 2-liter respirometry vessel held in a small temperature-controlled (± 0.2 C) cabinet at the same T_a as in the walk-in chamber. Flow rate was 200 ml/min. Because the sensitivity to disturbance increases toward the end of torpor bouts, these measurements were performed on days 2–4 of a bout. $\dot{V}O_2$ was not determined until oxygen concentration stabilized; these measurements lasted 3–6 h. The $\dot{V}O_2$ during these measurements was determined by integrating the trace of percent oxygen concentration on the chart paper over a 60-min period. T_b was measured immediately after removal of the animal from the respirometer by 4-cm rectal insertion of a 36-gauge thermocouple.

Oxygen consumption was monitored continuously with an Applied Electrochemistry S-3A oxygen analyzer. T_a was measured continuously in the respirometer by thermocouple and recorded along with oxygen concentration on a Leeds and Northrup Speedomax 250. Point readings of T_a were taken using a digital thermometer. The digital thermometer and thermo-

couples were calibrated to the nearest 0.1 C with a mercury Bureau of Standards thermometer.

RESULTS

During the central part of the hibernation season over which our measurements were made, the influence of air temperature on torpor duration was significant, whereas effects of season were insignificant (fig. 1). The duration of torpor measured

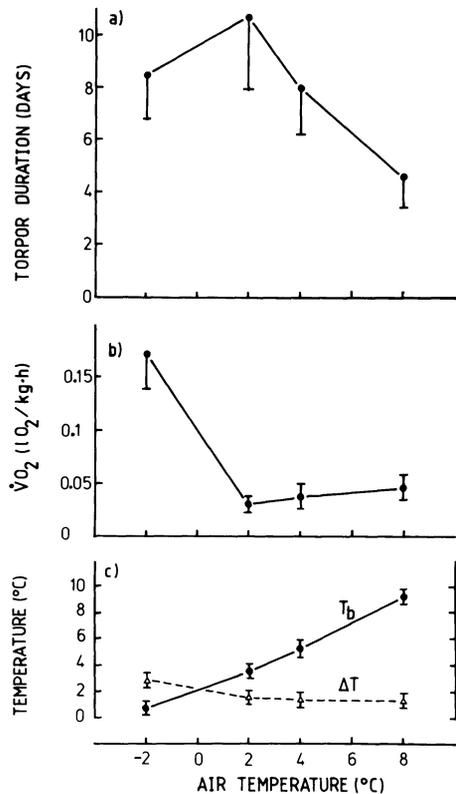


FIG. 2.—The influence of air temperature (T_a) on (a) duration of torpor, (b) oxygen consumption ($\dot{V}O_2$), and (c) body temperature (T_b ; solid lines) and $T_b - T_a$ (ΔT ; broken line) of hibernating *Spermophilus saturatus*. All values are means \pm SD. The torpor durations are the same values as in fig. 1, with the two determinations at T_a 4 C combined. The duration of torpor at the four T_a 's differed significantly (one-way ANOVA: $F = 27.4$; $df = 3, 67$; $P < .0001$). All pairwise comparisons were significantly different (Student-Newman-Keuls test; $P < .05$) except for the values at T_a 4 and -2 C. The T_b 's, ΔT 's, and $\dot{V}O_2$'s are the mean of seven individuals at each temperature. The mean mass of individuals used for $\dot{V}O_2$ measurements at the four temperatures was 248 ± 12 g. The torpor duration (TD) as a function of T_a from T_a 2 C to 8 C is described by the equation: $\log_{10} TD = 1.13 - 0.060T_a$ ($r^2 = .63$; $P < .0001$; $n = 51$).

at T_a 2 C in a series of intervals was stable, at about 10–11 days, over the entire 4.5-mo period of the measurements. When animals were exposed to different T_a 's, the duration of torpor changed distinctly. Torpor duration decreased when T_a was raised from 4 to 8 C and increased when T_a was lowered from 8 to 2 C. At T_a -2 C torpor duration was similar to that at 4 C. Because the duration of torpor at T_a 4 C in December and March/April did not differ significantly (fig. 1), we combined these measurements in further analyses.

When expressed as a function of T_a , torpor duration increased exponentially from a mean \pm SD of 4.6 ± 1.1 days at T_a 8 C to 10.7 ± 2.8 days at T_a 2 C (fig. 2a, see eq.). In contrast, a further decrease in T_a to -2 C resulted in a reversal of the pattern, and mean torpor bouts were only 8.5 ± 1.8 days, which was significantly shorter than at 2 C ($P < .05$; Student-Newman-Keuls test).

Rate of oxygen consumption (fig. 2b) and torpor duration (fig. 2a) showed opposite responses to T_a . The $\dot{V}O_2$ decreased from T_a 8 C to 2 C with a Q_{10} of 2.1, whereas torpor duration increased. The 20% reduction in torpor duration when T_a was decreased from 2 to -2 C was accompanied by a 5.5-fold increase in $\dot{V}O_2$. Similarly, the difference between T_b and T_a (ΔT) increased when T_a was lowered from 2 to -2 C (fig. 2c). In contrast, T_b decreased steadily over the entire range of T_a investigated (fig. 2c).

Linear and stepwise multiple regression analysis with torpor duration (TD in days) as dependent variable and T_b , T_a , and $\dot{V}O_2$ as independent variables suggests that within the T_a range where T_b in torpor approximates T_a (T_a 2–8 C), torpor duration is negatively related with T_b and T_a (TD vs. T_b : $r^2 = .68$, $P < .0001$, $n = 21$; TD vs. T_a : $r^2 = .66$, $P < .001$, $n = 21$), whereas $\dot{V}O_2$ was a weaker predictor of torpor duration (TD vs. $\dot{V}O_2$: $r^2 = .34$, $P < .01$, $n = 21$). Neither T_a nor $\dot{V}O_2$, when considered together with T_b , could explain more of the variation in torpor duration than T_b alone. When a linear regression analysis was performed over the whole temperature range (-2 to 8 C), T_b again explained more of the variation in torpor duration ($r^2 = .28$, $n = 28$, $P < .01$) than the two

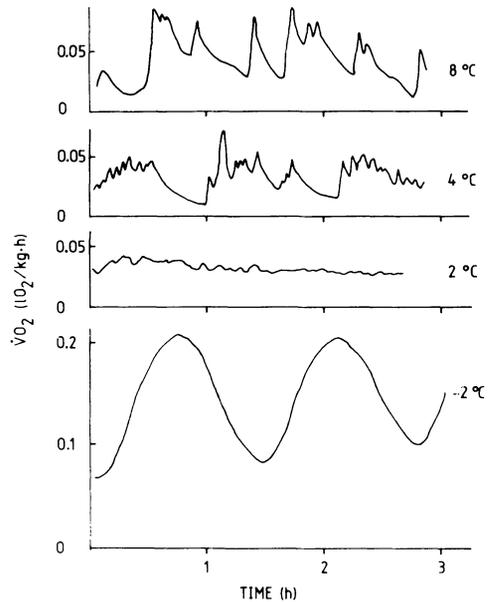


FIG. 3.—Representative cyclic patterns of oxygen consumption ($\dot{V}O_2$) in relation to air temperature (T_a) as reflected by different patterns of ventilation.

other variables. However, 63% of the variation in torpor duration was explained ($r^2 = .63$, $n = 28$, $P < .0001$), in a multiple regression where T_b was considered together with $\dot{V}O_2$.

The rate of oxygen consumption of torpid animals fluctuated in relation to ventilation over the course of the 3–6-h periods of measurement at most T_a 's, and the pattern of these fluctuations varied with air temperature (fig. 3). At T_a 8 C and 4 C, the $\dot{V}O_2$ alternated between low rates, during which intermittent apnea occurred, and high rates during polypnea (Cheyne-Stokes respiration). We noted these patterns of ventilation by visual observation of our animals in their transparent respirometers via a window in the environmental cabinet. In contrast to fluctuations in $\dot{V}O_2$ and ventilation at T_a 4 C and 8 C, the $\dot{V}O_2$ at T_a 2 C was stable, and ventilation was relatively even. At T_a -2 C, the $\dot{V}O_2$ showed a steady sinusoidal oscillation with a frequency of approximately 0.7 cycle/h. The pattern of breathing at -2 C was very regular, and the phase of increase in $\dot{V}O_2$ was accompanied by a ventilation rate of about 6 breaths/min, while the phase of decrease coincided with 3–4 breaths/min.

DISCUSSION

THERMAL AND METABOLIC DETERMINANTS
OF TORPOR BOUT LENGTH

It has been suggested that torpor bout duration in hibernation is determined by accumulation of metabolic wastes or depletion of energy reserves (Dubois 1896; Mrosovsky 1971; Galster and Morrison 1975; Krilowicz 1985; for review, Lyman et al. [1982]). For any such metabolic explanation, one should expect that torpor duration is determined by the summation of energy metabolism. Using linear and multiple regression analysis, we can now suggest that the duration of torpor bouts in *Spermophilus saturatus* is determined by T_b and T_a and only partly by metabolic rate. Our statistical determination that T_b accounts for more of the variation in torpor duration than $\dot{V}O_2$ indicates that accumulation or depletion of metabolites can only partly account for the length of torpor bouts. Because T_b is the best predictor of torpor duration, we suggest that the lengthening of torpor bouts may be due to a reduction in neural sensitivity to buildup of metabolites as T_b decreases. Two observations may lend support to this hypothesis:

1. $\dot{V}O_2$ explains only 34% of the variation in torpor bout duration over the T_a range of 8–2 C, whereas T_b explains 68% of the variation of torpor bout duration. The fact that T_b decreases by 6 C over this range (fig. 2) suggests that thermal sensitivity of the nervous system to stimuli for arousal may be reduced, which may contribute to the additional increase in bout length. The much more pronounced thermal sensitivity of torpor duration than of $\dot{V}O_2$ over this temperature range further supports this view. Similarly, Strumwasser, Schlechte, and Streeter (1967) proposed a model in which arousal from torpor occurs when a circadian pacemaker crosses a threshold that is lowered with the time spent in torpor. The lower the T_b , the slower the decrease in threshold and the longer the torpor bout. The view that a biological clock is involved in the timing of arousals is supported by the observations that the circadian rhythm is maintained during hibernation (Pohl 1987) and that arousal occurs at about the same time of

day regardless of the duration of torpor (Twente and Twente 1987). However, the model of Strumwasser et al. (1967) does not explain the decrease in torpor duration that we observed at T_a 's below the minimum T_b .

2. The sharp increase in $\dot{V}O_2$ when T_a was decreased from 2 C to –2 C is a much greater relative change than that at temperatures above 2 C, whereas torpor duration decreased only slightly below 2 C. The additional decrease of T_b by about 3 C over the T_a range of 2 to –2 C may further reduce the thermal sensitivity of the nervous system and thus allow longer torpor bouts at T_a 's below the $T_{b\text{minimum}}$. Observations on hibernating hedgehogs, *Erinaceus europaeus*, also illustrate the lack of a direct relationship between torpor duration and metabolism; when torpor bout length was decreased by half in response to lowering of T_a below the minimum T_b , the $\dot{V}O_2$ increased 22-fold (Soivio et al. 1968). Similarly, when torpor duration of the small marsupial *Planigale gilesi* decreased by half in response to colder T_a , the $\dot{V}O_2$ showed a fivefold increase (Geiser 1985).

Because our hypothesis of reduced neural sensitivity to metabolites at low T_b does not explain all of the variation in torpor duration, other possibilities must also be considered. The hypothalamic set point for T_b , T_{set} , in torpid animals gradually increases shortly before arousal (Florant and Heller 1977). The time of arousal may thereby coincide with the time when T_{set} rises far enough to induce arousal. However, if this effect were directly responsible, torpor duration at high T_b should last longer than at low T_b , in contrast to the observations presented here, because T_{set} at high T_b should reach the arousal stimulating difference from T_b later than at low T_b . If, however, the time of increase in T_{set} were related to T_b and the metabolic rate during torpor, the rise in T_{set} as an arousal stimulus may explain our observations.

Another possibility is that the increased sympathetic activity associated with temperature regulation at T_a –2 C increases the sensitivity or irritability of the animal. These phenomena may operate at the low T_a 's, whereas temperature-sensitive timing mechanisms may operate at the higher T_a 's. Therefore the reduction of the dura-

tion of torpor at $T_a -2$ C may reflect a switching of regulatory mechanisms for timing of arousals. The T_a of -2 C may be low enough to approximate T_{alarm} at which arousal is initiated, rather than a continuous proportional control of T_b at all T_a 's.

Willis, Goldman, and Foster (1971) proposed an alternative hypothesis for regulation of torpor bout duration that involves the loss of potassium ions from muscle during hibernation. An increase in potassium ion concentration outside of the membrane of excitable tissues should lead to depolarization and increased excitability. Irritability during hibernation has been shown to increase with bout duration (Twente and Twente 1968). The potassium ion hypothesis is supported by the observation of increased arousal frequency following injection of an isotonic mixture of KCl and NaCl that increased extracellular potassium concentration by about 20% (Fisher and Mrosovsky 1970). However, hyperkalemia was not detected at the end of a torpor bout in the serum of several species (Willis et al. 1971). Therefore, direct evidence for the involvement of potassium in determining natural torpor duration is lacking. Furthermore, no attempt has been made to integrate the potassium ion concept with the thermal response of torpor bout duration.

In agreement with earlier observations (Twente and Twente 1965; Twente, Twente, and Moy 1977) the duration of torpor in the present study increased exponentially with decreasing T_a in the T_a range above the T_{bminimum} . The maximum predicted torpor duration of *S. saturatus* (14 days) on the basis of extrapolation from the equation in figure 2 should occur at about T_a 0 C, because the observed T_{bminimum} was 0.8 C and ΔT during torpor is approximately 1 C (Lyman et al. 1982; present study). Pengelley and Fisher (1961) observed torpor durations similar to this prediction in the closely related and perhaps conspecific golden-mantled ground squirrel *S. lateralis* at T_a 0 C.

THERMAL SENSITIVITY OF BREATHING

The change that we observed in the short-term cycling of $\dot{V}O_2$ at different temperatures was striking. A transition between Cheyne-Stokes respiration and con-

stant breathing as temperature decreased to just above freezing has been observed previously in *Spermophilus lateralis* (Hammel et al. 1968). We interpret this change in breathing pattern as a preparation for thermostatic heat production during torpor, because the transition occurs at a temperature close to the minimum T_b . The great amplitude and steady sinusoidal oscillation of $\dot{V}O_2$ during torpor at $T_a -2$ C is possibly due to the long feedback time between a thermoregulatory error signal, thermoregulatory heat production, and heat distribution back to the brain (Heller and Colliver 1974). Because arterial CO_2 tension appears to provide the primary respiratory drive during hibernation (Millsom, McArthur, and Webb 1986), the breathing pattern of a thermoregulating animal that shows an increased CO_2 production should become more regular.

THERMAL REGIME OF NATURAL HIBERNATION

Our observation of a decrease in torpor duration below a critical T_a raises the question whether hibernators in the field are exposed to such temperature extremes. Hibernacula are warmer than outside air (Walhovd 1976; Maclean 1981), yet temperatures as low as -8 C have been reported in burrows of hibernating arctic ground squirrels, *Spermophilus parryi* (Mayer 1960). It is unlikely that all individuals in a population of "deep hibernators" such as *S. saturatus* occupy thermally optimal hibernacula. The ability to thermoregulate during torpor suggests that there must occasionally be a need to regulate T_b above T_a during torpor in the wild. In heterotherms like deer mice or dasyurid marsupials that show daily torpor and much higher minimum T_b 's of 10–20 C (Morhardt 1970; Geiser 1986b), the regulation of T_b substantially above T_a during torpor should be more common than in deep hibernators.

The selection of thermally appropriate hibernacula is important because both energy metabolism and torpor duration are influenced by T_a . Hibernation at high temperatures would result in higher metabolic rate during torpor and more frequent, energetically costly arousals. The same applies for the condition where environmental temperature falls below the

minimum T_b . Soil temperatures below 50 cm depth at a typical hibernaculum site of *S. saturatus* in a study area at 650-m elevation decrease to about 2 C during winter (Kenagy, unpublished), which is close to the temperature that yields the longest mean torpor-bout duration observed for

this species (10.7 days; fig. 2a). Further evidence for selection of appropriate microclimates during hibernation is available from bats, that select roosting positions where T_a is close to $T_{b\text{minimum}}$ (Twente 1955; Hall 1982).

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