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PATTERNS OF BODY TEMPERATURE CHANGE IN  
HIBERNATING ARCTIC GROUND SQUIRRELS

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*Brian M. Barnes and Douglas Ritter*

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## PATTERNS OF BODY TEMPERATURE CHANGE IN HIBERNATING ARCTIC GROUND SQUIRRELS

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### Introduction

Careful measurements of body temperatures in undisturbed animals over the entire hibernation season are fundamental to investigating the regulation of hibernation, its relationship to environmental variables, and sex differences in the timing and strategies of hibernation. Determining precise correlations between the frequency of periodic arousals from hibernation, euthermic arousal duration, and ambient and body temperatures should also be useful for examining hypotheses about arousal function (French 1982a, 1985; Geiser and Kenagy 1988). This is often not feasible under laboratory conditions due to disturbances related to noise and animal care; mimicking the smooth temperature changes in natural burrows is also difficult. Additionally, it is not possible to associate behaviors such as timing of immergence or emergence from burrows with use of torpor in animals in small cages. The need for measurements of hibernation patterns in animals living under natural or semi-natural conditions is illustrated by the frequent citations of the classic study of Wang (1979; see also Young 1990); however, in completely natural situations, variables such as temperature and food cannot easily be manipulated. This paper introduces a useful compromise: outdoor enclosures built for collecting hibernation patterns using telemetry.

### Materials and Methods

*Outdoor Enclosure Design.* Twenty enclosures (0.9 by 0.9 by 1.8 m) made of wire mesh (2.5 cm squares) were buried to 1.3 m in sandy soil

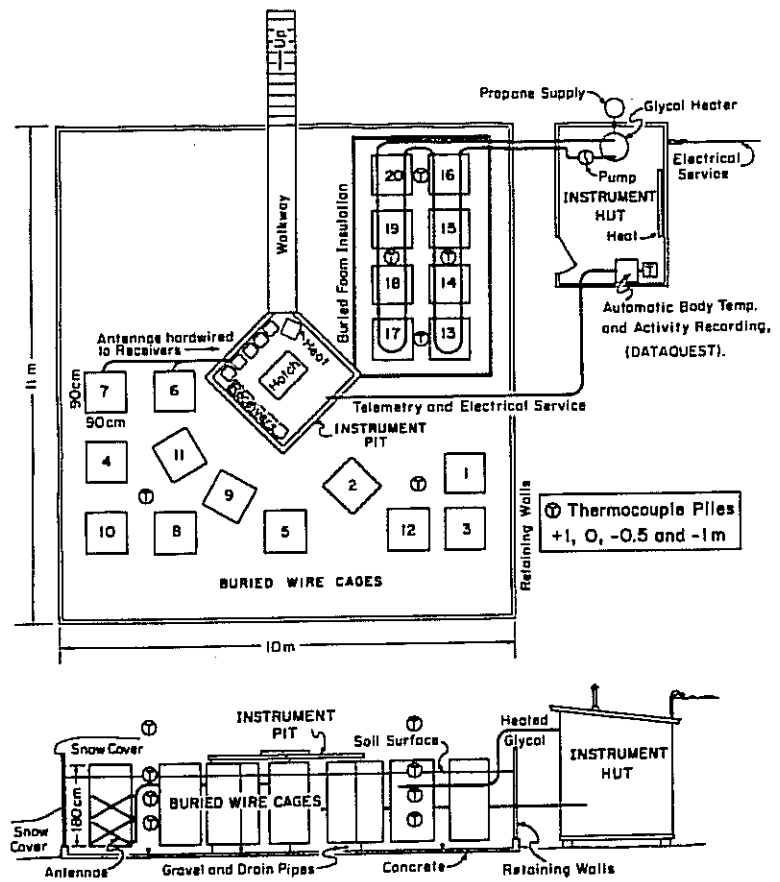


FIGURE 1 Outdoor enclosures for arctic ground squirrel hibernacula located in Fairbanks, Alaska. Animals dug their own burrows and remained outdoors throughout the seasons while changes in body temperature and activity were recorded via telemetry.

brought to a wooded area on the University of Alaska Fairbanks campus. Each enclosure was fitted with 4 copper loop antennas in plastic pipe buried at different depths and connected to coaxial leads. Leads connected to receivers that interfaced to a computerized data collection system (DataQuest III: Data Sciences, Inc. and Mini-Mitter, Co., Inc.).

Band pass filters were used to overcome commercial radio interference. The receivers and computers were housed in heated instrument sheds. To manipulate soil temperatures, copper piping (3/4") was buried 30 cm deep in two runs each that connected eight enclosures. The pipes were filled with a ethylene glycol-water mixture and connected to a hot water heater and circulating pump. Thermocouples allowed measurement of soil temperatures at differing soil depths. A schematic of the layout is shown in Fig. 1.

**Animals.** Arctic ground squirrels, *Spermophilus parryii kennicotti*, were captured in late August near the Toolik Research Station (68° 38"N, 149° 38"W, altitude 720 m) on the North Slope of Alaska. Animals were transported to Fairbanks and housed in cages exposed to 18 °C and day lengths of 18L:6D for 2 weeks. During this time they were implanted with abdominal temperature-sensitive radiotransmitters. In mid-September animals were released into their outdoor enclosures and given hay and cotton batting for bedding. Animals were fed Purina Laboratory Chow ad lib, with sunflower seeds, carrots and apples given each 1-2 days until they immersed. Timing of immersion and emergence was indicated by leaving markers over burrow entrances. Ten females and ten males began the experiment in 1989, but two females died while hibernating in especially shallow burrows (<25 cm) and one male never hibernated.

The soil above 4 males and 4 females was artificially warmed beginning 1 February. This caused soil temperatures ( $T_{\text{soil}}$ ) at -1 m to increase from -7.1 to 5.9 °C by 1 April in the experimental burrows, compared to rising from -6.3 to -2.9 °C in control burrows. Torpor bout lengths (TBL) were calculated as the time an animal was below core (abdominal) temperatures ( $T_c$ ) of 30 °C; euthermic arousal duration was defined as the interval  $T_c \geq 30$  °C.

## Results

Ground squirrels began to dig immediately after being released into the enclosures and burrowed for several weeks. When burrows were excavated the next year, spherical nests 25-30 cm in diameter were found at the end of branching tunnels 1-1.3 m deep.

**Daily Torpor Prior to Hibernation.** Before showing multi-day torpor bouts, almost all (12 of 14) animals for which there were clear records entered short (<12 hrs) torpor that began at night and ended with arousal before noon the next day (Fig. 2). After rewarming, animals usually showed above ground activity. Once an animal had extended daily torpor into a multi-day torpor bout, it did not show daily torpor

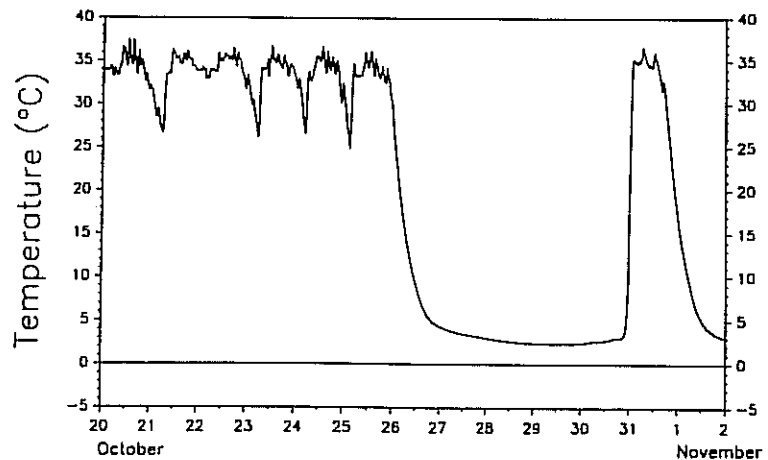


FIGURE 2 Body temperature of an arctic ground squirrel entering hibernation in an outdoor enclosure. Animals showed daily torpor before the first multi-day torpor bout.

again and remained in its burrow until spring. Minimum  $T_c$  reached during initial nightly torpor bouts were below 25 °C; these became progressively lower before the first multi-day bout, but this trend was not statistically significant ( $p > .08$ , ANOVA).

**Seasonal Changes in Euthermic Set Point.** In fall, before torpor began, euthermic  $T_c$  gradually decreased and showed greater daily variation compared to  $T_c$  and its variation after torpor ended in spring. This is apparent from the negative slope of euthermic  $T_c$  seen in most animals before they entered hibernation (Fig. 3), and from comparing average  $T_c$  and its SD during the last 10 days without torpor in fall with that during the 10 days after the last arousal in spring ( $34.76 \pm 1.08$  vs.  $36.12 \pm 0.76$  °C,  $n = 6$ ,  $p < .02$ ). These changes were apparent even in the animal that did not hibernate (Fig. 4). Minimum  $T_c$  during hibernation of  $-0.2$  to  $-2.3$  °C (average  $-1.5 \pm .2$  °C) were reached in February and March when  $T_{\text{soil}}$  at  $-1$  m averaged from 6 locations was  $-5.1 \pm .3$  °C.

**Torpor Bout Length vs. Date.** TBL increased in October and November, were longest and constant December to March, and became shorter in April and May (Fig. 5). The longest torpor bout measured was 26.5 days. TBL did not differ between sexes.

**TBL vs. Soil Temperature.** Soil temperatures at  $-1$  m nearest each hibernaculum significantly influenced torpor bout length ( $p < .001$ ,

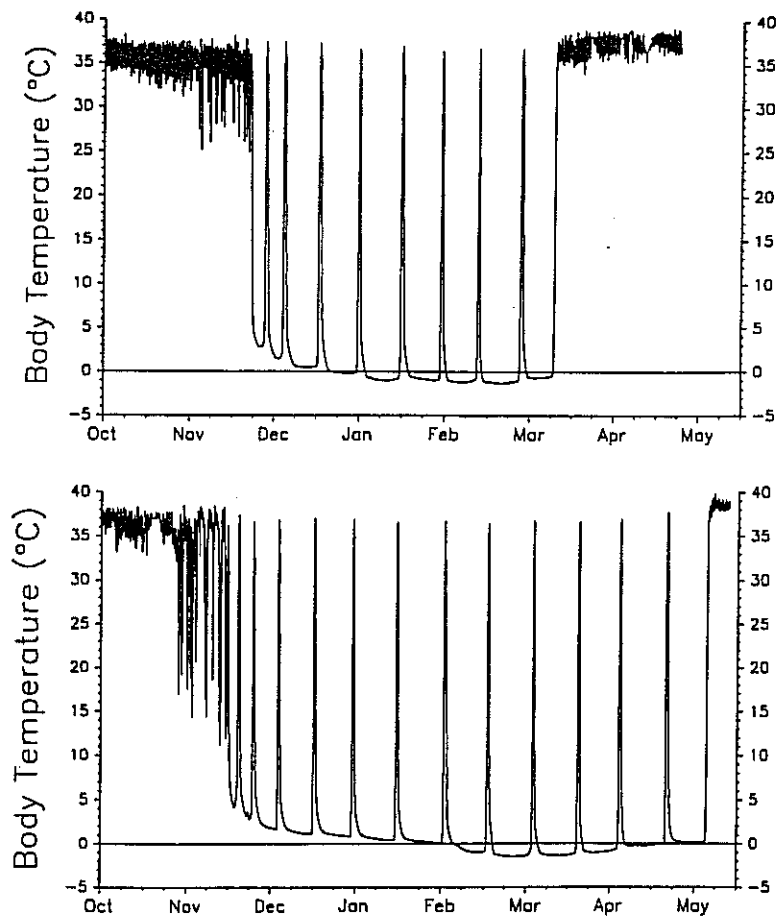


FIGURE 3 Body temperatures of a male (top) and female (bottom) arctic ground squirrel overwintering in outdoor enclosures in Fairbanks, Alaska.

ANOVA); however, this was only true for  $T_{\text{soil}} > 0^{\circ}\text{C}$ . In colder soils, from 0 to  $-7^{\circ}\text{C}$ , there was no significant influence of  $T_{\text{soil}}$  on torpor duration (Fig. 6;  $p > .5$ , ANOVA).

**TBL vs. Body Temperature.** Abdominal body temperatures, calculated as average  $T_c$  from two days after the beginning of a torpor bout to just before  $T_c$  began to rapidly rise during an arousal, also

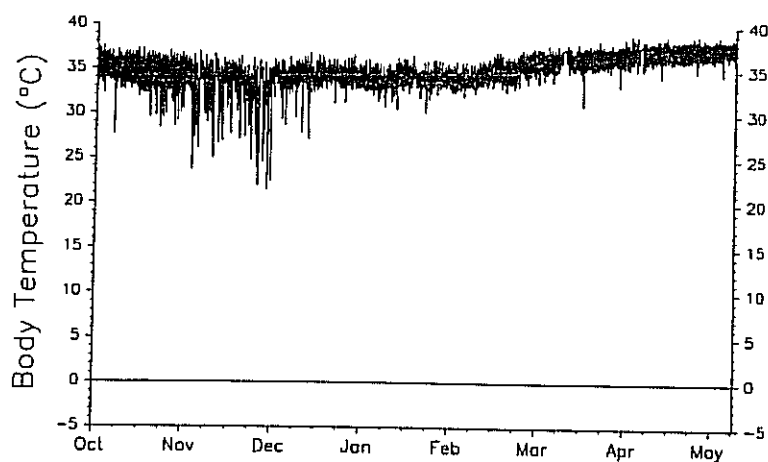


FIGURE 4 Body temperature of a male arctic ground squirrel that failed to hibernate, though he was kept in an outdoor enclosure. Food was provided bi-weekly.

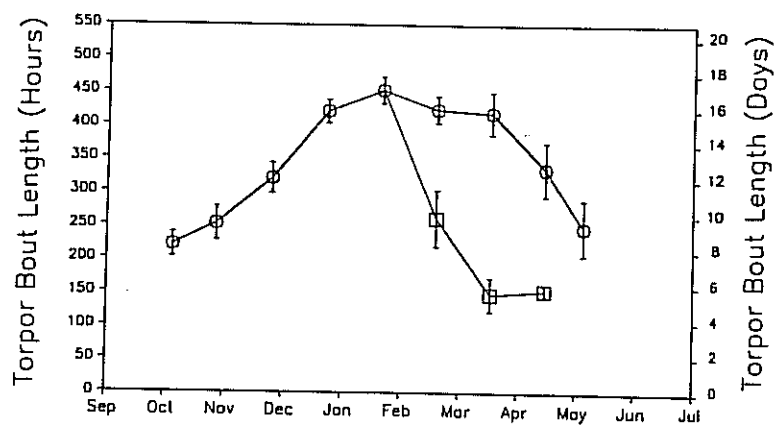


FIGURE 5 Torpor bout lengths of arctic ground squirrels hibernating in outdoor enclosures under natural conditions (circles,  $n=8-12$ ) or in enclosures in which the soil was warmed over two months from  $-7$  to  $+6$  °C beginning 1 February (squares,  $n=3-7$ ).

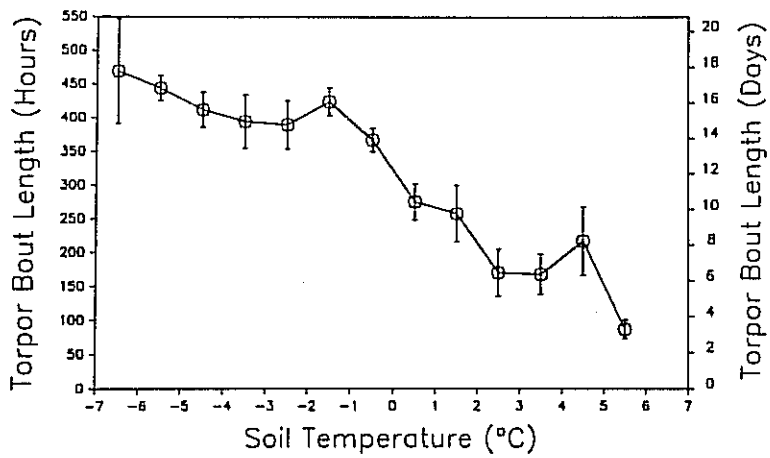


FIGURE 6 Torpor bout length versus soil temperature near burrow depth.

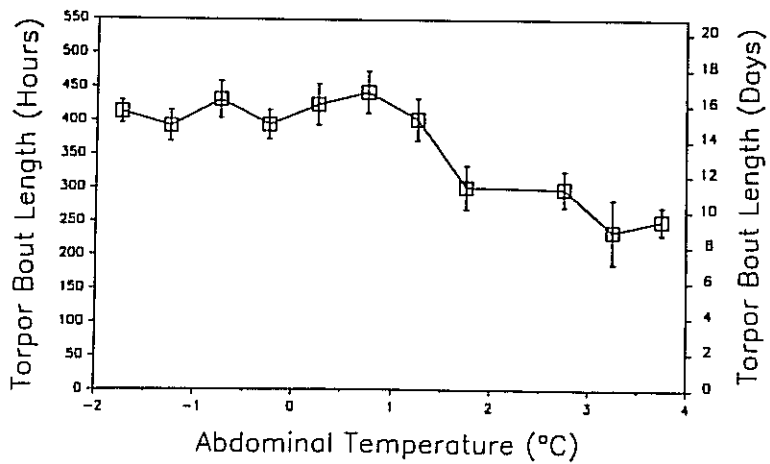


FIGURE 7 Torpor bout length versus average abdominal temperatures reached during steady state torpor.

influenced TBL ( $p < .01$ , ANOVA), but this effect was only significant for  $T_c > 1$  °C; below this body temperature, TBL was constant (Fig. 7).

**TBL vs. Delta T.** As the gradient between subzero  $T_{soil}$  and  $T_c$  increases, metabolic rates may increase in support of greater heat production. Greater rates of metabolism could cause TBL to shorten, however, TBL remained long and constant at  $T_{soil} < 0$  °C, even at delta T ( $T_c - T_{soil}$ ) as great as 5-6 °C (Fig. 8).

**TBL Versus Date,  $T_{soil}$ ,  $T_c$ , and Delta T.** A multiple regression model predictive of TBL was developed using a stepwise procedure; it included the variables  $T_c$ ,  $T_{soil}$ , and date as significant, however,  $T_c$  contributed the most (.43) to the combined  $r^2$  of .47.

**Warming the Soil.** Accelerating the rate that soils warmed after 1 February increased the frequency of arousals in experimental compared to control animals: mean TBL after 1 February was  $226.5 \pm 35.5$  hrs in the experimental group vs.  $381.2 \pm 19.0$  hrs in controls ( $p < 0.001$ , t-test; Fig. 5).

Warming the soil advanced the timing of emergence of males but not females. Emergence date averaged 6 Mar  $\pm 5.9$  d vs. 16 April  $\pm 15.0$  d in warmed and control males, respectively ( $p < .05$ ), and 10 April  $\pm 7.2$  d and 23 April  $\pm 6.7$  d in females ( $p > .2$ ).

**Spontaneous Arousals.** Spontaneous arousals lasted  $15.9 \pm 0.7$  hrs ( $n = 57$ ) between November and March (Fig. 9); arousals during April, which usually were the penultimate arousals, were longer, lasting  $24.3 \pm 4.1$  hr ( $n = 9$ ). Arousal duration was positively correlated with  $T_c$ , but weakly so ( $p < .001$ ,  $r^2 = .30$ ). Arousal duration was not significantly correlated with the length of the previous torpor bout nor with the integrated value below the curve of  $T_c$  during the previous torpor bout ("degree-hours").

Average  $T_c$ 's reached during spontaneous arousals was  $34.9 \pm 1.8$  °C ( $n = 6$ , 30 arousals) which is similar to the average  $T_c$  in the same animals 10 days pre-torpor ( $34.8 \pm 4.0$  °C), but significantly lower than their average  $T_c$  in the 10 days after hibernation ( $36.1 \pm 8.3$  °C;  $p < .05$ ). These changes are not accounted for by drift in the transmitters, which were recalibrated after recovery in spring.

**Circadian Rhythmicity.** Daily rhythms in body temperature were evident during euthermia before hibernation, daily torpor, and in a minority of animals that had  $T_c > 8$  °C during the first or second multi-day torpor bout; rhythms of  $T_c$  were not evident in later bouts when  $T_c$  was less than 8 °C, and the timing of spontaneous arousals generally could not be predicted on the basis of earlier periodicity.

**Sex Differences in Hibernation Patterns.** This experiment was repeated the next year, but without manipulating soil temperatures. Females entered hibernation earlier than did males (eg. Fig. 3);

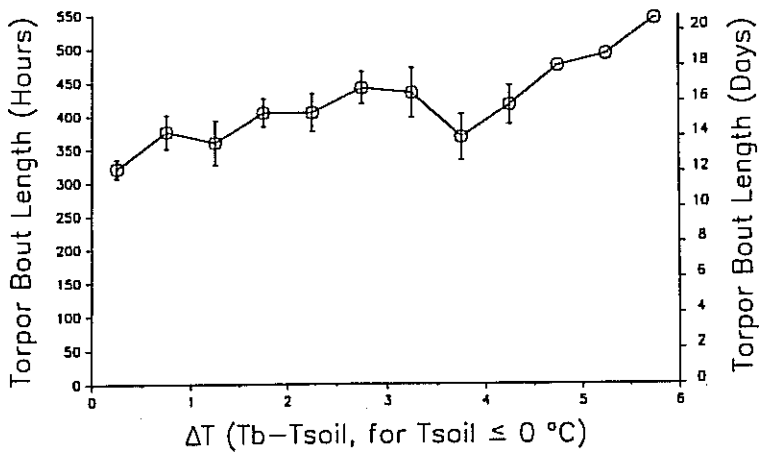


FIGURE 8 Torpor bout length versus the gradient between abdominal body temperature and soil temperature at -1 m, in subzero soil temperatures.

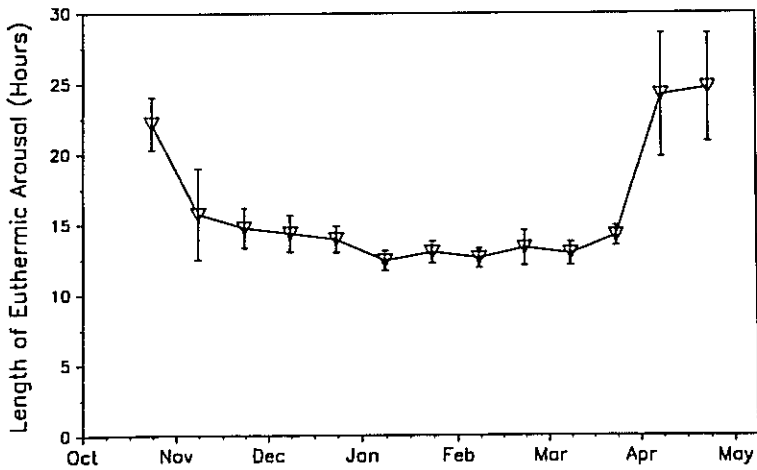


FIGURE 9 Duration of periodic arousals from hibernation measured as the interval T<sub>c</sub> ≥ 30 °C. Points are bi-weekly means ± SE representing 5-8 animals except for late April which is from 3 animals.

reproductively maturing males ended hibernation earlier than did females and non-reproductive males. Reproductive males ( $n=5$ ) remained sequestered within their burrows at euthermic  $T_c$  for 10-21 days (mean  $15.2 \pm 2.0$  d) before first appearing on the surface, whereas females ( $n=5$ ) and non-reproductive males ( $n=2$ ) emerged within 3-6 days of ending torpor.

### Discussion

The later immergence of males compared to females is unusual among hibernating Sciurids (Michener 1984) and may relate to the importance of food caches in arctic ground squirrel males, who end heterothermy in late March and early April when their environment is completely covered with snow which lingers until late May. Many cachable foods such as grass and berry seeds and fungi are not available until late summer, and thus males that delay immergence may accumulate larger caches (McLean and Towns 1981). Males end torpor early and sustain euthermy because a high  $T_c$  is required for testicular growth and development (Barnes et al. 1986a,b), which takes 3 weeks in this species (Barnes unpublished). Males would seem to prefer to remain sequestered within their hibernacula during most of this euthermic pre-emergence interval. Females and males that remain immature stay in hibernation until late April and early May and emerge within a few days of ending torpor. Females can become pregnant within eight days of their last arousal (Reed and Barnes unpublished).

Warming the soil above the hibernacula caused early emergence of males but not females, suggesting increasing  $T_{soil}$  can act as a cue for the timing of emergence in males. Increasing ambient temperatures also caused hibernation to end early in hibernating male *S. lateralis*, but the period and phase of the underlying circannual rhythm was not affected (Barnes and York 1990). Why there appears to be a sex difference in this effect in *S. parryii* is not clear.

Hibernating arctic ground squirrels express circadian rhythms in  $T_c$  when torpor is daily or during initial multi-day torpor bouts, if  $T_c$  remains above approximately 8 °C. At lower  $T_c$  that occur later in the season there is no discernible circadian cycling in  $T_c$ . The damping of the rhythm may relate to a need to suppress the arousing influence of the suprachiasmatic nucleus (Edgar et al. 1992) in order for torpor to extend past 24 hours. Alternatively, the function or expression of the circadian clock may be inhibited below body temperatures of 8 °C (Lee et al. 1990).

The seasonal pattern of torpor bout length in arctic ground squirrels is

similar to that reported in other ground squirrel species (Wang 1979; French 1982b; Barnes et al. 1986b). The lengthening of bouts in fall is probably related to decreasing  $T_{\text{soil}}$  and concomitant lowering of  $T_c$ , a relationship seen under lab conditions (Twente and Twente 1965), and shorter bouts in spring may be due in part to increasing  $T_{\text{soil}}$  and  $T_c$ , as was illustrated by the shortening effect on TBL of warming soils prematurely. However, TBL does not respond as predicted at  $T_{\text{soil}} < 0^\circ\text{C}$ . When ambient temperatures decrease below  $0^\circ\text{C}$ , arctic ground squirrels begin to thermoregulate, as body temperatures of the anterior including the head are not known to fall below  $0^\circ\text{C}$ , although  $T_c$  can reach  $-2.9^\circ\text{C}$  (Barnes 1989). In subzero  $T_{\text{soil}}$  as the difference between  $T_c$  and  $T_{\text{soil}}$  ( $\Delta T$ ) increases, metabolic costs of thermoregulation should increase, assuming that a  $\Delta T$  of 1-6  $^\circ\text{C}$  cannot be maintained at a constant rate of metabolism by reducing conduction. Metabolic theories of what governs TBL and the frequency of arousals predict that TBL should shorten with increasing metabolic rates (Galster and Morrison 1975; Geiser et al. 1990), yet in arctic ground squirrels, TBL remained constant or even lengthened as  $T_{\text{soil}}$  decreased to as low as  $-7^\circ\text{C}$ .

It is possible that the best correlate of TBL and arousal frequency is not  $T_c$  or metabolic rate, but rather the temperature of the brain, which remains between  $0-1^\circ\text{C}$  at  $T_{\text{soil}} < 0^\circ\text{C}$  and  $T_c < 1^\circ\text{C}$ , when TBL is constant, but increases with  $T_c$  and  $T_{\text{soil}}$  at temperatures above  $1^\circ\text{C}$  when TBL is decreasing. This hypothetical dependence of TBL and arousal frequency with brain temperature may relate to a temperature dependence of sleep debt kinetics with brain temperature and the hypothesized functional relationship of euthermic arousals from hibernation with sleep recovery (Daan et al. 1990, Trachsel et al. 1990, Barnes et al. this volume, Heller et al. this volume).

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