

TEMPERATURES OF HIBERNACULA AND CHANGES IN BODY COMPOSITION OF ARCTIC GROUND SQUIRRELS OVER WINTER

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Soil temperatures near hibernacula of free-living arctic ground squirrels (*Spermophilus parryii*) were recorded over 3 winters (October–April 1993–1996) at Toolik Lake, Alaska. Means and minima of soil temperature at 20 burrows averaged -8.9 and -18.8°C , respectively. Soil temperatures were $<-3^{\circ}\text{C}$ for, on average, >5 months, which represented the duration of winter that hibernating arctic ground squirrels were actively thermogenic. Individual burrows did not differ significantly in mean soil temperature over 3 years, but significant differences in mean and minimum soil temperatures were observed among burrows. Sites of burrows with shrubby vegetation accumulated more snow and had significantly higher soil temperatures over winter than windswept sites in non-shrubby vegetation. Female ground squirrels hibernated in burrows that had significantly higher mean and minimum soil temperatures than burrows of males, and adults hibernated in burrows with significantly higher soil temperatures than burrows of juveniles. Although ground squirrels occupying colder burrows were predicted to lose more body mass during hibernation than those in warmer burrows, changes in body, fat, and lean masses over winter were not correlated with soil temperature for any sex or age. Relationships between change in body composition of hibernating arctic ground squirrels and temperatures of their hibernacula may be confounded by use of food caches, differing thermal conductance of nests, or differences in individual's energetics of hibernating not related to the gradient between body and soil temperatures.

Key words: hibernation, hibernaculum, body composition, temperature, burrow, arctic, ground squirrel, *Spermophilus parryii*, Alaska

Factors that potentially influence differences in winter survivorship of hibernating mammals include variation in prehibernation body size and composition, use of food caches, and differences in energetic costs of hibernation (Arnold, 1993; Frank, et al., 1998; Kawamichi and Kawamichi, 1993; Michener and Locklear, 1990). Total energetic costs of hibernation vary with its length, frequency and duration of arousal episodes, and costs of thermoregulation during torpor and arousal (Wang, 1979). Energetic expenditure for thermoregulation during torpor or euthermia for solitary hibernators depends on thermal conductance of the animal and nest and the gradient of temperature between the hibernator's body and surrounding hibernaculum (Arnold, et

al., 1991; Chappell, 1981; Heldmaier and Ruf, 1992; Song, et al., 1997). Extent and nature of pre-hibernation fattening and timing and patterns of heterothermy differ with sex and age and may be linked to differential mortality during hibernation (Barnes and Ritter, 1993; Buck and Barnes, 1999; Frank et al., 1998; Michener and Locklear, 1990). Nevertheless, thermal conditions in the hibernaculum, which may or may not be similar among males and females and juveniles and adults, are poorly described. Conditions within the hibernaculum may be particularly important for survival at high elevations and latitudes where freezing soils force hibernators to be thermogenic and thermoregulatory costs can be significant.

Arctic ground squirrels (*Spermophilus*

parryii) are the northernmost hibernators in North America and the largest of their genus, attaining an adult body mass of >1 kg (Buck and Barnes, 1999; Nadler et al., 1982). Individuals are active for 3–5 months each year, during which they reproduce, grow, and fatten in preparation for hibernation (Mayer 1953; McLean and Towns, 1981). In northern Alaska, emergence into hibernation takes place from mid-August to mid-September in an overlapping sequence, beginning with females (adults before juveniles) and then males (adults before juveniles). Arctic ground squirrels spend the next 7–9 months sequestered in underground hibernacula. Emergence from hibernation begins in mid-April and lasts ca. 3 weeks with reproductive males emerging before females. Although reproductive males first appear in spring with no significant loss in body mass compared with autumn, loss in body mass of females over winter ranges from 11 to 47% (Buck and Barnes, 1999). Sources of this variation in loss of mass are not known.

The thermal environment of the hibernaculum could be a major factor in determining energetic costs associated with hibernation and change in body composition of arctic ground squirrels over winter. Depths of burrows in most of the northern range of *S. parryii* are limited to <1 m by permafrost (Carl, 1971), and hibernacula reach some of the lowest temperatures experienced by hibernating mammals. Mayer (1955) reported a minimum temperature of -26.7°C near nests of hibernating *S. parryii* in the Alaska Range, and Barnes (1989) recorded soil temperatures of -18.0°C at the depth of the hibernaculum in the northern foothills of the Brooks Range, Alaska. Hibernating ground squirrels exposed to ambient temperatures $\leq 0^{\circ}\text{C}$ increase metabolic rates to keep from freezing, and rates of thermogenesis rise proportionally with the increasing gradient between body and ambient temperature (Geiser and Kenagy, 1988; Heller and Collier, 1974). Thus, substantial differences in the thermal envi-

ronments of hibernacula should correspond to significant differences in energetic costs for inhabitants and, therefore, loss in body mass and change in body composition over winter. Our objectives were to record soil temperature at burrows of individual arctic ground squirrels, determine if temperatures varied among burrows or over years at individual burrows, and correlate that variation with changes in body mass and composition of the occupant over winter.

MATERIALS AND METHODS

Study area.—Our study was conducted along the shores of Toolik Lake ($68^{\circ}38'\text{N}$, $149^{\circ}38'\text{W}$; elevation, 809 m) in the northern foothills of the Brooks Range, Alaska, 300 km N of the Arctic Circle. The topography was gently rolling hills underlain by permafrost. The growing season for plants near Toolik Lake was brief, usually <10 weeks (Shaver, et al., 1986), with freezing temperatures and snowfall possible in each summer month. Snow in winter accumulated to depths of 10–75 cm (Benson and Sturm, 1993; Sturm et al., 1995). Winter was further characterized by extreme subzero temperatures for ca. 8 months, high winds, and darkness.

Handling of animals.—Free-ranging arctic ground squirrels were live-trapped in late summer (August and September) and spring (April and May) with Tomahawk traps baited with carrots. We trapped at marked burrows along a 4.0-km transect within 1.8 km of the northern and eastern shore of Toolik Lake. Between 40 and 80 traps were set in the morning and examined every 1–3 h until late evening. We set traps daily in 1993 (13 August–6 September), 1994 (9 April–10 May, 22 August–22 September), and 1995 (9 April–12 May). Most animals were captured twice weekly. Captured animals were transferred to the adjacent Toolik Field Station of the University of Alaska where they were weighed and assessed for reproductive status. Body composition (fat and lean mass) was estimated using body mass and total body electrical conductance (TOBEC—Buck and Barnes, 1999). In addition, all newly captured animals were ear-tagged and had their fur dyed in unique patterns for identification. The Institutional Animal Care and Use Committee at the University of Alaska Fairbanks approved all procedures.

Locations of hibernacula.—Locations of in-

dividual hibernacula were determined by radio-telemetry of animals 1–3 weeks prior to immergence into hibernation. Ground squirrels were fitted with radiotransmitters (Model P2—AVM Instrument Company, Ltd., Livermore, CA) fixed to plastic wire-ties that served as collars. Transmitters operated at frequencies from 150 to 160 MHz. The signal was transmitted from a 15-cm whip antenna and received by a portable receiver (Model LA12-DS—AVM Instrument Co., Dublin, CA) with a Yagi antenna. Animals were tracked to their sleeping nests at night. A ground squirrel that was tracked to the same burrow for ≥ 3 consecutive nights was considered the occupant of that burrow. In the following spring, burrows were confirmed as hibernacula by locating the hole in the snow through which the animal exited and subsequent capture of the same individual. Timing of immergence and emergence was inferred from sightings and success in trapping individuals. Duration of hibernation was calculated as the difference in number of days between dates of immergence and emergence.

Change in body mass and composition.—The combination of body, fat, and lean mass of individual ground squirrels on the date of their last capture in autumn was considered their immergent body condition. Those same measures at first capture in spring were considered their emergent condition. Measurements at emergence took place < 2 days of each animal's first appearance above ground, as indicated by disturbance of snow. We recorded characteristics of burrows of 21 female and 11 male ground squirrels. Of those, we collected both immergent and emergent measures of body composition and dates of immergence and emergence of 14 females and 9 males. We recorded aspect, direction of drainage, and primary type of vegetation for each site where burrows were located. Aspect and drainage direction of the site were determined with a magnetic compass corrected for magnetic declination. Vegetation type was classified as shrub, non-tussock tundra, or lacking vegetation (wind scour).

Temperature of soil and air.—In the last 2 weeks of August 1993, we outfitted 18 burrows with data loggers (Hobo-Temp II—Onset Computer Corporation, Pocasset, MA; accuracy $\pm 0.16^\circ\text{C}$ at ice point) for semi-continuous recordings (1 reading/4.8 h) of soil temperature at the maximum depth of thaw (depth of permafrost

table). Two additional burrows were added in 1995. Depth of thaw was determined by hammering a stainless steel rod through the active layer of the soil at five points surrounding each entrance to the burrow. Depth of thaw for that site was recorded as the mean of these measurements. Because ground squirrels can only dig through unfrozen soil, this depth represents the lower boundary for locating the hibernaculum and thus the warmest conditions at that site during winter. In addition to indicating depth of the permafrost table, hammering the rod through the active layer allowed us to estimate consistency of the soil based on resistance of the rod to insertion.

To avoid recording elevated temperatures due to thermogenic output of the hibernating occupant, we did not place thermistors directly into the nest chamber. Soil temperatures were measured by a thermistor in plastic pipe inserted through the soil to just above the permafrost table. To mimic thermal conductance of soil and inhibit convection, the pipe was filled to the surface of the soil with granular table salt and sealed. Granular table salt was chosen because it poured uniformly into the pipes and has a thermal conductivity similar to mineral soil (conductivity, salt = $6.0 \text{ W m}^{-1} \text{ }^\circ\text{K}^{-1}$, mineral soil = $5.4 \text{ W m}^{-1} \text{ }^\circ\text{K}^{-1}$ —Turcotte and Schubert, 1982). The thermistor was connected to a data logger placed above ground within a waterproof shelter. Of 18 burrows with temperature loggers, data were recovered from all for winter 1993–1994, 10 in 1994–1995, and six in 1995–1996. Reductions were due to failures of loggers or thermistors. Data on soil temperature were collected at five of the 18 burrows for 3 consecutive years.

Air temperatures at 1 m above ground were collected each hour at a meteorological station located at the Toolik Lake Research Station. Depth of snow < 1 m from the data logger at each burrow was measured to the nearest 5 cm on 12 April 1994 and 1995. Depth of snow was not measured in spring 1996.

Statistical analysis.—Comparisons of soil and air temperature were for October–April (overall $\bar{X} \pm 1 \text{ SE}$). Minimum soil temperatures were reported as the lowest value from October to April. A paired *t*-test was used for analyses of change in body composition over winter for each age and sex class and for comparing average soil temperatures of burrows in shrubby

versus non-shrubby sites. For comparisons of average air temperature and soil temperature among burrows and over years, we used repeated measures analysis of variance. To compare average soil temperatures of burrows belonging to different sex and age classes of ground squirrels, we used a two-way analysis of variance and Tukey's test for pairwise comparisons (Zar, 1984). To determine associations among individual changes in body, fat, or lean masses, and measures of soil temperature at each burrow, we used separate linear regressions. All tests were considered significant at $P < 0.05$.

RESULTS

Temperature at depth of the hibernaculum.—Depth of thaw of the soil at 20 burrows of arctic ground squirrels in late August averaged 97 ± 1.2 cm (range = 80–104 cm; Table 1). Means and minima of soil temperature at depth of the thermistor for all 20 burrows averaged -8.9 ± 0.4 (range = -13.5 – -4.7°C) and $-15.8 \pm 0.7^\circ\text{C}$ (range = -23.4 – -8.0°C), respectively. Soil temperatures decreased $<0^\circ\text{C}$ on 26 October ± 3 days. Among the 20 burrows and over 3 winters, both mean and minimum soil temperatures were positively correlated with depth of snow in spring (mean soil temperature, $r^2 = 0.49$, $d.f. = 26$, $P < 0.001$; minimum soil temperature, $r^2 = 0.53$, $d.f. = 26$, $P < 0.001$, Fig. 1) and to one another ($r^2 = 0.98$, $d.f. = 26$, $P < 0.001$), but not to the date that soil temperature decreased $<0^\circ\text{C}$ ($r^2 = 0.02$, $d.f. = 26$, $P = 0.08$). Depth of thaw was not significantly related either to mean ($r^2 = 0.029$, $d.f. = 26$, $P = 0.191$) or minimum soil temperature ($r^2 = 0.05$, $d.f. = 26$, $P = 0.28$) or to the date soil temperature decreased $<0^\circ\text{C}$ ($r^2 = 0.03$, $d.f. = 26$, $P = 0.83$).

Soil temperatures at maximum depth of the hibernaculum were collected at five burrows and air temperature above one burrow for 3 consecutive winters (Fig. 2; Table 2). Mean ($F = 15.58$, $d.f. = 8, 4$, $P < 0.001$) and minimum ($F = 16.93$, $d.f. = 8, 4$, $P < 0.001$) soil temperatures varied significantly among burrows over 3 years but did not vary at individual burrows over 3 years

(mean soil temperature, $F = 0.81$, $d.f. = 2$, $P = 0.48$; minimum soil temperature, $F = 2.30$, $d.f. = 2$, $P = 0.16$, Table 2). Air temperature averaged -24.5°C and did not vary among years ($F = 0.45$, $d.f. = 2$, $P = 0.64$).

By spring, snow averaged 34.1 ± 4.4 cm above burrows located in shrubby vegetation and 12.5 ± 2.4 cm above burrows in non-shrubby sites ($t = 3.70$, $d.f. = 34$, $P \leq 0.001$). Soil temperatures were higher in burrows with shrubs ($-7.0 \pm 0.46^\circ\text{C}$) compared with burrows without shrubs ($-10.67 \pm 0.51^\circ\text{C}$; $t = 4.12$, $d.f. = 34$, $P \leq 0.001$).

Loss of body mass and change in body composition.—Adult and juvenile males did not differ in amount of body, fat, and lean mass lost over winter (body mass, $t = -1.93$, $d.f. = 7$, $P = 0.10$; fat mass, $t = -0.41$, $d.f. = 7$, $P = 0.70$; lean mass, $t = -1.84$, $d.f. = 7$, $P = 0.11$) and were pooled for further analyses. Males averaged the same body mass at first capture in spring as they did at last capture in autumn ($t = 0.20$, $d.f. = 8$, $P = 0.85$) and showed no significant change in either mass of fat ($t = -0.34$, $d.f. = 8$, $P = 0.75$) or lean ($t = 0.47$, $d.f. = 8$, $P = 0.65$). Adult and juvenile females did not differ significantly in change in body condition over winter (body mass, $t = 1.54$, $d.f. = 12$, $P = 0.15$; fat mass, $t = 1.43$, $d.f. = 12$, $P = 0.18$; lean mass, $t = 0.31$, $d.f. = 12$, $P = 0.76$) and were pooled for further analyses. Average body mass of females was 35% less at emergence than immergence ($t = 13.99$, $d.f. = 13$, $P \leq 0.001$), including a 66.0% loss in mass of fat ($t = 13.99$, $d.f. = 13$, $P \leq 0.001$) and a 20.8% loss in lean mass ($t = -8.95$, $d.f. = 13$, $P \leq 0.001$).

For females, duration of hibernation (range = 223–255 days) was correlated positively to difference in body mass between immergence and emergence ($r^2 = 0.34$, $d.f. = 12$, $P = 0.03$). Therefore, we calculated rate of change in body mass and composition over hibernation by dividing loss of mass of individual females by number of days in hibernation (Table 3). During hibernation, individual females differed in

TABLE 1.—Characteristics of arctic ground squirrels and their burrows at Toolik Lake, Alaska.

| Site | Depth of active layer (cm) | Aspect | Vegetation ^a | Soil ^b | Mean depth of snow (cm) | | Soil temperature (mean, minimum, °C) | | | Age ^c | Sex |
|------|----------------------------|--------|-------------------------|-------------------|-------------------------|------|--------------------------------------|--------------|--------------|------------------|------|
| | | | | | 1994 | 1995 | 1993-1994 | 1994-1995 | 1995-1996 | | |
| 1 | 100 | S | SH | FSG | 35 | 50 | -8.9, -15.7 | -7.0, -12.3 | -7.2, -12.3 | A, J | ♀ |
| 4 | 92 | S | SH | FSG | 30 | 20 | -9.4, -17.5 | | -8.7, -15.6 | A, J | ♀ |
| 5 | 98 | SW | T | FSG | 10 | 30 | -12.0, -20.9 | -11.2, -18.8 | | J | ♂ |
| 6 | 97 | W | SH | C | 35 | 60 | -8.2, -15.1 | -6.7, -11.8 | -11.0, -18.8 | A | ♂, ♀ |
| 11a | 101 | W | SH | FS | 30 | 15 | -8.6, -16.3 | | | A, J | ♀ |
| 11b | 98 | SW | SH | FS | 20 | 15 | -9.4, -17.7 | | | A | ♂ |
| 12 | 93 | SW | SH | GC | 15 | 15 | -10.6, -18.8 | -10.6, -16.1 | | A, J | ♀ |
| 13 | 102 | NE | SH | FSG | 45 | 100 | -6.6, -11.5 | -4.7, -8.0 | | A | ♀ |
| 16 | 80 | NW | T | FS | 10 | 10 | -10.5, -18.8 | | | A | ♂ |
| 18 | 98 | S | T | FSG | 10 | 10 | -10.6, -19.1 | -9.7, -16.6 | -5.7, -12.8 | J | ♂, ♀ |
| 21 | 94 | SE | T | FS | | | | | | | |
| 22 | 90 | SE | T | FSG | | | | | -11.0, -21.0 | | ♂, ♀ |
| 23 | 100 | SW | SH | FSG | 45 | 30 | -11.7, -19.5 | | -5.6, -9.7 | J | ♂ |
| 31 | 89 | NW | WS | CB | 10 | 0 | -13.5, -23.4 | -13.0, -21.9 | -12.2, -20.8 | J | ♂ |
| 32 | 103 | SE | T | FS | 10 | 10 | -12.4, -21.6 | | | A | ♂, ♀ |
| 33 | 100 | SW | T | FSG | 35 | 10 | -10.6, -19.1 | -9.7, -16.1 | -8.9, -15.9 | A, J | ♂, ♀ |
| 34 | 96 | SE | SH | FSG | 40 | 45 | -5.6, -11.2 | -5.5, -9.7 | -5.0, -8.7 | A | ♀ |
| 39 | 100 | W | SH | FSG | 40 | 45 | -5.6, -11.2 | -5.8, -11.2 | | A | ♀ |
| 46 | 101 | W | SH | FSG | 10 | 10 | -7.2, -13.4 | | | A | ♂ |
| 53 | 104 | SW | T | FSG | 10 | 10 | -8.8, -15.6 | | | A | ♂ |

^a SH = shrub; T = tundra (non-tussock); WS = wind scout.

^b FS = fine soil; FSG = fine soil and gravel; C = cobble; GC = gravel and cobble; CB = cobble and boulder.

^c A = adult; J = juvenile.

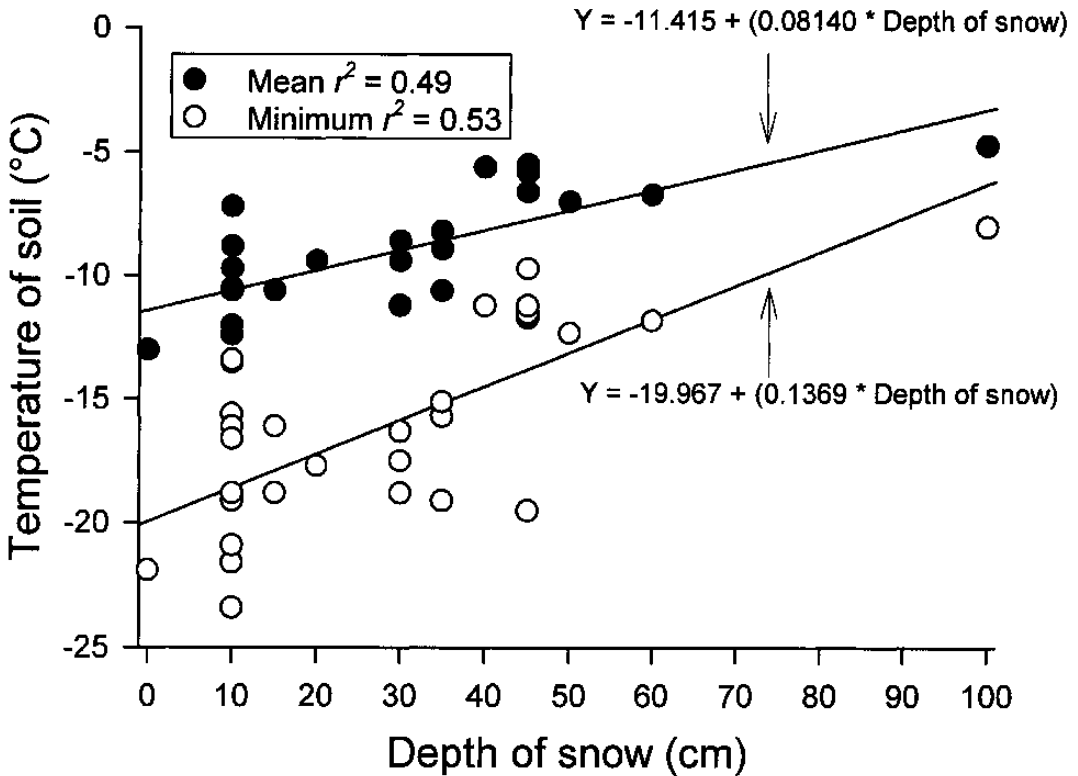


FIG. 1.—Relationship between snow depth and soil temperature at burrows of arctic ground squirrels on 12 April at Toolik Lake, Alaska (1993–1995). Mean and minimum soil temperature were significantly correlated with snow depth ($P < 0.001$).

rates of loss for body mass by $\leq 23\%$, for fat mass by 400%, and for lean mass by 1,220%.

Soil temperature and change in body composition.—We performed separate linear regression analyses of soil temperature at each burrow with differences between immergent and emergent body, fat, and lean mass to identify potential relationships between thermal conditions and change in body composition of the occupant over winter. There were no statistical relationships between loss in body mass and change in composition with respect to either mean or minimum soil temperature of the burrow for any age and sex class. Further, among females, the only class that had a significant change in body composition over winter, loss of body mass, fat mass, and lean mass per day of hibernation were

not related to either mean or minimum soil temperature.

Selection of burrows.—Arctic ground squirrels of different age and sex selected burrows with different mean soil temperature (sex, $F = 6.77$, $d.f. = 1, 29$, $P = 0.01$; age, $F = 9.71$, $d.f. = 1, 29$, $P < 0.01$) and minimum soil temperature (sex, $F = 6.38$, $d.f. = 1, 29$, $P = 0.02$; age, $F = 8.81$, $d.f. = 1, 29$, $P < 0.01$; Table 4). Adults hibernated at sites with higher mean temperature than juveniles (Tukey's $q = 4.41$, $P < 0.05$) and females hibernated at sites with higher mean temperature than males ($q = 3.68$, $P < 0.05$). Similarly, adults hibernated at sites with higher minimum temperature than juveniles ($q = 4.2$, $P < 0.05$), and females hibernated at sites with higher minimum temperature than males ($q = 3.57$, $P = 0.05$; Table 4).

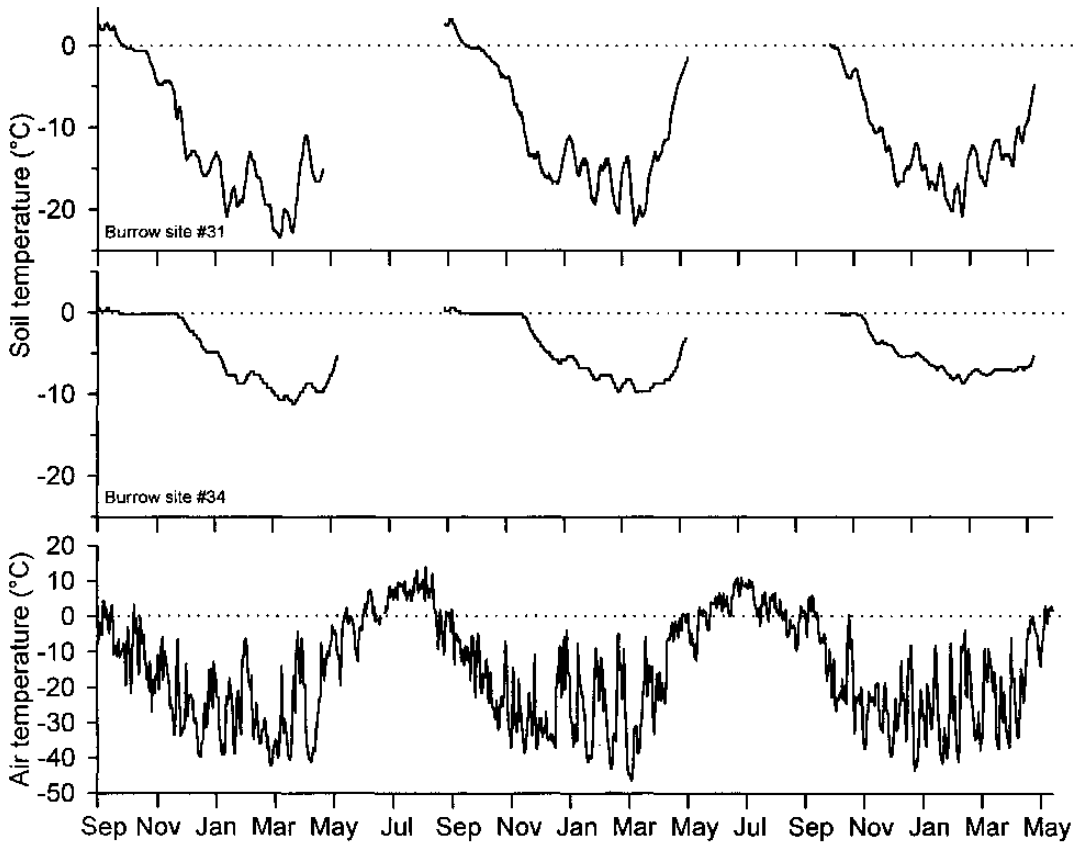


FIG. 2.—Average daily air temperature at 1 m above the ground and soil temperature recorded five times daily at depth of the coldest (#31) and warmest (#34) burrows of arctic ground squirrels monitored from 1993–1996 at Toolik Lake, Alaska.

Over 3 years, seven of 18 burrows were used exclusively by female ground squirrels and seven exclusively by males (Table 1). All burrows used exclusively by females

were located in areas with tall (ca. 25–100 cm) shrubby dwarf birch (*Betula nana*). Only two of seven burrows of males were in shrubby areas; four were in areas with

TABLE 2.—Mean and minima of soil temperatures (°C) collected October–April 1993–1996 at five burrows of arctic ground squirrels near Toolik Lake, Alaska. Mean and minima of air temperature (°C) are from the meteorological station of the Toolik Field Station.

| Temperature | Burrow number | 1998–1994 | | 1994–1995 | | 1995–1996 | | 3-year | |
|-------------|-------------------|-----------|---------|-----------|---------|-----------|---------|-----------|---------|
| | | \bar{X} | Minimum | \bar{X} | Minimum | \bar{X} | Minimum | \bar{X} | Minimum |
| Soil | 1 | -8.9 | -15.7 | -7.0 | -12.3 | -7.2 | -12.3 | -7.7 | -13.4 |
| | 31 | -13.5 | -23.4 | -13.0 | -21.9 | -12.2 | -20.8 | -12.9 | -22.0 |
| | 6 | -8.2 | -15.1 | -6.7 | -11.8 | -11.0 | -18.8 | -8.6 | -15.2 |
| | 34 | -5.6 | -11.2 | -5.5 | -9.7 | -5.0 | -8.7 | -5.4 | -9.9 |
| | 33 | -10.6 | -19.1 | -9.7 | -16.1 | -8.9 | -15.9 | -9.7 | -17.0 |
| | Overall \bar{X} | -9.4 | -16.9 | -8.4 | -14.4 | -8.9 | -15.3 | -8.9 | -15.5 |
| Air | | -24.9 | -42.3 | -25.7 | -46.5 | -24.7 | -43.4 | -25.1 | -44.1 |

TABLE 3.—Rates of loss of body, fat, and lean mass of female arctic ground squirrels ($n = 14$) during hibernation near Toolik Lake, Alaska. Data are combined for 1993–1995.

| Type | Mass lost (g/day) | | |
|-----------|-------------------|------|----------|
| | \bar{X} | SE | Range |
| Body mass | 1.1 | 0.07 | 0.7–1.6 |
| Fat mass | 0.6 | 0.07 | 0.3–1.2 |
| Lean mass | 0.5 | 0.08 | 0.09–1.1 |

low tundra vegetation of prostrate graminoids and forbs and one in a wind-scoured area with no vegetation. Two of four burrows that were used by both male and female ground squirrels were in tundra vegetation and the other two in shrubby areas. Eighty-five percent of burrows were in areas of fine soil or fine soil mixed with gravel, and 72% had a southern exposure.

DISCUSSION

Conditions of hibernacula.—Hibernacula of arctic ground squirrels were located in areas with an average depth of thaw of 97 cm, whereas depth of the active layer in the area of Toolik Lake averaged 44 cm in moist tundra and 58 cm in dry tundra (Bockheim et al., 1998). This suggests that arctic ground squirrels select sites with deeper than average permafrost table for digging burrows (Mayer, 1953). Despite their location in regions with deeper thaw, all burrows were very cold compared with conditions reported for lower-latitude hibernators, which only briefly or never reach freezing. Minimum soil temperature report-

ed for hibernacula are -2.6°C for *S. richardsonii* (Michener, 1992), ca. 0°C for *S. columbianus* (Young, 1990), 0.1°C for *Marmota monax* (Ferron, 1996), 0.5°C for *M. marmota* (Arnold et al., 1991), and 2°C for *S. saturatus* (Kenagy et al., 1989). The highest mean soil temperature that we recorded over 3 winters was -4.7°C , and the lowest was -13.5°C , with minimum soil temperatures from -23.4 to -8°C .

Burrows varied substantially and consistently from one another in temperature each year, with over a two-fold difference in mean soil temperature among burrows. Several factors could account for these differences. Variations in mean and minimum soil temperature were significantly correlated with differences in snow accumulated above burrows. Increases in accumulated snow cover are associated with increases in insulation due to increased depth and decreases in thermal conductivity (Sturm et al., 1995). This was apparent in the relative warmth of burrows located in association with shrubby dwarf birch that act as wind breaks, preventing dispersal of fallen snow and collecting wind blown-snow (Fig. 1; Table 1). Ground squirrels modify soil surrounding their burrows through digging and turnover of soil, and concentrations of phosphorous and nitrogen in soil near burrows are elevated due to deposition of urine and feces (Batzli and Sobaski, 1980; McKendrick et al., 1980). This fertilization could lead to increased growth and perseverance of shrubs, which also are stimulated by higher winter soil temperature (M.

TABLE 4.—Means and minima of soil temperature at burrows of arctic ground squirrels at Toolik Lake, Alaska (1993–1995).

| Class | n | Soil temperature ($^{\circ}\text{C}$) | |
|------------|-----|---|----------------------|
| | | $\bar{X} \pm SE^a$ | Minimum $\pm SE^a$ |
| Adult ♀ | 14 | -7.7 ± 0.06 a | -13.7 ± 1.0 a |
| Juvenile ♀ | 7 | -9.8 ± 0.60 b,c | -17.6 ± 0.98 b,c |
| Adult ♂ | 6 | -9.4 ± 0.61 c | -17.0 ± 1.2 c |
| Juvenile ♂ | 6 | -11.9 ± 0.55 d | -20.2 ± 0.98 d |

^a Different letters within a column indicate a significant difference (Tukey's test, $P < 0.05$) in either mean or minimum soil temperature at different burrows of different age or sex class.

Sturm, pers. comm.). These relationships may create positive feedback loops between presence of ground squirrels, shrub occurrence and height, snow accumulation, and soil temperature during winter.

Amount of water in the soil (percent saturation) also affects the pattern of change in soil temperature over winter. Heat is released as water freezes, causing soil temperature to remain at 0°C until all water in the soil is ice (Johnston, 1981). After soil is frozen, however, the facility with which it undergoes changes in temperature (thermal diffusivity) increases with percent saturation (Kerston, 1949). Burrows in wet soils, therefore, decrease below 0°C later in the season compared with drier sites but cool faster after all water is frozen. That heat is released as water freezes is evident in the pattern of soil temperature at the two burrows shown in Fig. 2. However, the increased thermal diffusivity predicted for the site that remained at 0°C longest is masked by the greater accumulation of snow at the warmer burrow (#34) than the colder burrow (#31), which insulated frozen soils from the air above.

Finally, burrows also could vary in thermal conductivity of soil. Most burrows were overlain with a thin (7–12 cm) organic layer and located in fine soil and gravel, and, thus, they should have similar rates of thermal conductance through soil. Only the coldest burrow (#31; Fig. 2), scoured by wind, lacked an organic layer and was in boulders and large cobble. It is likely that conduction through and free convection around boulders and cobble, combined with little or no accumulation of snow, contributed to the extreme cold recorded over 3 consecutive years at this site.

Temperatures of burrows and loss of body mass.—At temperatures <0°C, we presume that hibernating in cold compared with warm burrows is more energetically expensive. During torpor, arctic ground squirrels in nests thermoregulate to maintain core body temperatures $\geq -2.9^\circ\text{C}$ and head and neck temperatures $\geq 0^\circ\text{C}$, by in-

creasing metabolic rate as ambient temperatures decrease below 0°C (Buck, 1998; Barnes, 1989). For euthermic arctic ground squirrels, the lower critical temperature is 6–10°C (Erickson, 1956) and ca. 0°C for animals in nests (Chappell, 1981). Therefore, arctic ground squirrels during hibernation must be actively thermogenic, at least when soil temperature is $< -2.9^\circ\text{C}$. During hibernation, mean soil temperature was $< -2.9^\circ\text{C}$ at burrows of males for 71% (5.2 months) of the hibernating season and 66% (5.3 months) at burrows of females. If thermal conductance does not differ significantly among individuals and nests, and body temperatures during torpor are comparable among individuals, then rates of metabolism during torpor must increase similarly and proportionally with the increasing gradient between body and soil temperature. Frequency of arousal to euthermia also is correlated positively with metabolic rate during torpor in ground squirrels (Geiser and Kenagy, 1988). Thus, animals in colder burrows with higher metabolic rates should arouse more often and spend more total time at euthermic body temperatures than those in warmer burrows that have lower rates of metabolism.

A higher metabolic rate during torpor, more frequent arousals, and greater time spent euthermic suggests that arctic ground squirrels hibernating in colder burrows expend more energy, and, hence, lose more body mass, compared with those in warmer burrows. We tested this hypothesis by regressing mean and minimum soil temperatures of individual burrows against differences between immergent and emergent body, fat, and lean mass, and rates of loss of body, fat, and lean mass of each occupant. There were no significant relationships between changes in body composition and soil temperature over winter for either males or females. Those results were anticipated for males, which cache food in their hibernacula (McLean and Towns, 1981) and undergo an extended (2–3 weeks) interval of euthermia before emergence

(Barnes, 1996; Barnes and Ritter, 1993). During this time, they eat and recoup body mass lost during the heterothermic season (Buck and Barnes, 1999). Males in our study did not show losses in body, fat, or lean mass upon emergence in spring compared with autumn. Females, in contrast, do not cache food before hibernation (Buck and Barnes, 1999; McLean and Towns, 1981) and, under captive conditions, have only short intervals (3–6 days) of euthermy before emergence in spring (Barnes and Ritter, 1993). Neither female nor male arctic ground squirrels eat during periodic arousals from torpor. Although there was significant and substantial (2.3–12-fold) variation in the percentage and rate of loss of body, fat, and lean mass among females over winter (Table 3), those changes in body composition were not related to differences in soil temperature.

One assumption of our study is that soil temperature recorded at maximum depth of thaw closely approximates thermal conditions experienced by the hibernating ground squirrel. Because arctic ground squirrels cannot dig into permafrost, but otherwise place their nests as deep as possible (Barnes, 1989; Carl, 1971; Mayer, 1953), maximum depth of the active layer approximates the lower boundary of the hibernaculum and, thus, the temperature of the soil surrounding the bottom of the nest. Soil temperature at this stratum should be relevant to estimating the thermal gradient between body and soil that arctic ground squirrels experience during hibernation.

Lack of significant linear regressions between soil temperature and changes over winter in body composition of females could be due to three confounding factors. First, both immergent and emergent dates were inferred from success of capture. However, measures of body mass and composition at last capture in autumn and first capture in spring may not be strictly representative of values immediately pre- and post-heterothermy. Time that ground squirrels are euthermic underground after last

capture in autumn or before first capture in spring could have significant consequences on body mass and composition in either a positive or negative manner depending if the animal was eating from a cache. More precise information on changes in body mass will require knowledge of when heterothermy begins and ends in the field and assessing body composition close to those dates.

Second, arctic ground squirrels may build nests with differing values of thermal conductance. Without knowledge of conductance of each nest of our animals, the influence of differences in size and insulation of nests on rates of loss of body mass cannot be ruled out. However, we believe it unlikely that differences in thermal conductance of the nest are responsible for confounding relationships between soil temperature and change in body condition. Previous studies have shown that arctic ground squirrels construct nests of similar size and thermal conductivity. Animals that wintered in self-dug burrows in outdoor enclosures each constructed nests ca. 30 cm in diameter (Barnes, 1989), and nests from hibernacula near Point Barrow, Alaska, ranged from 22.5 to 30 cm in diameter, and all consisted of dry grass and lichens (Mayer, 1953). It is reasonable to assume that arctic ground squirrels within our population use similar materials for construction of similarly sized nests for adequate insulation.

Even if variation in thermal conductivity of nesting material occurred, significant changes in conductivity (20% increase) were associated with <1% change in metabolic rate in a model of heat exchange for hibernating marmots (Webb and Schnabel, 1983). Building larger nests will decrease rates of heat loss. However, heat loss from a spherical nest was estimated as (Kreith, 1973):

$$Q = kv(4\pi r_i)(4\pi r_o) \cdot (T_2 - T_1) / (r_o - r_i),$$

where Q is total heat flow in W/m^2 , k is thermal conductivity (assumed constant), r_i is estimated radius of a hibernating squirrel

(10 cm), r_0 is radius of the nest, T_1 is soil temperature, and T_2 is minimum core body temperature that ground squirrels can sustain during hibernation (-2.9°C —Barnes, 1989). From this equation, doubling nest diameter (30 to 60 cm) results in only a 25% decrease in rate of loss of heat and, therefore, a corresponding 25% difference in energetic costs of hibernation and loss of body mass. We consider it unlikely that arctic ground squirrels are building nests that differ in size and thermal conductance enough to offset two-fold differences in average temperatures of burrows.

Third, diets rich in unsaturated fatty acids decrease energetic costs of mammalian hibernation. Rodents fed diets containing high levels of the polyunsaturated fatty linoleic acid or the monounsaturated oleic acid enter hibernation sooner, reach lower body temperatures and lower rates of metabolism during torpor and have fewer arousals than those with diets consisting of more saturated fat (Florant et al., 1993; Frank, 1992; Geiser et al., 1994). Because episodes of arousal represent the major energetic expense during hibernation (Wang, 1979), animals with fewer arousals and lower rates of metabolism should expend less energy during the heterothermic season. Although diet-related differences in patterns of hibernation have not been demonstrated in *S. parryi*, the effect has been shown in five other species, including two ground squirrels (Florant et al., 1993; Frank, 1992; Geiser and Kenagy, 1987, 1993; Geiser et al., 1994; Thorp et al., 1994). Polyunsaturated fatty acids are essential nutrients for mammals, and marmots and ground squirrels obtain them by eating plants and seeds (Florant et al., 1990; Frank, 1994). Natural diets and consequent concentrations of polyunsaturated fatty acids in depot fat varied substantially in a population of free living *S. saturatus* (Frank et al., 1998), which raises the possibility that rates of loss in body mass in arctic ground squirrels are influenced by diet before hibernation. Differentiating between alternative hypotheses of

what controls loss of weight in arctic ground squirrels over winter will require additional information from field and laboratory studies on the nutritional, thermal, and energetic limits to hibernation in mammals.

Burrow preferences.—Arctic ground squirrels of different age and sex classes were found at burrows that differed significantly in soil temperature. This may indicate that ground squirrels discriminate and prefer burrows based in part on thermal characteristics. Female ground squirrels hibernated at warmer burrows than males, and adults occupied warmer burrows than juveniles. Perceived qualities of burrows may differ between sexes, and access by juveniles to favored sites may be limited by competition with adults. Carl (1971) described a period of overt territoriality and aggression among arctic ground squirrels in late summer that was associated with competition for and guarding of hibernacula. Thermal conditions may be only one of several preferred features that include drainage, availability of food, visibility of surrounding terrain, and cover for protection from predators, particularly for newly emerging young-of-the-year.

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LITERATURE CITED

- ARNOLD, W. 1993. Energetics of social hibernation. Pp. 65–80, in *Life in the cold: ecological, physiological, and molecular mechanisms*. (C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, eds.). Westview Press, Boulder, Colorado.

- ARNOLD, W., G. HELDMAIER, S. ORTMANN, H. POHL, T. RUFF, AND S. STEINLECHNER. 1991. Ambient temperatures in hibernacula and their energetic consequences for alpine marmots (*Marmota marmota*). *Journal of Thermal Biology*, 16:223–226.
- BARNES, B. M. 1989. Freeze avoidance in a mammal: body temperatures below 0°C in an Arctic hibernator. *Science*, 244:1593–1595.
- . 1996. Relationships between hibernation and reproduction in male ground squirrels. Pp. 71–80, in *Adaptations to the cold*. (F. Geiser, A. J. Hulbert, and S. C. Nicol, eds.). University of New England Press, Armidale, Australia.
- BARNES, B. M., AND D. RITTER. 1993. Patterns of body temperature change in hibernating arctic ground squirrels. Pp. 119–130, in *Life in the cold: ecological, physiological, and molecular mechanisms*. (C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, eds.). Westview Press, Boulder, Colorado.
- BATZLI, G. O., AND S. T. SOBASKI. 1980. Distribution, abundance, and foraging patterns of ground squirrels near Atkasook, Alaska. *Arctic and Alpine Research*, 4:501–510.
- BENSON, C. S., AND M. STURM. 1993. Structure and wind transport of seasonal snow on the Arctic slope of Alaska. *Annals of Glaciology*, 18:261–267.
- BOCKHEIM, J. G., D. A. WALKER, L. R. EVERETT, F. E. NELSON, AND N. I. SHIKLOMANOV. 1998. Soils and cryoturbation in moist nonacidic and acidic tundra in the Kuparuk River basin, Arctic Alaska, U.S.A. *Arctic and Alpine Research*, 30:166–174.
- BUCK, C. L. 1998. Physiological ecology of the arctic ground squirrel: energy metabolism, torpor, and behavioral endocrinology. Ph.D. dissertation, University of Alaska Fairbanks, Fairbanks.
- BUCK, C. L., AND B. M. BARNES. 1999. Annual cycle of body condition and hibernation in free-living arctic ground squirrels. *Journal of Mammalogy*, 80:430–442.
- CARL, E. A. 1971. Population control in arctic ground squirrels. *Ecology*, 52:395–413.
- CHAPPELL, M. A. 1981. Standard operative temperature and cost of thermoregulation in the arctic ground squirrel, *Spermophilus undulatus*. *Oecologia*, 49:397–403.
- ERICKSON, H. 1956. Observations on the metabolism of arctic ground squirrels (*Citellus parryi*) at different environmental temperatures. *Acta Physiologica Scandinavica*, 36:66–81.
- FERRON, J. 1996. How do woodchucks (*Marmota monax*) cope with harsh winter conditions? *Journal of Mammalogy*, 77:412–416.
- FLORANT, G. L., H. S. AMEEDNUDDIN, AND D. A. RINTOUL. 1993. The effect of a low essential fatty acid diet on hibernation in marmots. *American Journal of Physiology*, 264:R747–R753.
- FLORANT, G. L., L. C. NUTTLE, D. E. MULLINEX, AND D. A. RINTOUL. 1990. Plasma and white adipose tissue lipid composition in marmots. *American Journal of Physiology*, 258:R1123–R1131.
- FRANK, C. L. 1992. The influence of dietary fatty acids on hibernation by golden-mantled ground squirrels (*Spermophilus lateralis*). *Physiological Zoology*, 65:906–920.
- . 1994. Polyunsaturate content and diet selection by ground squirrels (*Spermophilus lateralis*). *Ecology*, 75:458–463.
- FRANK, C. L., E. S. DIERENFELD, AND K. B. STOREY. 1998. The relationship between lipid peroxidation, hibernation, and food selection in mammals. *American Zoologist*, 38:341–349.
- GEISER, F., AND G. J. KENAGY. 1987. Polyunsaturated lipid diet lengthens torpor and reduces body temperature in a hibernator. *American Journal of Physiology*, 252:R897–R901.
- . 1988. Torpor bout duration in relation to temperature and metabolism in hibernating ground squirrels. *Physiological Zoology*, 61:442–449.
- . 1993. Dietary fats and torpor patterns in hibernating ground squirrels. *Canadian Journal of Zoology*, 74:1182–1186.
- GEISER, F., B. M. MCALLEN, AND G. J. KENAGY. 1994. The degree of dietary fatty acid unsaturation affects torpor pattern and lipid composition of a hibernator. *Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology*, 164:299–305.
- HELDMAIER, G., AND T. RUF. 1992. Body temperature and metabolic rate during natural hypothermia in endotherms. *Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology*, 162:696–706.
- HELLER, H. C., AND G. W. COLLIVER. 1974. CNS regulation of body temperature during hibernation. *American Journal of Physiology*, 227:583–589.
- JOHNSTON, G. H. 1981. *Permafrost engineering design and construction*. John Wiley & Sons, New York.
- KAWAMICHI, M., AND T. KAWAMICHI. 1993. Factors affecting hibernation commencement and spring emergence in Siberian chipmunks (*Eutamias sibiricus*). Pp. 81–89, in *Living in the cold: ecological, physiological, and molecular mechanisms*. (C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, eds.). Westview Press, Boulder, Colorado.
- KENAGY, G. J., S. M. SHARBAUGH, AND K. A. NAGY. 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia*, 78:269–282.
- KERSTON, M. S. 1949. *Thermal properties of soils*. Minnesota University Institute of Technology, Minneapolis.
- KREITH, F. 1973. *Principles of heat transfer*. Third ed. Intext Educational Publishers, New York.
- MAYER, W. V. 1953. A preliminary study of the Barrow ground squirrel, *Citellus parryi barrowensis*. *Journal of Mammalogy*, 34:334–345.
- . 1955. The protective value of the burrow system to the hibernating ground squirrel, *Spermophilus undulatus*. *The Anatomical Record*, 122:437–438.
- MCKENDRICK, J. D., G. O. BATZLI, K. R. EVERETT, AND J. C. SWANSON. 1980. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arctic and Alpine Research*, 12:565–578.
- MCLEAN, I. G., AND A. J. TOWNS. 1981. Difference in body mass changes and the annual cycles of male and female arctic ground squirrels. *Arctic*, 34:249–254.
- MICHENER, G. R. 1992. Sexual differences in over-winter torpor pattern of Richardson's ground squirrels in natural hibernacula. *Oecologia*, 89:397–406.

- MICHENER, G. R., AND L. LOCKLEAR. 1990. Over-winter weight loss by Richardson's ground squirrels in relation to sexual differences in mating effort. *Journal of Mammalogy*, 71:489-499.
- NADLER, C. F., R. S. HOFFMAN, N. N. VORONTOV, J. W. KOEPL, L. DEUTSCH, AND R. I. SOKERNIK. 1982. Evolution in ground squirrels II: Biochemical comparisons in Holarctic populations of *Spermophilus*. *Zeitschrift für Säugetierkunde*, 47:198-215.
- SHAVER, G. R., F. CHAPIN, III, AND B. L. GARTNER. 1986. Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaska tussock tundra. *Journal of Ecology*, 74:257-278.
- SONG, X., G. KORTNER, AND F. GEISER. 1997. Thermal relations of metabolic rate reduction in a hibernating marsupial. *American Journal of Physiology*, 273: R2097-R2104.
- STURM, M., J. HOLMGREN, AND G. E. LISTON. 1995. A seasonal snow cover classification system for local to global applications. *Journal of Climate*, 8:1261-1283.
- THORP, C. R., R. P. KODANDA, AND G. L. FLORANT. 1994. Diet selection alters metabolic rate in the yellow bellied marmot (*Marmota flaviventris*) during hibernation. *Physiological Zoology*, 67:1213-1229.
- TURCOTTE, D. L., AND G. SCHUBERT. 1982. *Geodynamics applications of continuum physics to geological problems*. John Wiley & Sons, New York.
- WANG, L. C. H. 1979. Time patterns and metabolic rates of natural torpor in Richardson's ground squirrel. *Canadian Journal of Zoology*, 57:149-155.
- WEBB, D. R., AND R. R. SCHNABEL. 1983. Functions of fat in hibernators: thermal aspects. *Journal of Thermal Biology*, 4:369-374.
- YOUNG, P. J. 1990. Hibernating patterns of free-ranging Columbian ground squirrels. *Oecologia*, 83:504-511.
- ZAR, J. H. 1984. *Biostatistical analysis*. Second ed. Prentice-Hall, Inc. Englewood Cliffs, New Jersey.
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