BODY TEMPERATURE AND ACTIVITY PATTERNS IN FREE-LIVING ARCTIC GROUND SQUIRRELS

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We investigated influences of the thermal environment on patterns of body temperature (T_b), activity, and use of burrows during the active season in a population of free-living arctic ground squirrels (*Spermophilus parryii*). Arctic ground squirrels normally exhibited a daily 5°C range in T_b, and had higher T_b when above ground than when in burrows ($P < 0.0001$). This difference decreased as standard operative temperature (T_{es}; an index of environmental heat load) increased. Ground squirrels entered burrows more frequently on warmer compared to average or cooler days and when T_b exceeded 39°C. On cool days with heavy precipitation, ground squirrels remained almost exclusively below ground, and peaks in T_b were associated with brief aboveground forays. Time on the surface was maximal (about 80% between 0500 and 2200 h) at $T_{es} = 17–33$°C and decreased proportionately with decreasing T_{es} from 17°C to −2°C. Forty-six percent of variation in timing of presence above ground could be explained by a series of thermal and nonthermal variables related to environmental heat transfer. This suggests that diurnal activity patterns in this arctic environment with 24-h daylight result from a strategy that minimizes thermoregulatory costs.

Key words: arctic ground squirrel, behavioral thermoregulation, body temperature, hyperthermia, multiple regression, *Spermophilus parryii*, standard operative temperature

Behavior plays a central role in thermoregulation and physiological ecology of ectothermic reptiles and amphibians (Belliure et al. 1996). However, comparatively less is known about the role of behavior in thermoregulation and activity of endothermic mammals. Behavior is likely important for small mammals living in environments with wide ranges in temperature. Because of high body surface area to volume ratios, less insulation, and rapid rates of heat exchange with the environment, small mammals are more susceptible than large mammals to rapid changes in body temperature (T_b) and, therefore, to the need for rapid adjustments in their allocations of time, activity, and energy (Tracy 1977). This influence of the thermal environment on small mammals can structure time available for foraging in thermally stressful environments and create trade-offs between daily needs for energy from foraging and increased costs of thermoregulation (Melcher et al. 1990).

Behavioral choices of retreating to burrows or using shade restrict activity and time for foraging in rodents living in both

desert (Bacigalupe et al. 2003; Bennett et al. 1984; Chappell and Bartholomew 1981a; Recht 1979; Sharpe and Van Horne 1999) and temperate (Byman 1985; Morhardt and Gates 1974; Vispo and Bakken 1993) climates. However, studies of thermal energetics in arctic and montane rodents such as the arctic ground squirrel (*Spermophilus parryii*) have largely focused on requirements of hibernation. In one study of thermoregulation and activity of arctic ground squirrels, Chappell (1981) demonstrated correlation between thermoneutral environmental temperatures and stable T_b, with foraging occurring nearly continuously during daytime. That study was for 1 week in early August, but arctic ground squirrels in northern Alaska have active seasons that last 3–4 months, and include weeks of complete snow cover in spring and occasional hot conditions in summer (Buck and Barnes 1999a). As a result, arctic ground squirrels often experience temperatures well outside the critical limits of their thermoneutral zone, and their activity and foraging strategies likely evolve in response to thermal constraints imposed by the environment over the course of their active season.

We used light-sensitive radiocollars together with implanted temperature-sensitive dataloggers to test the hypothesis that arctic ground squirrels attempt to maximize time above ground for foraging, but use burrows strategically to cool or warm as environmental temperatures dictate.

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MATERIALS AND METHODS

Study site.—Our study was conducted near the Toolik Field Station operated by the Institute of Arctic Biology (University of Alaska Fairbanks) in the northern foothills of the Brooks Range, Alaska (68°38′N, 149°38′W; elevation 809 m) from 10 May to 10 August 2001. The study site encompassed about 50 ha along the eastern shore of Toolik Lake. Vegetation is cotton grass–tussock tundra dominated by dry heath (*Eriophorum vaginatum*) with dwarf shrubs of willow (*Salix*) and birch (*Betula*—Shaver et al. 1986). Shade is minimal and most of the site is potentially fully exposed to continuous sunlight throughout the summer. Terrain is generally flat with rocky soils underlain by permafrost usually within 1 m (Buck and Barnes 1999b).

Animal handling and body temperature.—Free-ranging ground squirrels were livetrapped from 10 to 17 May. On initial capture, ground squirrels were anesthetized with methoxyflurane vapor for surgery, ear-tagged, implanted subcutaneously between the shoulder blades with a passive integrated transponder (Schooley et al. 1993), and their pelage was marked with hair dye. Core T_b was recorded at 5-min intervals throughout the study period by using temperature-sensitive dataloggers (modified StowAway Tidbit, Onset Computer Corporation, Bourne, Massachusetts) that were surgically implanted into the peritoneal cavities of 14 adult ground squirrels (body mass = 500–1,000 g). Dataloggers were calibrated before implantation, and their total mass was 12–13 g. Focal ground squirrels were generally released at the site of capture the day after surgery and were recaptured weekly during the study to monitor reproductive status (scrotal testes in males and pregnancy or lactation in females), body mass, and overall health. When temperature loggers were removed by a 2nd surgery 4–10 August 2001, no adverse physiological or anatomical effects were evident in abdominal cavities of ground squirrels. All procedures were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks, and were in compliance with American Society of Mammalogists Animal Care and Use Committee (1998) guidelines.

Telemetry.—Radiotelemetry was used to determine whether focal ground squirrels were above or below ground at about 5-min intervals throughout the study. Before release after surgery, ground squirrels were fitted with light-sensitive radiotransmitters (model TXP-1/L, Televilt International AB, Lindesberg, Sweden) attached to neck collars formed from 30-cm antennas covered with soft plastic tubing (Hut et al. 1999). Radiocollars also were placed on 4 additional ground squirrels not implanted with temperature loggers. Collars weighed 18–20 g. Combined mass of radiocollars and temperature loggers (about 30 g) did not exceed 7% of body mass of ground squirrels (range 500–1,000 g) and was <5% for most ground squirrels.

Presence of telemetered ground squirrels above or below ground was indicated by the interpulse interval of the transmitters, which varied discreetly between 2,000 ms in light levels < 0.03 lux (below ground) and 1,200 ms in light levels > 0.03 lux (above ground—Hut et al. 1999). Each collar was identified by a unique frequency. Location and behavior of telemetered ground squirrels was observed and recorded at 1-min intervals over 1 daily active period each to corroborate telemetry data with presence of ground squirrels above or below ground.

Telemetry signals from each ground squirrel were recorded every 1–5 min by 1 of 4 multichannel data-logging receivers (model RX900, Televilt, and model TR-5, Telonics, Mesa, Arizona). Aberrant values resulting from positional changes of the ground squirrels, general frequency noise, and missed pulses were filtered out before analyses, based on criteria developed by Hut et al. (1999).

Environmental conditions.—Operative, or effective, environmental temperatures (T_e—Bakken 1976, 1980), which integrate measures of radiant and convective thermal input to an organism, were measured in the field along with wind speed (V). T_e and V were then combined with laboratory data published by Chappell (1981) to calculate standard operative temperature (T_{es}—Bakken 1976; Gagge 1940). T_{es} expresses a combination of thermal parameters (e.g., radiation, convection, air temperature, and T_b) on a single scale, then corrects this measurement to standard convective conditions (Chappell and Bartholomew 1981b). A detailed description of the features and theory of T_{es} is provided by Bakken (1980, 1992).

We measured T_e in the field by using pelt-covered hollow copper models of arctic ground squirrels constructed by following the methods of Chappell (1981). Each model was fitted internally with a 4-channel thermocouple attached to a datalogger (HOBO 4-Channel External, Onset Computer Corporation) that recorded temperature every 5 min throughout the study. Two models were placed in a microhabitat typical of the study site. One was posed in a quadrupedal posture and the other in an alert bipedal posture. The temperature of the quadrupedal model was used for T_e when calculating T_{es}, because the pelt of the bipedal model was damaged by rodents early in the study. We assumed the influence of dye marks on T_e to be negligible (Vispo and Bakken 1993).

Wind speeds were obtained from a weather station on the study site. Wind speed at 3 m above ground was recorded every minute (model 014A anemometer, Campbell Scientific, North Logan, Utah). Wind speed at 20 cm (a mean height for arctic ground squirrels) was estimated by assuming a logarithmic wind profile of decreasing speeds closer to the ground (Pielke 2002). Cloud cover was recorded categorically (clear, partly cloudy, or overcast), as was precipitation (none, snow, or rain). Soil temperatures were recorded at a depth of 1 m every 4 h at 5 locations in the study site by temperature dataloggers (HOBO Pro Series, Onset Computer Corporation) during summer 2002 as an indicator of burrow temperatures. Soil temperatures during 2001 were measured only during winter. However, between-year differences in soil temperatures at this site are sufficiently small to warrant the use of temperature data collected in 2002 for burrow temperatures during the summer of 2001 (Buck and Barnes 1999b).

Standard operative temperature (T_{es}) was calculated from the following equation (Chappell and Bartholomew 1981b):

$$T_{es} = T_b - (r_{es}/r_e)(T_b - T_e), \qquad (1)$$

where r_{es} is the total resistance (s/m) to heat flow of a live ground squirrel in standard convective conditions and r_e is the total resistance of the ground squirrel when T_e is measured in the field. We used previously published data for arctic ground squirrels to estimate the ratio of thermal resistance in standard conditions to thermal resistance in the field (r_{es}/r_e): total thermal resistance of live ground squirrels (r_t^a) in unstirred air at temperatures below thermoneutrality (Scholander et al. 1950; Withers et al. 1979), and total thermal resistance of the pelt-covered models at various wind speeds (Chappell 1981). Based on these data, the ratio of thermal resistance in standard conditions to thermal resistance in the field was calculated as the ratio of live-animal resistance in unstirred air to estimated live-animal resistance at wind speeds observed in the field. For simplicity, we assumed a constant T_b of 38.5°C when calculating T_{es}.

At temperatures below thermoneutrality, minimum conductance (K, the inverse of resistance) for arctic ground squirrels under standard conditions (V about 0.1 m/s) is about 0.19 W/°C and basal metabolic rate is about 3.5 W (Scholander et al. 1950; Withers et al. 1979). We followed the assumption of Chappell (1981) that the upper critical temperature in *S. parryii* is 36°C at $T_b = 41$°C, with about 50% of heat production lost as evaporation. Based on this assumption, maximum dry conductance at temperatures above thermoneutrality was estimated to be 0.35 W/°C (Chappell 1981). These conductances were converted

to total live-animal resistances. Thermal resistance was assumed to be maximal below the lower critical temperature ($T_e < 18°C$—Chappell 1981), minimal above the upper critical temperature ($T_e > 36°C$), and intermediate within the thermoneutral zone.

Dependence of live-animal thermal resistance on wind speed can be estimated from measured values of the thermal resistance of the pelt-covered models. Differences between model resistance and live-animal resistance occur primarily because models lack the vasomotor components of resistance (Chappell and Bartholomew 1981b). Nevertheless, because tissue resistance is not directly affected by wind, live-animal resistance should decrease in parallel with model resistance as wind speed increases (Chappell 1981). Therefore, live-animal resistance can be predicted in the field at various wind speeds by fitting the slope of the regression of model resistance against wind speed through the minimal (predicted) and maximal resistance values obtained for live animals in standard conditions (V about 0.1 m/s). Thus, at temperatures below thermoneutrality,

$$r_t^a = 310 - 54.2V^{0.5}, \qquad (2)$$

and at temperatures above thermoneutrality,

$$r_t^a = 176 - 54.2V^{0.5}. \qquad (3)$$

Live-animal resistance (r_t^a) at temperatures within the thermoneutral zone was assumed to be proportionately intermediate between resistance values at the upper and lower critical temperatures. Equations 2 and 3, along with the known and predicted resistance values for live animals in standard conditions, can be substituted into equation 1 to calculate T_{es}, so that at temperatures below the lower critical temperature,

$$T_{es} = 38.5 - [293/(310 - 54.2V^{0.5})](38.5 - T_e), \qquad (4)$$

and at temperatures above the upper critical temperature,

$$T_{es} = 38.5 - [159/(176 - 54.2V^{0.5})](38.5 - T_e), \qquad (5)$$

where V is wind speed when T_e is measured in the field.

Data analyses.—Data analysis generally was restricted to data collected between 0500 and 2200 h each day, because ground squirrels were rarely observed on the surface outside of this interval. Because environmental, T_b, and telemetry data were not always collected at precisely the same moment, criteria were developed to determine for each measurement of T_{es} or T_b if focal animals were above or below ground. Samples for individual ground squirrels were included in analyses if their telemetry signal was recorded within 5 min before and after the logging of T_e or T_b, and if these signals consistently indicated light or dark ambient conditions. The number of ground squirrels included in each analysis varied (from 5 to 11) because of predation and equipment failures. For analyses of T_b, frequency of burrow use, and timing of emergence, days were categorized as cold ($T_{es} < 18°C$) or average ($18°C < T_{es} < 36°C$) based on which thermal category was prevalent for >50% of the day between 0500 and 2200 h, or were categorized as hot if T_{es} exceeded 36°C for >2 h consecutively during that period. Categories were chosen based on the upper (predicted) and lower critical temperatures of *S. parryii* (Chappell 1981). All statistical analyses were performed by using Proc GLM and Proc REG in SAS version 8.0 (SAS Institute Inc. 2000).

We qualitatively examined the relationship between T_b and surface activity by constructing daily plots of T_b and telemetry data for each ground squirrel throughout the study period. In addition, mixed-model analyses of variance with ground squirrel identification (ID) and the interaction between ground squirrel ID and the fixed factor (either presence above or below ground within a daily thermal category, or just the daily thermal category) included as random factors were used to test

for differences in T_b above compared to below ground, as well as for differences in frequency of burrow use, across the 3 daily categories of T_{es} (Neter et al. 1996). Least-squares means were compared in these analyses to account for differential sample sizes among ground squirrels within fixed factors, and residual plots were examined to ascertain adherence to assumptions. Significance was assigned based on alpha ≤ 0.05.

We calculated the proportion of time spent on the surface both for individuals and for the study population by 2°C intervals of T_{es} and by hour. Population means were weighted by sample size. Confidence intervals for the population were constructed by use of a binomial distribution and were conservative, because this distribution tends to overestimate *SE* (Bowden et al. 1984; Bowyer 1991).

We used stepwise multiple regression with ground squirrel ID forced into the model as an independent variable to examine the effects of several potentially important thermal and nonthermal predictor variables on time spent on the surface (Neter et al. 1996). The proportion of time spent above ground was used as the dependent variable, and independent variables included T_{es}, wind force (wind speed squared), hours since solar noon, time of day (24-h clock time), Julian date, body mass, precipitation (included as an ordinal variable), and cloud cover (included as a binomial variable). Cloud cover was ranked as 0 if >50% of the day was clear or partly cloudy (defined as <50% cloud cover) or 1 if >50% of the day was overcast (defined as >50% cloud cover). Precipitation was ranked similarly as 0 for no precipitation, 1 for snow, and 2 for rain. The likelihood of T_{es} and precipitation interacting in their effects on surface activity was indicated by preliminary analysis of telemetry data, so we included this interaction term as an independent variable. Body mass was typically recorded weekly upon capture and was assumed to be constant between these measurements. Daily mean values were used for all variables to help meet assumptions of independence, and we used a standard arcsine-square root transformation on proportion of time spent above ground and a log transformation on wind force to meet assumptions of normality. Alpha for entry into the model was 0.15, and was 0.10 to remain.

A correlation matrix was examined to detect colinearity between independent variables ($|r| \geq 0.50$ was considered to be correlated). The initial matrix indicated precipitation was highly correlated with the interaction term (T_{es} by precipitation; $r = -0.78$, $P < 0.0001$), and time of day was highly correlated with hours since solar noon ($r = -0.99$, $P < 0.0001$). To eliminate the effects of colinearity, Mallow's C_p and adjusted R^2 were used as criteria to select the best model from a set of models containing uncorrelated combinations of 8 of the 10 initial independent variables (including ground squirrel ID). The model that included the T_{es} by precipitation interaction term along with hours since solar noon resulted in the combined lowest C_p and highest adjusted R^2 values ($C_p = 14.00$, adjusted $R^2 = 0.46$, compared with $C_p = 14.00$, adjusted $R^2 = 0.45$ for the next-best model, which included precipitation with hours since solar noon). Consequently, these 2 variables were included in stepwise selection, and precipitation and time of day were eliminated as predictor variables. Robustness of the final model was evaluated by performing backward stepwise selection.

RESULTS

Body temperature and burrow use.—Although individual ground squirrels in northern Alaska exhibited a labile T_b, both hourly (Fig. 1) and monthly (Fig. 2) mean T_bs for the population remained relatively stable; overall mean for the season was 38.48°C $\pm$ 0.005 2 *SE*. T_b of individual ground squirrels fluctuated rapidly, and at the extreme, varied as much as 10.5°C
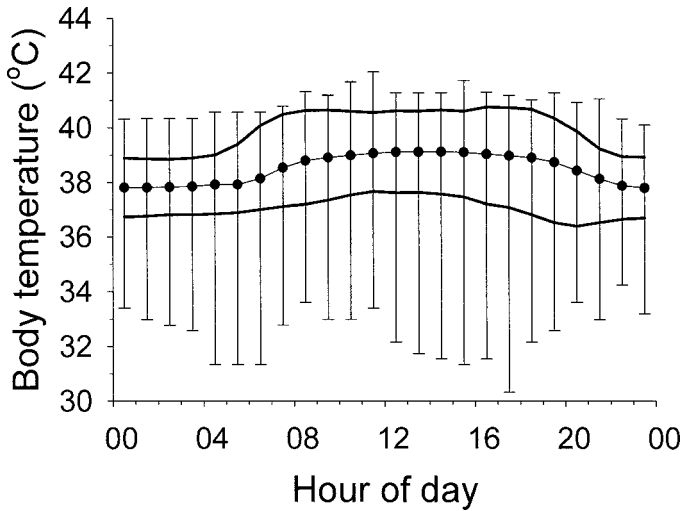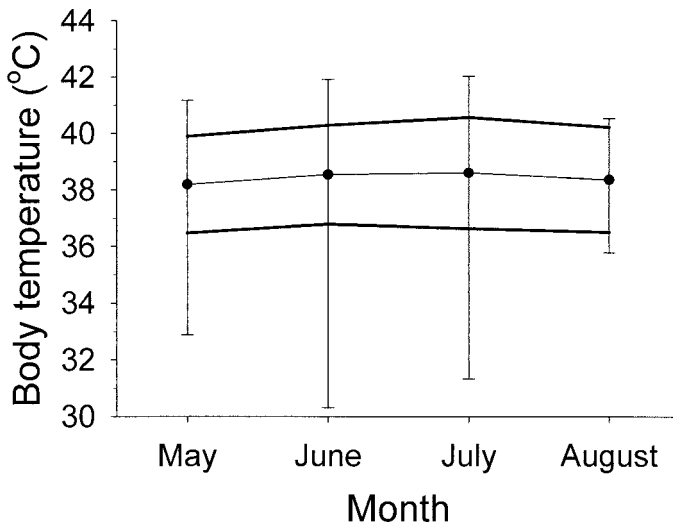
FIG. 1.—Mean body temperatures of 11 free-living *Spermophilus parryii* determined at hourly intervals near Toolik Lake, Alaska, May–August 2001. Error bars encompass range and thick lines represent mean ± 2 *SD*.

(30.32–40.82°C) between 0500 and 2200 h within a single day, although more typical fluctuations in T_b ranged 3–5°C (Fig. 3). Minimum and maximum T_b for the season were 30.32°C and 42.04°C, respectively. Both the magnitude and the rate of daily fluctuations in T_b differed considerably between ground squirrels. However, distinct, consistent diurnal and hourly patterns were found in T_b and burrow use among ground squirrels that were especially evident during hot ($T_{es} > 36$°C) and cold ($T_{es} < 18$°C) days. Increases in T_b of 1–2.5°C typically preceded morning emergence from burrows, and decreases of 1–2°C followed final immergence into burrows at night. On hot days ($n = 14$), T_b rose with time above ground, and rapid

FIG. 2.—Mean body temperatures of 11 free-living *Spermophilus parryii* determined at monthly intervals near Toolik Lake, Alaska, May–August 2001. Error bars encompass range and thick lines represent mean ± 2 *SD*.
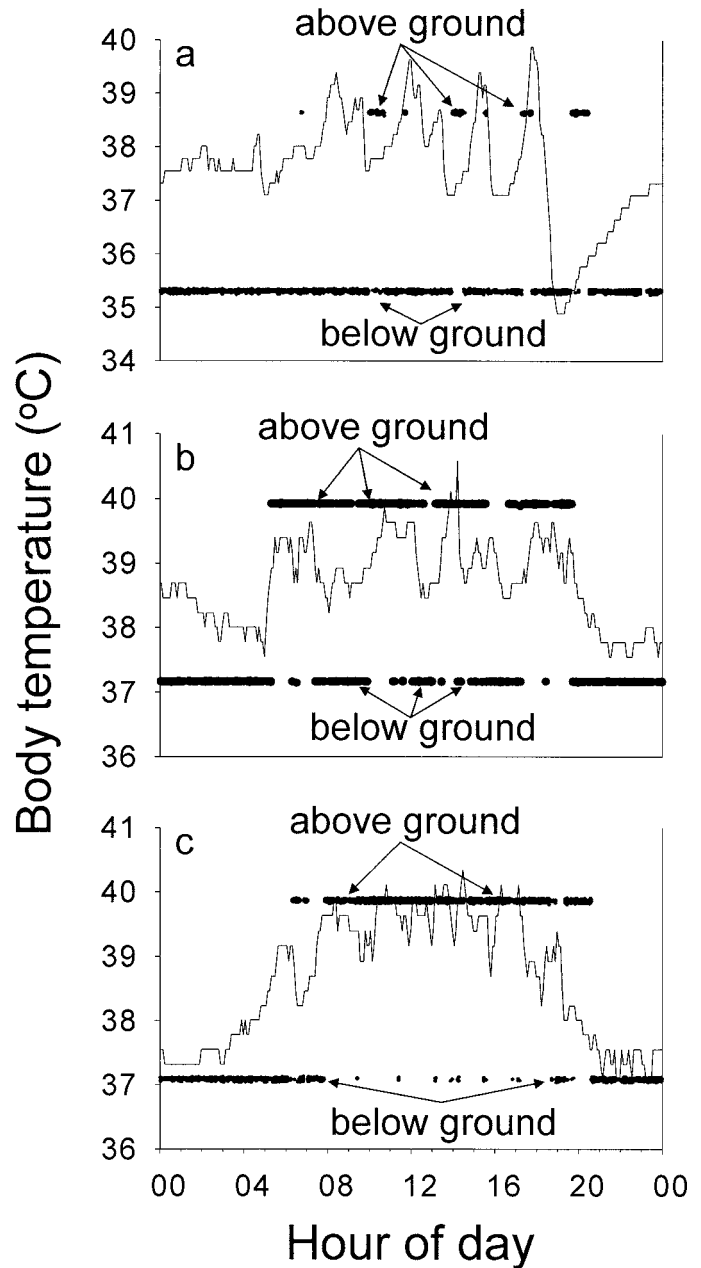

FIG. 3.—Body temperature (T_b; °C) and burrow use patterns of a representative free-living *Spermophilus parryii* (male 1) near Toolik Lake, Alaska, during a) a cold day (29 July 2001; standard operative temperature < 18°C for most of the day), b) a hot day (2 July 2001; standard operative temperature > 36°C for >2 consecutive hours between 0500 and 2200 h), and c) an average day (27 July 2001; 18°C < standard operative temperature < 36°C for most of the day). The continuous lines represent T_b, and presence above or below ground is indicated by data points for 1 of 2 general classes of interpulse intervals (above ground about 1,200 ms and below ground about 2,000 ms).

decreases in T_b occurred shortly after return to the burrow, after T_b had reached or exceeded 39°C (Fig. 3b). Just before squirrels returned to burrows on hot days, body temperature was 39.07 ± 0.11°C. On cold days ($n = 23$) that included precipitation for >50% of the day ($n = 12$), ground squirrels spent most of

their active period below ground, and 2–3°C peaks in T_b were associated with 5–7 brief aboveground forays (Fig. 3a). This same pattern was less obvious on cold days with little or no precipitation. No consistent patterns of T_b coinciding with burrow use were evident on days with average temperature ($18°C < T_{es} < 36°C$; $n = 39$). On those days, ground squirrels tended to remain above ground despite T_b reaching the highest levels recorded (Fig. 3c).

Ground squirrels had significantly higher T_b when they were above ground ($39.22 \pm 0.09°C$, $39.28 \pm 0.04°C$, and $39.12 \pm 0.08°C$ on cold, average, and hot days, respectively) than when they were below ground ($38.08 \pm 0.11°C$, $38.45 \pm 0.16°C$, and $38.56 \pm 0.34°C$ on cold, average, and hot days, respectively) at all levels of T_{es} ($F = 99.01$, $d.f. = 5, 1,530$, $P < 0.0001$). The difference in mean T_b above compared to below ground decreased as T_{es} increased. Frequency of entry into burrows also was significantly higher on hot days (8.62 burrow entries/day $\pm$ 1.44 2 SE) than on either cold (3.35 ± 1.36 burrow entries/day) or average days (4.52 ± 0.89 burrow entries/day; $F = 16.17$, $d.f. = 2, 93$, $P < 0.0001$). In both analyses, differences among ground squirrels also were significant ($F = 6.03$, $d.f. = 4, 1,530$, $P < 0.0001$ and $F = 16.05$, $d.f. = 6, 93$, $P < 0.0001$, respectively), as were the interaction terms ($F = 4.09$, $d.f. = 20, 1,530$, $P < 0.0001$ and $F = 6$, $d.f. = 12, 93$, $P < 0.0001$, respectively).

Timing of morning emergence from burrows was relatively consistent across all categories of T_{es} throughout the season, and emergence most frequently occurred between 0600 and 0630 h, with few ground squirrels emerging before 0500 h or after 0930 h, regardless of T_{es} or season.

Environmental conditions.—Standard operative temperature often was outside the limits of the thermoneutral zone of *S. parryii* during all hours of the day (Fig. 4). Less than 30% of 33,072 measurements of T_{es} used in our analyses were between the lower critical temperature of 18°C and the upper critical temperature of 36°C. Ground squirrels were most often exposed to T_{es} above thermoneutrality at midday, although such temperatures occasionally occurred as early as 1100 h and as late as 1830 h. Ground squirrels were potentially exposed to T_{es} well below thermoneutrality during all hours of the day.

Mean wind speed at 20 cm above ground was 1.31 m/s $\pm$ 0.006 2 SE. Wind speed tended to be highly irregular throughout the day, and gusts of up to 3.6 m/s were recorded occasionally. General weather patterns also were variable during our study. Of 76 days included in our analyses, 49% were categorized as clear or partly cloudy, 51% were overcast, 74% had no substantial precipitation, 8% were days with snow, and 18% were days with rain. No seasonal patterns of cloud cover or precipitation were evident, and a nearly equal number of days from every category occurred during each summer month.

Soil temperatures measured at 5 burrow locations during the summer of 2002 ranged from a low of $-7.3°C$ in early May to a high of 10.65°C in mid-July. Greatest variability in soil temperatures among burrow locations (maximum difference of 10.67°C) also occurred during mid-July. Regardless of this increased variability, maximum soil temperatures during mid-July of 2002 were still about 6°C lower than the mean value of T_{es} ($16.61 \pm 0.23°C$) recorded during this time in 2001.

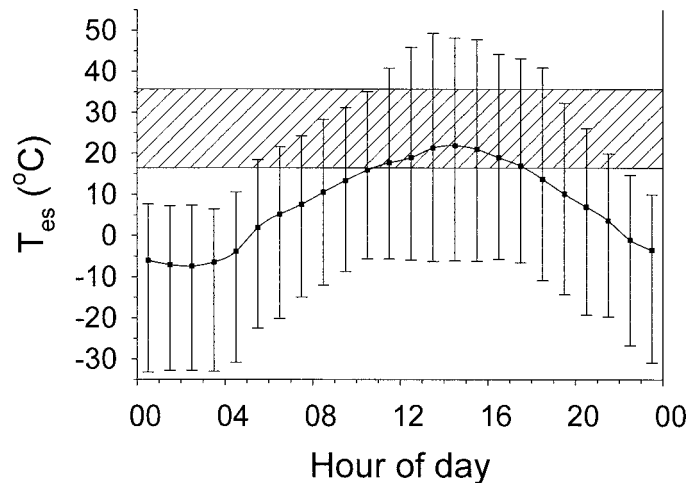FIG. 4.—Hourly mean and range of standard operative temperature (T_{es}; °C) on the study site near Toolik Lake, Alaska, May–August 2001. The hatched band includes temperatures within the thermoneutral zone of *Spermophilus parryii*.

Surface use relative to time of day and T_{es}.—The percentage of time spent on the surface by arctic ground squirrels tended to increase uniformly during the morning to a maximum around midday and decrease later in afternoon (Fig. 5). However, the interval during which mean percentage of time spent on the surface by ground squirrels exceeded 50% increased from about 7 h during May to 12 h during June and 14 h during July, and then decreased to 11 h during August (Fig. 5). In addition, throughout June, July, and August, surface time appeared to decrease slightly from maximum levels for a short period of time around 1200 h and 1600 h. These times generally represented the hottest portions of the day.

Time spent on the surface between 0500 and 2200 h increased proportionately as T_{es} increased from $-2°C$ to 17°C, remained nearly constant from T_{es} 17°C to 33°C, and, for most ground squirrels, appeared to decrease slightly from T_{es} 33°C to 47°C (Fig. 6). To control for the potential correlation of surface activity with nonthermal variables that are not randomly distributed with respect to T_{es}, we constructed a multiple-regression model that included several nonthermal predictor variables in addition to T_{es}; daily proportion of time spent on the surface was used as the response variable. The final regression model accounts for about 46% of the total variance in surface activity (adjusted $R^2 = 0.46$; Table 1). T_{es} was the most important variable in the model, and alone accounted for 33.5% of the variance in surface activity.

DISCUSSION

Arctic ground squirrels, with one of the longest hibernation seasons among sciurid rodents, experience extremely short active seasons, with individuals active above ground for only 3–4 months per year (Barnes 1996). Such a short active season should select for individuals to maximize the length of their daily activity periods, particularly in Arctic Alaska, where the sun at the Toolik Field Station remains above the horizon from
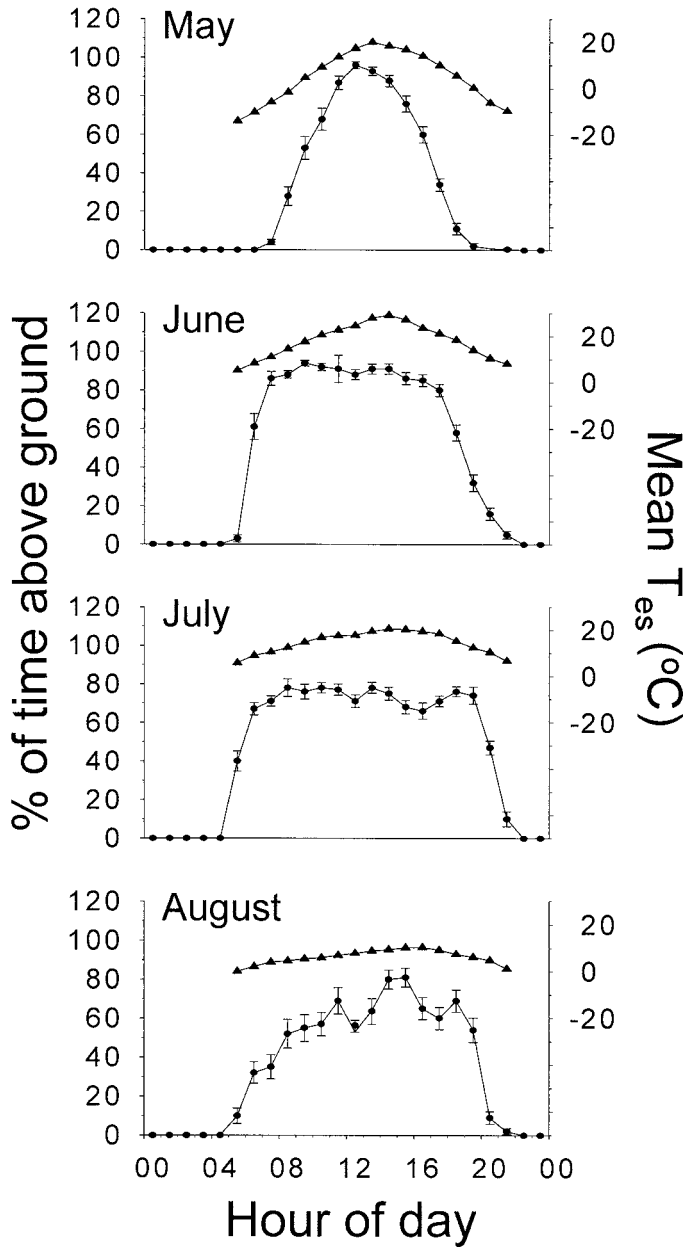
FIG. 5.—Portion of each hour (%) spent on the surface by arctic ground squirrels (points with error bars) and mean hourly standard operative temperature (T_{es}; °C) between 0500 and 2200 h (triangles) during May, June, July, and August 2001 ($n = 3–7$ ground squirrels). Combined number of telemetry locations for each hourly interval during each month ranged from 223 to 864 ($\bar{X} = 486$). Percentage data are represented as mean $\pm$ 2 *SE*, and means are weighted by number of telemetry locations for individual ground squirrels.

FIG. 6.—Percent of time spent on the surface between 0500 and 2200 h during May–August 2001 at different standard operative temperature (T_{es}; °C; $n = 3–7$ ground squirrels). Combined number of telemetry locations for each 2°C interval of T_{es} ranged from 82 to 2,603 ($\bar{X} = 998$). Data for the population are represented as mean $\pm$ 2 *SE*, and means are weighted by number of telemetry locations for individual ground squirrels. Points without error bars represent data for a single ground squirrel.

mid-May to late July. However, results from this study indicate that the thermal environment likely imposes substantial constraints on the length and pattern of the daily activity period in arctic ground squirrels.

Ground squirrels in our study experienced a wide range of thermal conditions throughout their active season, with >70% of our me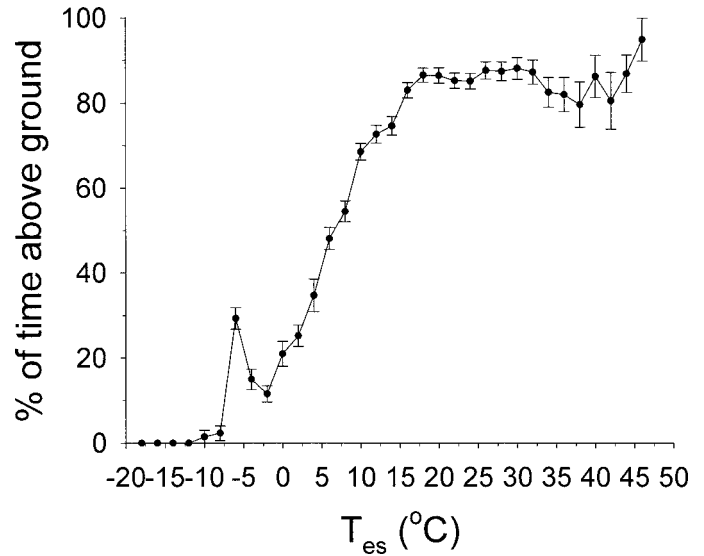asurements of T_{es} exceeding the critical limits of this species' thermoneutral zone. Although T_e was measured in only 1 microhabitat, the tundra and heath environment near Toolik Lake, Alaska, is relatively homogeneous. Thus, we believe that temperatures recorded by our model provided an accurate index of T_e for purposes of calculating T_{es}.

Daily patterns of burrow use and length of time spent above ground were correlated with daily variation in the thermal environment, and seasonal changes in the duration of the daily activity period reflected seasonal changes in the availability of favorable T_{es} (Fig. 5). The shortest activity periods were observed in May when temperatures often were below thermoneutrality throughout the day, whereas activity periods lengthened during June and July when temperatures generally became more favorable, with the exception of decreases in activity during the hotter midday hours. Ground squirrels seldom were observed on the surface when T_{es} was consistently below thermoneutrality regardless of season; this includes all hours between 2200 and 0500 h (Figs. 4 and 5). Accordingly, avoidance of thermal stress by arctic ground squirrels likely is an important factor in their adaptive development of strictly diurnal activity patterns in the face of near-continuous daylight throughout their active season (Chappell 1981). This hypothesis is supported by the consistency of the timing of 1st morning emergence from burrows across all categories of T_{es}. Morning emergence from burrows typically occurred between 0500 and 0700 h, the time interval when range of T_{es} 1st included thermoneutral temperatures (Fig. 4).

On cold days that included steady precipitation, arctic ground squirrels remained almost exclusively below ground. Arctic ground squirrels construct nests in their burrows (Krog 1954;

Mayer 1953) that likely provide enough insulation to allow for maintenance of high T_b with basal levels of metabolic heat production (Chappell 1981). As a result, ground squirrels potentially can return to their burrows to conserve energy when thermoregulatory costs of being active on the surface outweigh benefits gained from foraging. Heat production by exercise rarely compensates for thermoregulatory heat requirements in small mammals (Bartholomew 1977). Vispo and Bakken (1993) observed this pattern in the behavior of 13-lined ground squirrels (*Spermophilus tridecemlineatus*) and concluded that, during cold conditions, ground squirrels maximized energy intake over periods of >24 h rather than daily. An exception to the proportional decrease in activity time with decreasing T_{es} was the increase in surface activity exhibited at T_{es} between −10°C and −5°C (Fig. 6). This exception may occur because a large proportion (44%) of the temperatures recorded in this range were in May during the 1st few weeks of the active season, which corresponds with mating activities of *S. parryii* (Buck and Barnes 2003; Byrom and Krebs 1999). Arctic ground squirrels display a serially polygamous mating system with an importance of male–male aggressive interactions and male–female courting behaviors, most of which occur above ground (Buck and Barnes 2003).

Free-living arctic ground squirrels displayed T_b that normally remained within a 5°C range and within 3°C of the seasonal mean over the 24-h cycle, similar to other diurnal small mammals (Refinetti 1999a). However, individuals frequently tolerated T_b minima below 34°C and maxima above 40°C. Lowest T_b occurred both in day and night and did not occur in a regulated pattern suggestive of daily torpor; instead T_b below and above the range of 2 *SD* around the mean should be considered regular occurrences of hypothermia and hyperthermia, respectively. The alternative would be to broaden the range of T_b accepted as normothermic within this species. The consistent 1–2°C increases in T_b that anticipated regular morning activity and usually preceded emergence from the burrow on cold and wet days suggests that thermoregulation occurs to generate T_b > 39°C, which may be optimal for arctic ground squirrels active on the surface. Increases in T_b regularly precede the onset of daily activity in mammals (Refinetti 1999b), but increases in T_b that precede activity forays are less well described. Warming may occur before emergence such that T_b is optimal for locomotion or digestion while on the surface (Huey and Kingsolver 1993), or warming may occur in anticipation of the rapid rates of heat loss associated with being above ground, effectively countering decreases that otherwise could reduce T_b to <36°C. Given the T_b increases that precede 1st emergence and later emergences even on average and hot days, the former seems the more likely explanation, although both may play a significant role on cold and wet days.

When environmental temperatures were above thermoneutrality, arctic ground squirrels maximized surface time by tolerating transient hyperthermia and shuttling from surface to burrows. In an environment with almost no shade, periodically reducing T_b from hyperthermic levels by conduction in a burrow is an effective means of cooling for an animal that neither pants nor sweats (Chappell and Bartholomew 1981a). Bennett et al.

TABLE 1.—Stepwise multiple regression model used to describe the effects of standard operative temperature (T_{es}; °C) and several nonthermal variables on the daily proportion of time spent above ground by free-living arctic ground squirrels (*Spermophilus parryii*) near Toolik Lake, Alaska. Alpha for entry into the model was 0.15 and was 0.10 to remain. The sampling unit was 1 ground squirrel day.[a]

Variable	d.f.	Parameter estimate	SE	P	Partial r^2
T_{es}	1	0.0238	0.0020	< 0.0001	0.3349
Hours since solar noon	1	−0.0275	0.0059	< 0.0001	0.0514
Julian date	1	0.0021	0.0008	0.0068	0.0372
Cloud cover	1	0.0888	0.0387	0.0224	0.0180
Wind force	1	0.2771	0.1035	0.0079	0.0116
T_{es} × precipitation	1	0.0056	0.0022	0.0117	0.0127

[a] $n = 275$, adjusted $R^2 = 0.4591$, $F = 20.38$, $P < 0.0001$.

(1984) reported that Cape ground squirrels (*Xerus inauris*) used their bushy tails as portable parasols to prolong surface bouts, and Melcher et al. (1990) showed that yellow-bellied marmots (*Marmota flaviventris*) alternate foraging with cooling periods by perching on rocks where higher wind speeds reduced T_{es}. With relatively small tails and generally low wind speeds, such strategies would not likely be as effective for these ground squirrels, especially compared with utilizing the large thermal gradient for conductive loss that exists between burrow temperatures of ≤10°C and T_b of 38–42°C to quickly cool.

Arctic ground squirrels briefly tolerate core T_b up to 42.04°C. However, ground squirrels did not typically allow T_b to rise as high on hot days compared to cold and average days, and T_b was more tightly regulated at high T_{es}. Narrow regulation maintains a margin between current and lethal T_b when high radiant heat loads reduce the time needed for T_b to rise to lethal levels. Although the pattern of shuttling thermoregulation seen in Fig. 3b was consistent for ground squirrels on hot days, the total amount of time spent on the surface at high T_{es} varied among ground squirrels. Most ground squirrels decreased total surface time at T_{es} > 33°C, but a few maintained maximum levels of surface time even at the highest T_{es}. This difference may occur because energy demand and efficiency of foraging, which can be affected by age, habitat quality, or reproductive status (Kenagy et al. 1989; Koivula et al. 2003; Melcher et al. 1989), will influence foraging time requirements (Vispo and Bakken 1993) and result in demands for total activity time that vary by individual. Social status and differential habitat use (Chappell and Bartholomew 1981a) also could account for interindividual differences in surface activity, but why such differences occurred only at high T_{es} is difficult to discern. In our regression model, however, when we controlled for interindividual variability and included several important nonthermal predictor variables, T_{es} was still the most important factor influencing surface activity. Other variables with the potential to influence surface activity, such as predator avoidance and requirements for sleep, were not included in our analyses because of the difficulty associated with their measurement. The inclusion of such variables in the regression model may further explain variability in time spent on the surface but would not likely diminish the significance of T_{es} as a predictor of surface use.

Although a strategy of shuttling thermoregulation at high environmental temperatures has been demonstrated for a number of ground squirrel species at lower latitudes, including 13-lined ground squirrels (Vispo and Bakken 1993), antelope ground squirrels (*Ammospermophilus leucurus*—Chappell and Bartholomew 1981b), Columbian ground squirrels (*Spermophilus columbianus*—Belovsky 1986), and Cape ground squirrels (Bennett et al. 1984), this is the 1st observation in an arctic species. Chappell (1981) reported that arctic ground squirrels spent little time ($<5\%$) in burrows during the day. During the relatively short duration of that study (early August), however, T_{es} was nearly always within the thermoneutral zone. Similarly, examination of our data demonstrates that on days when environmental temperatures are mostly within thermoneutrality, ground squirrels remain almost exclusively on the surface.

Several of our conclusions are based on the assumption that energy intake through foraging is maximal when surface time is maximal, and that foraging time is not limited by factors such as digestive capacity. This seems a reasonable assumption for arctic ground squirrels, because behavioral observations indicate that after the mating season, most of surface time is spent foraging regardless of T_{es}. In addition, our findings that time on the surface increases proportionately with increasing T_{es} are inconsistent with the hypothesis that arctic ground squirrels choose high-quality foods to minimize time on the surface (Vispo and Bakken 1993). In our experimental design, we did not consider a potential interaction between thermal conditions and food availability. Bacigalupe et al. (2003) reported that degus (*Octodon degus*) increase activity in hot environments when food is supplemented, despite an associated increase in thermoregulatory costs. If food availability changes naturally with temperature, then its inclusion as a covariate in our regression model may diminish the importance of T_{es} as a predictor of surface activity.

Arctic ground squirrels on the North Slope of Alaska frequently face potential energy costs for physiological thermoregulation during their active season. Our results indicate that ground squirrels respond to these costs behaviorally by using burrows to maximize foraging time on hot days and minimize energy expenditure for thermoregulation on cold days. We conclude that the thermal environment represents the most immediate constraint on foraging behavior in these small mammals.

ACKNOWLEDGMENTS

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