

Standard Operative Temperatures and Cost of Thermoregulation in the Arctic Ground Squirrel, *Spermophilus undulatus*

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Summary. Body temperatures (T_b) and daily activity patterns of free-living arctic ground squirrels (*Spermophilus undulatus*) were determined via telemetry at a field site in northern Alaska. Simultaneous measurements were made of ambient temperature (T_a), wind speed (V), and incident solar radiation. The operative environmental temperature (T_e) for ground squirrels was obtained from fur-covered, thin metal taxidermic models of the animals. Standard operative temperature (T_{es}), a comparative index of heat flow, was calculated from T_e , V , and laboratory measurements of thermal conductivity.

During the period of the study (August), *S. undulatus* were active for about 14 h per day (06.00 to 20.00 h). T_b was high throughout the daily cycle, averaging 38–39° C. Circadian variations in T_b were slight; average T_b values dropped <1° C at night. Daytime T_b fluctuations were not closely correlated to activity or to changes in environmental conditions. Air temperatures during the study were low, usually between 10 and 15° C during the day. However, T_{es} in exposed areas was normally higher, even though skies were generally overcast. During periods of sunshine, T_{es} may be as high as 34° C. The absence of nocturnal activity may result from increased costs of thermoregulation at night, which sharply reduces foraging efficiency. The high and stable body temperatures of *S. undulatus* probably result from thermoneutral daytime T_{es} , low activity levels, and the use of well-insulated nests.

Introduction

For many small mammals living in cold environments, a major portion of total energy expenditures is used to pay a “cost of thermoregulation” (Bartholomew 1977; Chappell 1980c), defined as any additional heat production above basal metabolism necessary for maintenance of normal body temperature (T_b). This cost will be especially important to hibernators which must not only survive and reproduce during the summer, but must also accumulate large fat stores. Unfortunately, little information exists on the bioenergetic regimes of hibernators in their natural habitats. Morhardt and Gates (1974) examined thermal energy exchange in Belding’s ground squirrel (*Spermophilus beldingi*), a hibernator from the mountains of California. They demonstrated that despite poor insulation, *S. beldingi* is energetically well adapted to its cool habitat, because the intense solar radiation typical of high altitudes compensates for ambient tempera-

tures which are usually below thermoneutrality. Consequently, the cost of thermoregulation in *S. beldingi* is probably low, although it was not specifically measured. At high latitudes, maintaining a favorable energy balance is potentially more difficult for hibernators, since ambient temperatures are lower and solar energy is less intense. Therefore, the summer-season energy balance and cost of thermoregulation of the arctic ground squirrel *Spermophilus undulatus*, a medium-sized (~1 kg) arctic hibernator, are of considerable comparative interest.

Calculations of the cost of thermoregulation require an understanding of thermoregulatory physiology, activity patterns and habitat selection. Also necessary is a quantitative index of the thermal characteristics of the habitat. Most studies of bioenergetics have used air temperature (T_a) as the predominant thermal index, but a rigorous assessment of energy balance requires consideration of the effects of wind and solar radiation as well as T_a (Porter and Gates 1969). All of these parameters are incorporated into the concept of “standard operative temperature” (T_{es}), which is easy to measure in the field and has been shown to be an accurate index of heat exchange in white-crowned sparrows (Bakken 1980) and antelope ground squirrels (Chappell and Bartholomew 1981a, b) in a variety of convective and radiative environments. Therefore, the T_{es} concept was used for the study presented in this paper: an analysis of the energetics, thermoregulatory costs, and activity patterns of arctic ground squirrels in northern Alaska, USA.

Materials and Methods

Study area

Arctic ground squirrels were observed near Driftwood Creek, a field camp on the north slope of the Brooks Range, Alaska, USA (69° N. latitude). The area is a river valley (altitude 300–400 m) lying between low hills and ridges. Plant cover consists of riparian willow thickets surrounded by wet tundra vegetation and barren rocky ridges. There is 24-h sunlight in late June and early July. At the time of this study (early August) the sun was above the horizon approximately 19 h per day.

Behavioral Observations

Activity patterns and habitat selection at various times of the day were monitored by counting visible animals while walking a standard route around the airstrip adjacent to the camp. The squirrels quickly became accustomed to this procedure and showed no signs of alarm unless the observer approached within 5 m. During census walks I made brief behavioral observations; at other times I followed individuals for up to 1 h, recording movements and feeding habits.

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Telemetry

Temperature-sensitive transmitters (J. Stewart Enterprises TT-1U's) were surgically implanted in the peritoneal cavities of five adult squirrels. These telemeters weigh 12 g and have a transmission range of about 1 km (decreasing to ~100 m when the animals enter burrows). Temperature is transduced as click frequency (30–50 pulses/minute at 35–40°C). Squirrels were released the morning following surgery and followed for 1 wk. Signals were acquired with a Telonics TR-2 receiver and analyzed with a Telonics Digital Processor displaying interpulse intervals and signal strengths. Comparison of interpulse intervals with a calibration curve yielded body temperature ($\pm 0.3^\circ\text{C}$); activity data were inferred from variations in signal strength. Signals from quiet animals were of uniform intensity, but signal strengths from active animals varied continuously, presumably due to changes in transmitter orientation (Morrison 1978). I validated these criteria with observations of alert animals prior to and after their release. All of the telemetered animals appeared healthy and behaved normally throughout the course of the study. Four were killed and dissected at the conclusion of observations; no abnormalities were noted, and the calibration of recovered transmitters had not changed.

Environmental Conditions

In order to estimate the energetic effects of the thermal regime an animal experiences in the field it is convenient to integrate the effects of important parameters (radiation, wind, air temperature, etc.) into an index value that can be directly compared to the animal's physiological performance under controlled conditions. This was done by (1) measuring in the field an integrated temperature (T_e) which combines the effects of air temperature, wind, and sun, (2) determining the effects of wind on thermal conductance, and (3) combining these data into a comparative index of heat flux for the animals in the field (T_{es}).

The operative, or effective environmental temperature (T_e) is the temperature at which an animal would equilibrate if it lacked metabolic heat production and evaporative water loss (Bakken 1976). I determined T_e from thermocouples attached to pelt covered, hollow copper models of the animals (Bakken and Gates 1976; Chappell 1980b). Two models were built in a normal quadrupedal posture and one was fabricated in the bipedal "alert" posture (Carl 1971). I did not use curled models because ground squirrels were never observed to curl up when outside of their burrows.

During T_e measurements I posed the models naturally in microhabitats commonly utilized by squirrels and made simultaneous measurements of air temperature, incident solar radiation, and wind speed. Radiation was measured with a silicon-cell pyranometer and wind speeds (averages of one-minute samples) were taken with a hand-held anemometer. I also obtained air and ground temperatures in several burrow systems. All of the microclimate temperatures and T_e 's were measured with a digital thermocouple thermometer.

Model animals were also used in the laboratory to determine the effects of wind on the thermal properties of ground squirrel pelts. For this purpose I equipped two models with constantan wire resistance heaters attached to the copper core with epoxy glue and heat-sink grease. Thermal resistance of the models could then be calculated from steady-state power input, model temperature, and air temperature at various air speeds in a wind tunnel (Chappell 1980a).

Although T_e is a much better index of the thermal potential which drives heat flow than is T_a , it does not incorporate the effects of changes in thermal conductance. Conductance changes are very important for the bioenergetics of endothermic homeotherms; in cold conditions, endotherms maintain nonequilibrium thermal steady-states by adjusting both thermal conductance and heat production to balance heat loss. Gagge (1940) and Bakken (1976) have proposed another index, the "standard" operative temperature (T_{es}) which takes conductance changes into account and allows direct comparisons to the animal's physiological performance under standard conditions (e.g., metabolism chambers). T_{es} can be calculated from T_e using the following equation (Bakken 1980):

$$T_{es} = T_b - (K_e/K_{es})(T_b - T_e) \quad (1)$$

where K_{es} is thermal conductance under standard conditions (here, defined as blackbody radiant conditions in the absence of forced convection) and K_e is thermal conductance when T_e is measured in the field. Differences between K_e and K_{es} result primarily from the effects of wind, and $T_{es} = T_e$ at low wind speed.

Evaporation of water from the skin is also affected by wind. However, since ground squirrels do not sweat, evaporative heat loss (λE) is primarily respiratory and therefore does not affect conductance across the pelt. Rates of evaporative cooling are probably small in the cool, humid Driftwood environment (Withers et al. 1979).

Endotherms change conductance in order to regulate heat balance within the thermal neutral zone (Bartholomew 1977); this must be accounted for when calculating T_{es} from T_e . For arctic ground squirrels, minimum conductance under standard conditions is about 0.19 W/°C, and basal metabolic rate is about 3.5 W (Scholander et al. 1950; Withers et al. 1979). The upper critical temperature (T_{uc}) of *S. undulatus* is not well known; it was assumed to be 36°C at $T_b = 41^\circ\text{C}$, with about 50% of heat production lost as evaporation. Therefore, the maximum dry conductance [= (heat production - λE)/ $(T_b - T_{uc})$] will be 0.35 W/°C. When computing T_{es} for field conditions, conductance was assumed minimal when $T_e < 18^\circ\text{C}$ (the species' lower critical temperature), maximal when $T_e > 36^\circ\text{C}$, and proportionally intermediate within the thermal neutral zone. This assumption introduces a small error ($< 2^\circ\text{C}$) into T_{es} calculations, since animals probably adjust conductance in response to T_{es} instead of T_e . This small inaccuracy is unimportant for bioenergetic studies because it only occurs when T_{es} is within or close to thermoneutrality.

To calculate K_e/K_{es} , conductances were converted into total resistances (r_t^e and r_t^{es} , respectively) and partitioned into body and external resistances according to the methods described in Robinson et al. (1976) and summarized in Appendix 1. Body resistance (r_b) in a live ground squirrel consists of tissue resistance (from subcutaneous fat and peripheral vascular adjustments) plus coat resistance. External resistance (r_{ex}) is a function of wind effects on the boundary layer of still air adhering to the animal. Coat resistance may also be affected by wind, but the thermal properties of ground squirrel pelts do not change greatly at wind speeds like those encountered in the field (see Results). Therefore, all differences between r_t^e and r_t^{es} are due to wind-induced changes of r_{ex} in the field. Since resistance is the inverse of conductance; $K_e/K_{es} = r_t^{es}/r_t^e$, and:

$$T_{es} = T_b - (r_t^{es}/r_t^e)(T_b - T_e) \quad (2)$$

Values of r_t^e and r_t^{es} were calculated from data obtained in wind tunnels (see Results).

Thermoregulatory cost to ground squirrels maintaining normal euthermic body temperatures in subterranean nests was estimated in the laboratory. Several artificial nests of dry grass, roughly 35 cm long by 25 cm diameter with wall thicknesses varying from 5 to 10 cm, were snugly fitted around the heater-equipped models. The materials and dimensions used are the same as observed for real arctic ground squirrel nests (Mayer 1953; Krog 1954; personal observations). The artificial nests containing the heated models were placed in large cardboard boxes and covered on all sides with several inches of soil to simulate the thermal effects of the burrow substratum. These assemblies were then placed in a controlled-temperature room maintained at 4°C. The heat production necessary for maintaining the models at 35–40°C could then be calculated from the power input to the heater.

Results

Environmental Data

During the study, days were overcast 80–90% of the time, with occasional light rain. Nights were always 100% overcast. The longest interval of continuous sunshine was 2 h. Consequently, the average insolation (Q_T) was rather low, about 180–350 W/m² at midday. Maximum irradiance observed when the sky was clear was 600 W/m² at 13.00 h; this is considerably less than the 1,000 W/m² Q_T typical in temperate latitudes. Average

and maximum irradiance throughout the day is plotted in Fig. 1. The maximum Q_r curve was constructed from readings obtained during the sporadic periods of direct sunlight.

Wind speed (V ; m/s) was quite low at night, always less than the minimum anemometer resolution of 0.4 m/s. During the day, V was higher, but irregular; gusts of up to 3 m/s occurred occasionally but average V was 1–1.5 m/s (Fig. 1). Measurements of V were made 20 cm above the ground (shoulder height of a ground squirrel sitting on its hind legs); presumably wind speed closer to the ground was smaller because of boundary layer effects. Average air temperature (T_a) usually varied 10° C between day and night (Fig. 1). Maximum midday T_a was normally about 15° C, but in shaded areas near ground T_a was only 1–2° C cooler than T_a in open areas. At night, temperatures in open areas and under shrubs were similar, falling from 12° C at sunset (22.00 h) to 6° C at dawn (05.00 h).

The temperatures of 6 burrows were all approximately 4° C throughout the day at depths of 20 cm or more. The deepest burrow measured had air and soil temperatures of 3.4° C at a depth of ~70 cm (the study site is in a permafrost area, but the depth of frozen soil was not known). Ground surface temperatures in shaded areas were approximately equal to T_a . In open areas surface temperature averaged 15–20° C, but varied $\pm 5^\circ$ C with soil moisture content, terrain relief, and changes in Q_r .

Convection

Total thermal resistance of the models (r_t^m ; all resistances in s/m) decreased approximately as the square root of wind speed ($r_t^m = 221 - 54.2 V^{0.5}$; $r^2 = 0.956$; $n = 31$) within the range of V tested (Fig. 2). This result is similar to that obtained from birds (Gessaman 1972; Robinson et al. 1976; Chappell 1980a). Total resistance of models is composed of body resistance (r_b^m) and the external resistance r_{ex} , both of which may be influenced by V . In models body resistance is comprised only of the coat resistance r_c ; live animals also possess a subcutaneous tissue resistance r_s , which arises from the insulatory fat layer and peripheral vascular control. Therefore, $r_t^m = (r_c + r_{ex})$, and r_t^a (total resistance of live animals) = $(r_s + r_c + r_{ex})$, or $(r_t^m + r_s)$.

External resistance can be calculated from T_a , V , and the diameter of the animal (Robinson et al. 1976; Appendix 1); $r_b^m (= r_c)$ is obtained by subtracting r_{ex} from r_t^m . In the arctic ground squirrel r_c appears to remain relatively constant until V exceeds 1.5–2 m/s. At higher air speeds r_c begins to decrease (Fig. 2). Again, the rate of decrease is accurately predicted by a linear function of the square root of V ($r_c = 172 - 47.9 V^{0.5}$; $r^2 = 0.956$; $n = 17$). This observation is consistent with theoretical predictions (Davis and Birkebak 1974) that r_c should be constant up to a "critical" windspeed. However, almost all wind speeds measured at Driftwood were < 2 m/s, so r_c of animals in the field was probably little affected by wind.

Figure 2 also shows measured and predicted thermal resistances of live animals (r_t^a) at various wind speeds. Values of r_t^a at low V (~ 0.1 m/s) were calculated from previously published measurements of metabolic rates, thermal conductances, and body temperatures obtained in unstirred air (Scholander et al. 1950; Withers et al. 1979). These values are $\sim 50\%$ larger than the thermal resistances of models (r_t^m). The difference occurs because models lack the subcutaneous tissue resistance r_s , which has a maximum value of about 90 s/m at temperatures below thermoneutrality. Nevertheless, it is likely that the external resistance r_{ex} and the thermal properties of pelts of models closely resemble those of live animals. Since tissue resistance is not directly affected by air movement, r_t^a should decrease in parallel

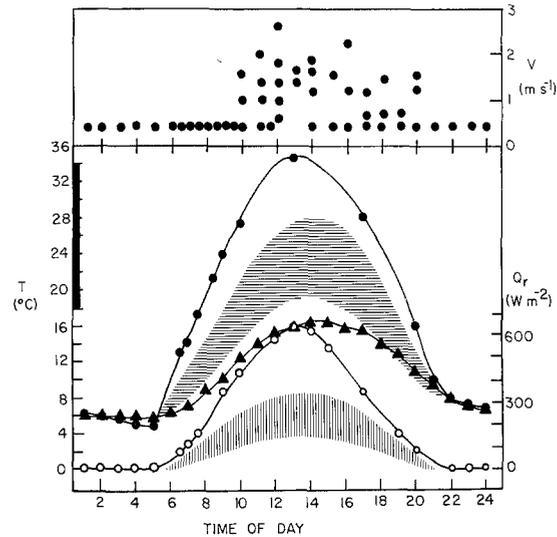


Fig. 1. Microclimate data from the Driftwood area. Upper section shows wind speeds (many data points overlap). Lower section shows maximum (open circles) and average (vertical shading) Q_r , average air temperature (triangles), and maximum (dark circles) and average (horizontal shading) T_{cs} in open areas (shade T_{cs} was very similar to air temperature). Black bar at left indicates the thermal neutral zone for arctic ground squirrels

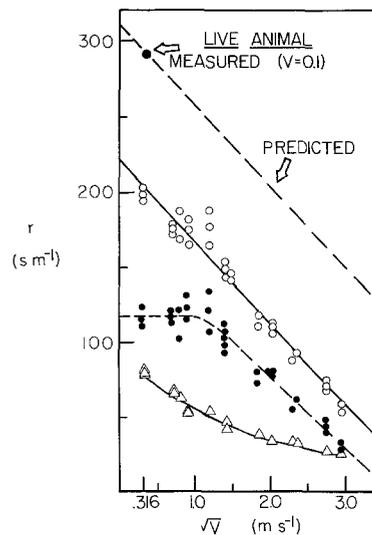


Fig. 2. Maximum thermal resistance for models and live animals at various wind speeds (data from different models are lumped). Open circles are wind tunnel measurements of total thermal resistance of models (r_t^m), black circles are values of coat resistance (r_c) obtained by subtracting calculated external resistance (triangles) from r_t^m (see text). Dashed line at top of figure is a prediction of the total resistance of live animals (r_t^a), obtained by redrawing the data from models through measurements from live animals in metabolism chambers at $V \sim 0.1$ m/s (black circle at top) according to Eq. (3). (The value of 0.316 on the x-axis denotes the square root of 0.1)

with the measured values of r_t^m as V increases (Fig. 2). The equation used to calculate r_t^a at temperatures below thermoneutrality is:

$$r_t^a = 310 - 54.2 V^{0.5} \quad (3)$$

At the highest wind speeds that could possibly be experienced by ground-dwelling squirrels (5 to 9 m/s), maximal thermal resis-

tance of a live animal is only half that possible in the absence of forced convection.

Equation (3) can be substituted into Eq. (2) to calculate T_{es} . Since r_f^* values (thermal resistance of live animals in standard conditions) are defined at wind speeds of ~ 0.1 m/s, at temperatures below thermoneutrality:

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

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

Operative Temperatures

In contrast to air temperature, T_e varied over a considerable range, from about 6° C at night to as much as 34° C in sunshine. In open areas, T_e averaged 5 to 15° C higher than T_a . This is rather surprising because of the prevalence of cloud cover and associated low irradiance levels. In deep shade, T_e was not significantly different from T_a . There were only slight and inconsistent differences between T_e values for model animals in different orientations or between the bipedal sitting posture and the quadrupedal walking posture, perhaps because the overcast skies reduced the directionality of the solar beam.

Standard operative temperature in open areas averaged somewhat higher than T_a , although it was seldom as high as T_e because of convection (Fig. 1). During the day, open-area T_{es} was usually between 15 and 25° C, with a maximum of 29° C. Considerable fluctuation occurred in T_{es} as a result of changes in both Q_r and V . It is significant, however, that most of the midday T_{es} values lie within the thermal neutral zone of *S. undulatus*. Figure 1 also shows the highest T_e values, which were measured during periods of sunshine. In the absence of any forced convection, these would also be the maximum possible T_{es} values. However, T_{es} was never maximal because convection was always significant in open areas. In shaded areas, V was usually < 0.4 m/s, and hence shade T_{es} was seldom different from T_e and T_a .

Nighttime values of T_e and T_{es} were equal to ambient temperature during this study, but only because the sky was consistently overcast and forced convection was negligible. For an animal exposed to wind, or to a clear night sky, T_{es} will be considerably less than T_a . Calculations based on clear-night T_e measurements made in Barrow, Alaska (71° N) indicate that T_{es} will be 12–17° C cooler than T_a on a cloudless night with near-ground wind speeds of 1–2 m/s.

Thermoregulation in nests

Experiments with artificial nests indicate that arctic ground squirrels in their burrows can easily maintain high body temperatures with basal levels of metabolic heat production, despite the cold ($\sim 4^\circ$ C) substratum. The power input needed to maintain model animals at 35 to 40° C averaged 3.2 W, or about 90% of basal metabolism. Presumably live animals in natural conditions could maintain T_b with greater precision through postural adjustments of vasomotor control, and possibly by manipulation of nest structure. During these experiments temperatures inside the nest cavity varied between 15 and 24° C, and soil temperatures 5 cm from the outer edge of the nest were 5 to 7° C. The net effect of the nest was to approximately double the thermal resistances of the model ground squirrels.

Activity Patterns and Body Temperatures

Arctic ground squirrels have long daily activity cycles during the summer, but do show a definite inactive period at night.

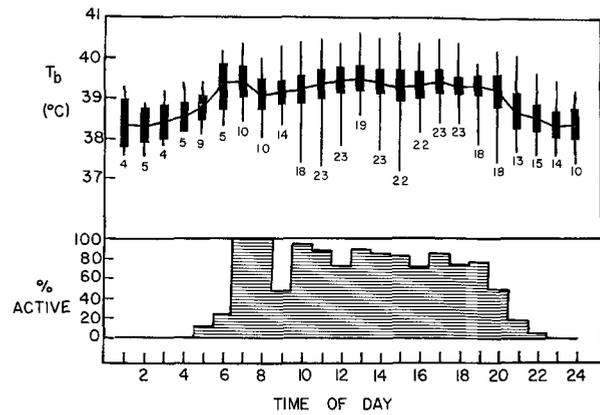


Fig. 3. Body temperature and activity data obtained by telemetry. Upper section shows range (vertical lines) and 2 standard errors of the mean (rectangles) of T_b ; mean values are joined by the horizontal line. Numbers of observations apply to both T_b and activity data

The telemeter-equipped animals were active for roughly 14–16 h per day, as determined by analysis of signal-strength variations. The bulk of activity was concentrated between 07.00 and 20.00 h, and all individuals were quiet and in burrows between 22.00 and 05.00 h (Fig. 3). Information from direct visual observations during census walks confirmed the telemetry data: activity was intense during the day, but no animals were visible above ground and no vocalizations were heard before 06.00 and after 21.00 h.

Activity was essentially constant throughout the day; from 07.00 to 20.00 h about 80% of the telemetered animals were active at any one time (Fig. 3). Simultaneous visual and telemetric observations suggested that most of the midday “quiet” periods actually represented episodes of alert, “watchful” behavior while the animals sat erect at burrow entrances. Squirrels were seldom underground during the day unless obviously frightened or during brief interludes while delivering nesting materials. No animals were ever observed in a curled posture and none were ever seen sleeping while outside of their burrows.

The body temperatures of the five telemetered animals were relatively constant throughout the daily cycle (Fig. 3). Mean T_b at night (21.00–05.00 h; $n=39$) was 38.4° C; mean daytime T_b (06.00–20.00 h; $n=264$) was 39.3° C. Body temperature was more variable during the day (range 37.2 to 40.7° C) than at night (range 37.5 to 40.1° C). Much of the variation in T_b was between animals. Individual squirrels usually displayed a fairly constant T_b , both daily and throughout the duration of observations. Nevertheless, every individual had T_b 's $< 38^\circ$ C and $> 40^\circ$ C at least once during the study.

Daytime T_b , like activity, does not seem to be closely coupled to any of the measured environmental variables. There is no correlation between T_b and T_{es} ; mean T_b at $T_{es} > 20^\circ$ C (39.36° C) was slightly higher than mean T_b at $T_{es} < 20^\circ$ C (39.30° C), but the difference is statistically insignificant. Activity also seemed to have little effect on T_b . Measurements from active animals (mean 39.4° C, $n=209$) tend to be slightly warmer than those from quiet animals (mean 39.2° C, $n=55$), but again the difference is statistically meaningless.

The lack of correlation between T_b and activity may be an artifact of discontinuous sampling. Activity can change instantly while T_b changes gradually; therefore, even if T_b were tightly coupled to activity, some T_b measurements will unavoidably be ‘out of synchronization’ with activity measurements. On several occasions I monitored T_b continuously for ~ 30 min while simultaneously observing the telemetered animals. During these

intervals, bursts of activity were almost always followed by rises in T_b . However, a bout of vigorous activity seldom lasted longer than 30 s, and the concomitant rise in T_b was usually 0.2–0.3° C and never exceeded 0.4° C. Should sustained, intense activity occur (e.g., lasting several minutes), it is likely that a substantial rise in T_b would result.

Discussion

Cost of Thermoregulation

The importance of using a rigorous thermal index like T_{es} for bioenergetic studies, as opposed to the physiologically less realistic T_a , is shown by a simple calculation: The lower critical temperature (T_{lc}) for arctic ground squirrels is about 18° C (Schlander et al. 1950; Withers et al. 1979). Since air temperature is usually considerably cooler than T_{lc} ($T_a = 8$ –12° C during the day at Driftwood), analysis of the thermal budget based on T_a predicts that squirrels must spend appreciable amounts of energy for thermoregulation. However, if T_{es} is used as the thermal index, a different picture emerges. On clear calm days T_{es} rises above the lower critical temperature by 08.00 h and remains within the thermal neutral zone until 20.00 h, a period encompassing the bulk of the animals' above-ground activity. Even on overcast days T_{es} reaches the lower critical temperature by 09.00–10.00 h and stays within thermoneutrality until 18.00–19.00 h (Fig. 1).

Behavioral observations indicate that arctic ground squirrels in the Driftwood area spend much of their active time (60–80%) in open areas, and most of the remainder under shrubs or in other shady areas. Very little time (<5%) is spent in the burrow during the day, unless the animals are harassed by predators to an unusual extent. By combining the habitat selection, T_{es} , and activity data in Figs. 1 and 3, we can calculate the cost of thermoregulation (heat production above basal metabolism required to maintain T_b) with the following equation:

$$C_{th} = \sum_{t=6}^{20} [k(T_b - T_{es(ot)}) - BMR](A_o) + [k(T_b - T_{es(st)}) - BMR](A_s) \quad (5)$$

where C_{th} = daily cost of thermoregulation, t = time of day when squirrels are active in units of 1 h (06.00–20.00 h; at night, animals are in thermoneutral nests), k is thermal conductance (0.19 W/°C), BMR = basal metabolic rate (3.5 W), $T_b = 38$ C, A_o = proportion of time spent in open areas (0.7), $T_{es(ot)}$ = average T_{es} in open areas during each hourly interval, A_s = proportion of time spent in shaded areas (0.3), and $T_{es(st)}$ = average T_{es} in shaded areas during each hourly interval. The small amount of time spent in burrows was ignored for this calculation. When T_{es} exceeded the lower critical temperature (18° C), the term $[k(T_b - T_{es}) - BMR]$ was set to zero. Exercise heat production was not considered, because it does not compensate for thermoregulatory heat requirements in most small mammals (Bartholomew 1977).

Solution of this equation for an average day at Driftwood yields an estimate of about 20 KJ/day for the cost of thermoregulation, or about 7% of the BMR of an adult ground squirrel (300 KJ/day). On clear days, T_{es} is higher and the cost of thermoregulation decreases to approximately 5–10 KJ/day, or 2–3% of BMR. On heavily overcast days with little insolation, the cost of thermoregulation is about 70–80 KJ/day, or 30–40% of BMR.

Preferential utilization of open, sunlit areas is probably an important energy conservation strategy for arctic ground squir-

rels. In the Driftwood Creek area, willow scrub (*Salix spp.*) covers approximately 60–70% of the ground surface. Therefore, a ground squirrel using the habitat unselectively will be in open areas less than half the time, instead of 60–80% as estimated from behavioral observations. The cost of thermoregulation will be about 55–60 KJ/day for a nonselective squirrel, instead of 20 KJ/day for a squirrel spending 70% of its time in sunlit areas. During periods of above-ground activity, a nonselective animal will spend 3.5–4 KJ/h for thermoregulation (equal to 30% of BMR), while a selective animal will spend only 1.3 KJ/h (equal to 10% of BMR). Assuming that weather conditions are fairly similar over the 60–70 day period of fat accumulation (late July through September), the additional cost to a nonselective animal is equivalent to roughly 65 g of fat, or 19% of the 350 g total fat storage (Morrison and Galster 1975).

When wind speed is low and the sky is clear, T_{es} in open areas may exceed the upper critical temperature of arctic ground squirrels. Such conditions did not occur during the present study, but probably are fairly frequent during June and July (as estimated from U.S. National Weather Service data). High T_{es} in open areas should not create severe problems for the Driftwood squirrels, because of the abundance of shaded areas under willow bushes. However, animals living in less heavily vegetated areas may have to retreat periodically to their burrows or resort to evaporative cooling on hot days. Carl (1971) mentioned that trapped squirrels often died of apparent heat stress on warm, calm days.

Thermoregulatory costs of arctic ground squirrels are very low compared to those of other small arctic mammals. For example, in lemmings (*Lemmus* and *Dicrostonyx*, about 75 g) inhabiting the arctic coastal plain of Alaska, the cost of thermoregulatory heat production in summer is equivalent to about 180% of BMR when the animals are outside of their nests, and averages about 120% of BMR over the entire summer season (Chappell 1980c). The disparity between lemmings and ground squirrels results from a variety of factors, but is primarily due to the order-of-magnitude size difference. Average environmental temperatures are about 8° C cooler in lemming habitat, but there is little difference between the species' lower critical temperatures (due to the unusually thick pelage of lemmings). However, the larger ground squirrels are much less tightly coupled to convective heat loss than are lemmings, and consequently benefit more from the effects of solar radiation (Porter and Gates 1969). Behavioral factors are also important. Lemmings spend most of their time in shaded runways where $T_{es} = T_a$, while ground squirrels remain primarily in open areas where T_{es} is considerably higher than T_a .

Activity patterns

The summer activity patterns of the arctic ground squirrel are of special interest because the species experiences long day lengths within a very short annual activity period. Most temperate-zone ground squirrels, subjected to a summer light:dark cycle of about 14 h light:10 h dark, are strictly diurnal. One might expect that *S. undulatus*, which must accumulate its energy supply for an entire year in 16 weeks or less, experiences selective pressures to fully utilize the long summer days for foraging activities. Nevertheless, despite a ratio of about 19 h light:5 h dark at the time of the study (with enough light for easy visibility for humans during the "dark" phase), the Driftwood squirrels were active for at most 16 h per day. Almost all entered burrows well before the sun set and emerged an hour or more after

sunrise. A similar rhythm was noted by Mayer (1953) and Carl (1971) during 24-hour sunlight.

A major factor in the avoidance of nighttime activity may be nocturnal increases in the cost of thermoregulation, which decrease the efficiency of foraging. As can be seen in Figs. 1 and 3, the active periods of ground squirrels coincided closely with times when T_{es} was within or close to their thermal neutral zone. At Driftwood, temperatures were 10 to 20 degrees cooler at night than during the day; T_{es} usually fell to 10° C below the lower critical temperature for several hours before dawn. Squirrels active in these conditions experience at least a 50% increase in heat loss rates above daytime levels and require a compensatory increase in metabolic heat production.

An adult ground squirrel stores about 350 g of fat over 60–70 days in preparation for hibernation (Morrison and Galster 1975), or about 5 g fat per day. Assuming that animals are active for 16 h per day (Fig. 1), during an hour of activity they can gather enough food to sequester about 0.3 g of fat (equivalent to 12 KJ). Thus, a ground squirrel active for an extra 8 h at night could accumulate an additional 96 KJ of fat per day, provided that no extra maintenance costs are incurred by nocturnal activity and that animals can gather food at night as rapidly as during the day. This would shorten the period necessary for fat storage to 47 days. However, on an overcast night when T_{es} is about 8° C, a ground squirrel faces an additional heat production requirement of about 6.5 KJ/h, or 52 KJ over 8 h. This metabolic cost will cut the rate of energy storage at night by at least 55%. On clear or windy nights, T_{es} may drop to 0° C or below, or about 20° C below the lower critical temperature. In such conditions a foraging ground squirrel would need to produce an extra 13 KJ/h of metabolic heat, completely obviating any possible gain in energy storage.

Another possible disadvantage of nocturnal foraging is reduced visual acuity. This could result in sharply decreased food-finding abilities (exacerbating the problem of increased thermoregulatory costs) and increased vulnerability to predation (Carl 1971). At Driftwood, potential ground squirrel predators are abundant and diverse, including grizzly bear (*Ursus arctos*), red fox (*Vulpes vulpes*), wolf (*Canis lupus*), golden eagle (*Aquila chrysaetos*), rough-legged hawk (*Buteo lagopus*), and gyrfalcon (*Falco rusticolus*). Many of these predators are nocturnally active.

Temperature regulation

The overall pattern of body temperature regulation in free-living arctic ground squirrels is similar to that observed in captive specimens (Folk and Folk 1964), in Richardson's ground squirrels (*S. richardsoni*; Wang 1972), in Belding ground squirrels (*S. beldingi*; Morhardt and Gates 1974), and in Abert's squirrels (*Sciurus aberti*; Golightly and Ohmart 1978). However, the range of body temperatures observed in arctic ground squirrels (3.5° C) is somewhat less than the T_b variation seen in Richardson's and Belding ground squirrels or Abert's squirrels (6.2, 5.0, and 5.9° C respectively). One factor affecting the relatively stable daytime T_b of arctic ground squirrels may be their comparatively inactive life style, which minimizes exercise heat production. Sustained, intense activity was seldom observed. Animals ran only when pursued by predators, or occasionally at moderate speed across large open areas, perhaps to shorten exposure time in areas lacking cover. Much of an arctic ground squirrel's day is spent feeding, primarily on green grass, forbs, and young willow leaves. Foraging animals walk slowly, often pausing to manipulate and chew food items. A large proportion of time

is spent sitting alertly at burrow entrances. Mayer (1953) described long-distance movements (up to 1 Km) by foraging squirrels, but during the present study all telemetered animals remained within 200 m of their burrows. Earlier in the season, male squirrels are much more active because of their aggressive defense of territories (Carl 1971).

The lack of significant nocturnal decreases in body temperature in *S. undulatus* is surprising. In theory, even the shortest possible complete cycle of torpor or hypothermia may result in significant energy savings (Tucker 1966; Bartholomew 1972; French 1976), but my observations revealed very little circadian body temperature variation and no indication of hypothermia or torpor. This stability of T_b is probably due in large part to the relatively large size and well-insulated nests of arctic ground squirrels, which prevent them from cycling T_b rapidly enough for selection to favor the evolution of daily torpor. In a prewarmed nest, a dead arctic ground squirrel will take approximately 2 h to cool from 38° C to 30° C at average soil temperatures, and a live animal with its metabolic heat production will cool about as slowly even if it activates heat loss mechanisms such as vasodilation. Calculations based on maximum thermal conductance and a Q_{10} of 2.5 suggest that a live animal in a nest will take at least 2 and probably 4–5 h or longer to lower T_b from 38° C to 30° C. The necessary pre-activity rewarming will also require a substantial period. Thus, an arctic ground squirrel inactive for 8 h nightly can cycle its T_b only a few degrees, with insignificant energy savings resulting. Predation pressure may also be a factor selecting against nocturnal hypothermia. A torpid squirrel might not be able to arouse quickly enough to escape if its burrow were excavated by a grizzly bear or wolverine (Carl 1971).

In summary, arctic ground squirrels have very low thermoregulatory costs during their summer activity periods, despite high and stable body temperatures and cool ambient conditions. This metabolic parsimony results from moderate body size, low thermal conductance, selective utilization of sunlit parts of the habitat, cessation of activity during the coldest part of the daily cycle, and the use of well-insulated nests. Behaviors such as selection of warm microclimates may save enough energy to increase the rate of accumulation of winter fat stores by 15–20%, an important advantage for an animal which can forage for only 3–4 months of the year.

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Appendix 1

Values of r_{ex} were obtained with the following equations (Robinson et al. 1976):

$$r_{ex} = (r_a \cdot r_r) / (r_a + r_r)$$

$$r_a = (r_{ro} \cdot r_{fr}) / (r_{ro} + r_{fr})$$

$$r_{ro} = k(d/V)^{0.5}$$

$$r_{fr} = 820[d/T_s - T_a]^{0.25}$$

$$r_r = \rho c_p / 4\sigma \epsilon (T_a^3)$$

where r_{ex} is a parallel equivalent resistance of the combination of resistance to convective heat flow (r_a) and an apparent radiative resistance (r_r).

r_{ro} = resistance to forced convection

r_{fr} = resistance to free convection

T_s = surface temperature

[here, assumed to equal $T_c + 0.5(T_b - T_c)$]

V = wind speed
 d = animal diameter
 k is a constant; =307 for laminar flow (wind tunnels) and 210 for turbulent flow (outdoors)
 ε = pelt emissivity (0.99)
 σ = Stefan-Boltzman constant ($5.7 \times 10^{-8} \text{ W m}^{-2} \text{ }^\circ\text{K}^{-4}$)
 ρc_p = heat capacity of air ($1,200 \text{ J m}^{-3} \text{ }^\circ\text{C}^{-1}$ at 20°C)

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