

The field energetics of winter-dormant black bear (*Ursus americanus*) in northeastern Minnesota

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Black bears (*Ursus americanus*) can spend half of their lives in a severe winter climate using only internal sources of energy and exchanging energy only as heat with their external environment. This paper presents the energy requirement to maintain a bear, and the magnitude of the heat transfer pathways to the bear's surroundings. Flux rate densities of the heat budget were measured for two denning black bears. It was found that the surface area of an oblate spheroid simulating the shape of the curled-up bears balanced the budgets. From these data a simulated bear–den system was constructed for a 75-kg animal; a fur-covered spheroid that was electrically heated and maintained at 36°C. The energy requirement and heat transport were measured through the skin and in the den over winter, as was the oxygen consumption of a live bear in a similar den nearby. Over a 145-day denning period, mass loss due to fat catabolism would have ranged between 24 and 28% for the simulated bear with the entrance sealed or open, respectively. Using the amount of oxygen consumed and holding body water constant, the mass loss of the live bear over the same period would have been 19% if just fat had been catabolized. However, additional protein catabolism near the end of the denning period caused the loss to increase to 31%, primarily through urination. Once net protein catabolism began, dehydration and not starvation became life threatening.

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Les Ours noirs (*Ursus americanus*) peuvent passer la moitié de leur vie en climat d'hiver rigoureux en utilisant seulement leurs sources internes d'énergie et en limitant à des échanges de chaleur leurs échanges d'énergie avec l'environnement. On trouvera ici les résultats d'une étude sur la quantité d'énergie nécessaire à la survie des ours et sur l'importance des voies de transfert de chaleur à l'environnement. L'intensité des échanges calorifiques a été mesurée chez deux Ours noirs dans leur repaire. La surface d'une sphéroïde aplatie simulant la forme d'un ours recroquevillé suffit à équilibrer les budgets. À partir de ces données, un système ours–repaire a été construit pour un «animal» de 75 kg, une sphéroïde couverte de fourrure chauffée par électricité et maintenue à 36°C. Les besoins énergétiques et le transport de chaleur à travers la peau et dans le repaire ont été mesurés durant l'hiver; de plus, la consommation d'oxygène a été évaluée chez un ours vivant aux environs, dans un repaire semblable. Au cours d'une période d'hibernation de 145 jours, la perte hypothétique de masse due au catabolisme des graisses chez l'ours simulé se situait entre 24 et 28%, selon que l'entrée était scellée ou ouverte. D'après l'oxygène consommé et en considérant comme constant le contenu hydrique du corps, la perte de masse de l'ours vivant au cours de la même période aurait dû être de 19% si les graisses seules avaient été catabolisées. Cependant, le catabolisme des protéines à la fin de la période d'hibernation a entraîné une augmentation de la perte jusqu'à une valeur de 31%, surtout à cause de l'élimination d'urine. À partir du moment où les protéines sont catabolisées, c'est la déshydratation et non l'inanition qui menace la vie de l'ours.

[Traduit par la revue]

Introduction

Black bears in northeastern Minnesota spend about 6 months each year in a winter den (Rogers 1977a). During the dormancy period, body temperatures range between 31 and 36°C as compared with the summer–active temperatures of 37–39°C (Hock 1957; Nelson et al. 1973; Rogers 1977b; Watts et al. 1981). Metabolic rates at freezing temperatures are about half the typical rate under standard conditions for fasting homeotherms of the same size (Watts et al. 1981). Black bears usually do not eat, drink, urinate, or defecate during the dormancy period. The average mass lost by 18 bears in the wild during the denning period was 23 ± 8% of their fall mass (L. L. Rogers, unpublished data); for 3 bears in captivity the loss was about 25% (Nelson et al. 1973). The amount of mass lost by a

bear depends on the metabolic rate required to maintain a particular deep-body temperature for a given type of fur, den, and weather, and on the type of substrate (ratio of fat to protein) used for metabolism.

For the dormant bear to maintain itself for an extended period, fat must supply the energy for metabolism (Nelson 1980). Should fat reserves be depleted to the extent that protein becomes an energy source, urination occurs, mass loss results, and dehydration becomes life threatening.

The energy requirement for metabolic maintenance is a function of the rate at which heat is transferred from the bear to its surroundings. Determining the heat budget of an organism has been a basic method used by agricultural meteorologists to couple the functioning of plants to their physical environment (Suomi and Tanner 1958). This principle was brought to the

attention of many field biologists for use on animals by D. M. Gates 1962) and has been used as the basis for a series of publications by Gates and others (Bartlett and Gates 1967; Birkebak 1966; Gates 1970; Porter and Gates 1969).

The energy budget of any animal may be written as:

$$\left[\begin{array}{l} \text{Heat produced} \\ \text{by metabolism} \end{array} \right] = \left[\begin{array}{l} \text{Net loss by} \\ \text{radiation} \end{array} \right] + \left[\begin{array}{l} \text{Net loss by sensible heat} \\ \text{transfer through the skin} \\ \text{to the air and ground,} \\ \text{and by breathing} \end{array} \right] \\ + \left[\begin{array}{l} \text{Loss by latent heat} \\ \text{transfer through the} \\ \text{skin and by breathing} \end{array} \right] + \left[\begin{array}{l} \text{Increase in heat} \\ \text{storage within} \\ \text{the body} \end{array} \right]$$

The heat transfer equations associated with each term are reviewed by Birkebak (1966). Because of the engineering difficulties in continuously monitoring all terms, budgets for free-roaming animals under field conditions are nonexistent. The loss of metabolic heat by small birds and mammals has been studied often under controlled laboratory conditions (Birkebak 1966), and hypothetical models have been tested in the field by comparing the predicted and observed behavior of lizards (Bartlett and Gates 1967). However, dormant animals offer the opportunity to directly measure the terms of the energy budget under field conditions. Thorkelson and Maxwell (1974) did this using a simulated model for a denning raccoon.

The objectives of the present study were to (i) measure the heat budget of denning bears in the field; (ii) use that information to construct a simulated bear-den system, and monitor the energy demand and heat budget of the model in the field for a typical winter denning season; and (iii) simultaneously monitor the oxygen consumption and mass loss of a live bear to determine its metabolic rate under similar conditions.

Materials and methods

Initial field study

During the winter of 1971–1972, a field experiment was conducted to measure the heat budget of two radio-collared bears at their selected den sites in Lake County, Minnesota. One bear was a yearling male with a fall mass of 45 kg, which wintered in a secure, earthen den. The other was a 5-year-old female with a fall mass of 72 kg, which selected an open den in a rock-raked windrow (a man-made pile of soil, rock, and slash left after logging). Because the young male moved and dug a new den after the fall weighing, we omitted the results for the first half of the winter for this animal. Both animals were weighed in early January and in mid-March before leaving their dens. The male and female would have lost 30 and 26% of their fall mass, respectively, based on a 180-day denning period. The heat budget measurements were taken in January and March only.

The measurement system consisted of (i) a set of temperature sensors made of fine wire thermocouples to measure the temperature gradient in the fur, air temperature, and den wall surface temperature; (ii) heat flux plates¹ to measure the flow through the den floor in contact with the bear; (iii) a miniature net radiometer² to measure the net radiative loss; (iv) an infrared thermometer³ to determine the effective radiative surface temperatures of the bear and den walls; and (v) a microvoltmeter⁴ to serve as the readout device for the thermocouples and thermopiles. Also required to compute the energy budget were

measurements of the characteristic length of the curled-up bear, den size, air space above the bear, nest thickness, fur thickness, breathing rate, and the fraction of the bear in contact with the ground.

The energy budget (neglecting evaporation of water from the skin and change in heat storage) for a denning bear may be written as follows:

$$[1] \quad M = A_s(\dot{R}_N + \dot{C}) + A_k\dot{K} + C_b + E_b$$

where

M = heat produced from metabolism (W)

\dot{R}_N = flux rate density of net radiation (W/m²)

\dot{C} = flux rate density of convective heat (W/m²)

\dot{K} = conductive heat loss through the nest (W/m²)

C_b = convective heat loss through breathing (W)

E_b = evaporative heat loss through breathing (W)

A_s = surface area of the bear above the nest or "in contact with air" (m²) and

A_k = surface area of the bear in contact with the nest or "in contact with ground" (m²)

In this experiment, M was computed assuming that mass loss was equivalent to fat loss (Nelson 1980); \dot{R}_N and \dot{K} were measured directly; \dot{C} was estimated using measured temperature differences and standard empirical engineering relationships to estimate the convective heat transfer coefficient (Kreith 1959); C_b was estimated by computing the volume of oxygen required to respire the mass of fat consumed (2.0 L of O₂ required for 1 g of fat, assuming 25% of O₂ inhaled is used for respiration) with the exhaled air at deep-body temperature; and E_b was estimated by computing the mass of water from respiration that had to be dissipated if body water content was to remain constant (1 g fat releases 1.1 g H₂O; latent heat of evaporation at 36°C is 575 cal/g H₂O; 1 cal = 4.1868 J).

The factor most difficult to approximate before the study was the total heat transfer area, A_t , from fur to the bear's surroundings ($A_t = A_s + A_k$). This number was left as the unknown quantity in eq. 1 and its magnitude was calculated as that surface area required to balance the energy budget. For the calculation, the fraction of A_t in contact with the nest was estimated visually (0.3 for the yearling male, 0.4 for the 5-year-old female). Then the fractions of A_t and the heat budget data were inserted into eq. 1, and the total transfer area, A_t , was computed.

Model bear-den system

To increase the sampling frequency of metabolic rate and gain better control over the complex convective heat transfer coefficient, a model bear-den system was installed at the Kawishiwi Field Laboratory of the North Central Forest Experiment Station (U.S. Department of Agriculture Forest Service) about 13 km southeast of Ely, Minnesota. The experiment was conducted in a 12 × 25 m forest clearing adjacent to a heated and electrified building that housed the switching, recording, and readout apparatus. A simulated bear and den were placed about 12 m from the building in sandy glacial till.

Using the results of the initial field experiment, we designed an artificial bear in the shape of an oblate spheroid to simulate a denning 75-kg animal (Fig. 1). There is a 1:1 correspondence between the electrical energy required to keep a mass at a constant temperature using a heating coil and the food required for a similar-sized homeotherm's metabolism given the same rate of heat loss (Kleiber 1961; Thorkelson and Maxwell 1974). The transport of heat from the base of the fur (i.e., next to skin) to the surroundings depends on the physical properties of the system and not how the heat is generated. Although transfer coefficients determined in this manner are empirical and therefore a function of the system, they were obtained under field conditions for a typical size and shape of bear and den.

The model bear was constructed by potting 36 individually calibrated (Fuchs and Tanner 1968) heat flux plates, similar to those described by Deacon (1950), in fiber glass with a total thickness of about 0.27 cm. A submersible pump and heating tape were mounted in the liquid-filled model, and a thermostat system supplied power to

¹Middleton and Co., CSIRO model CN3, Port Melbourne, Australia. Mention of trade names does not imply endorsement by the U.S. Department of Agriculture.

²Middleton and Co., Funk model CN6, Port Melbourne, Australia.

³Barnes Engineering, model PRT-10-L, Stamford, CT.

⁴Keithley model 155, Cleveland, OH.

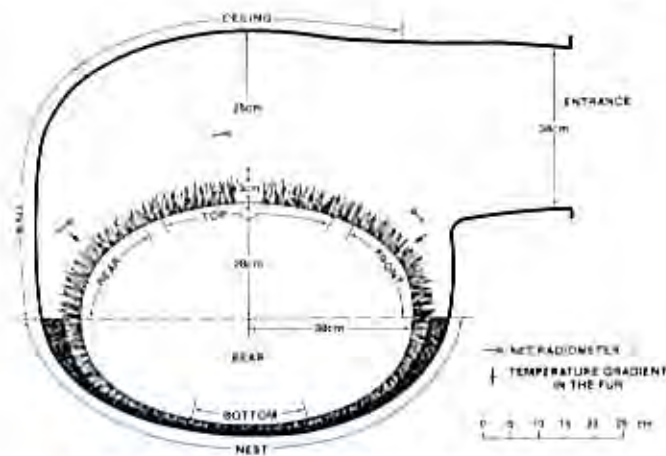


FIG. 1. Geometry of the simulated bear-den system.

maintain a constant deep-body temperature of 36°C. A black bear hide with a skin area of 0.924 m² was attached to the fiber glass. The model was filled with an antifreeze-water mixture to prevent freezing in the event of a power failure, and a high-temperature power cutoff was installed to prevent boiling in case of thermostat failure. The outputs from the heat flux plates were monitored at least twice each week. Because snow covered the den most of the season, more frequent measurements were not necessary.

A den was constructed that surrounded the bear, with a 5-cm nest beneath the "animal" (which compressed to about 1 cm) and a maximum 25-cm air space above the bear. The entrance was cylindrical and about 40 cm in diameter and in length. With a chamber area of 1.91 m², the den contained 20 flux plates that were monitored using the same procedure as with the simulated bear. In the case of the bear, the fiber glass did not affect the heat transfer coefficients through the fur because the model began at the base of the hair. The roughly 1.5°C temperature drop across the fiber glass did affect the rate of energy demand but constituted less than 6% of the thermal resistance through the fur. The fiber glass wall of the den affected the partitioning of heat loss from the bear. Because the thermal conductivity of fiber glass is less than one-half that of soil, the den wall acted as a barrier to heat flow when the entrance was not sealed by snow; this caused a higher proportion of "metabolic" heat to be transferred out through the entrance than would have occurred if the walls had been soil. To minimize this effect, the walls were made as thin as possible (0.18 cm) and at least 15 cm of soil covered the den. The loss by convection and radiation through the entrance was taken as the difference between metabolic heat generated and the flux through the wall.

A portion of the den was in contact with the nest, and the remaining portion was in contact with air in the den. To determine the variation in flux between regions, we partitioned the den into three areas besides the entrance (Fig. 1): (i) the region in contact with the nest, (ii) the wall region above the nest (nearly vertical), and (iii) the ceiling region above the model bear (nearly horizontal).

Three miniature shielded net radiometers (Funk 1962), 1.2 cm in cross section, were mounted about 10 cm above the fur near the den entrance, the ceiling, and the back wall (Fig. 1). Thirty-seven copper-constantan thermocouples were also installed in the model bear and den to determine the temperature field. Absolute temperatures were taken in the bear, in the center of the den floor, in the center of the den ceiling and in nearby soil; temperature differences were taken from these base points. Sensors also monitored deep-body, skin-surface, den air, wall, ceiling, floor, surrounding soil, and outside air temperatures, as well as the temperature gradient through the fur and nest. The temperature gradient through the fur was sampled at two locations: facing the den entrance and facing the back wall. Sensors were mounted on the skin, within 0.5 cm of the skin, at 1-cm intervals through the fur, and in the free stream air above the fur.

The measurement that sums all of the heat losses from the bear initially and then from the den is the electrical power required by the

simulated bear to maintain constant body temperature at a particular level (36°C was used during the field study). This power requirement is analogous to a live bear's metabolic rate, and may be expressed as mass rate of fat catabolized, volume rate of oxygen consumed, or watts (1 W is equivalent to 2.20 g fat respired per day or 4.30 L O₂ consumed per day). We determined the daily power requirement by measuring the amount of time power was supplied to the bear and printing the daily total at midnight.

During the 1973-1974 field season, the pump and heating tape were cycled simultaneously; their power consumption times the percentage of time running gave the energy requirement for the simulated bear. However, because the pump ran only about 20% of the time (e.g., 30 s on, 150 s off) we felt that thermal stratification of the liquid inside the model during the off time was a source of error. The following year we reduced power to the pump and tape, and the pump was run continuously at 44 W. The heating tape, now using 195 W, was cycled by the thermostat and operated between 5 and 15% of the time depending on the weather.

Energy requirement of the live bear

For the 1974-1975 field season, a similar den housing a 2-year-old female was installed inside a 5 × 5 × 2 m cyclone fence enclosure adjacent to the model bear-den system. The metabolic rate of the live bear was determined by the open-system method (Kleiber 1961) using the measured³ steady-state rate of oxygen consumption in the den. The metabolic heat liberated is 4.7 kcal/L O₂ consumed if fat is the substrate used for respiration; protein yields about 4.5 kcal/L O₂. Carbohydrate is disregarded as it constitutes a relatively small percentage of an animal's mass (less than 1% in farm animals; Kleiber 1961). Although the heat liberated per unit volume of oxygen consumed does not differ very much between the respiratory substrates, the heat of combustion per unit mass loss of the animal does: 4.8 kcal/g of protein compared with 9.5 kcal/g of fat (Kleiber 1961). For a given rate of oxygen consumption, the rate of mass lost between substrates can differ by a factor of about two. The oxygen data were recorded at the same time as the heat flux measurements, at least twice a week. The procedure was to seal the den entrance, turn on the pump, and monitor the oxygen concentration in the exhaust air until the system reached steady state; this took from 30 min to 2 h. The system was designed so the oxygen analyzer could be calibrated with outside air (20.9% O₂) and with a calibration gas of 17.2% O₂.

Results

Initial field study

The total transfer area that balanced the heat budget of the denning bears is presented in Table 1. These results were then compared with the outline surface areas computed using the animal's early fall mass (i.e., the typical "bear skin rug" area for a given mass as computed by Kleiber (1961); the area in square metres is 0.1 times the ²/₅ power of mass in kilograms). The two areas differ by a factor of about two. Because a denning bear is curled and forms an approximate oblate spheroid, this geometric surface area was also computed using the field observations of height and diameter of the curled bears. Agreement between the area that balanced the budget and the area of an oblate spheroid was within 2-16%. Using the area that balanced the heat budget equation to determine areas A_s and A_g, the percentages of metabolic heat lost through the various heat transfer mechanisms (eq. 1) are presented in Table 2.

Model bear-den system (1973-1974)

During the winter of 1973-1974, only the simulated bear-den system was operated. The data, presented in Fig. 2, were grouped into analysis periods of about 10 days duration which included three sets of recordings of heat flux and temperature,

³Beckman model OM-11 Oxygen Analyzer, Fullerton, CA.

TABLE 1. A comparison of computed surface areas for a bear and an oblate spheroid

	Total surface area, A_t (m ²)		
	5-yr-old female (72 kg)		1-yr-old male (45 kg)
	Jan. 8	Mar. 11	Mar. 11
Total skin area of a bear using fall mass	1.72	1.72	1.27
Transfer area to balance the heat budget of a curled-up bear	0.91	0.80	0.51
Area of an oblate spheroid simulating a curled-up bear	0.76	0.76	0.52

TABLE 2. Partitioning of metabolic heat in three denning situations

	Heat source = Sum of heat sinks (%) ^a					
	M	$A_s \dot{R}_N$	$A_s \dot{C}$	$A_s \dot{K}$	C_b	E_b
Jan. 8						
5-yr-old female	100	32	8	49	4	7
Mar. 11						
5-yr-old female	100	13	10	65	5	7
1-yr-old male	100	34	10	45	4	7

^a $M = A_s \dot{R}_N = A_s \dot{C} + A_s \dot{K} + C_b + E_b$. See eq. 1 in the text for a description of the terms.

and daily recordings of power consumption ("metabolic heat") and mean daily air temperature at Winton, MN, the closest climatological station (13 km away). The time periods were shortened for analyses 13 and 14 because the system was artificially sealed and less subject to change. Because of equipment malfunction, we are missing data for mid-April.

The values in Fig. 2 dampen the sensitivity of metabolic rate to outside air temperature and degree of entrance closure because they are 10-day averages. Greater extremes may be found when the data are analyzed on a daily basis. For example, during one 5-day period when the entrance was open, daily mean outside air temperature rose from -24 to -3°C , and metabolic rate decreased steadily from 150 to 97 g fat/day, a 35% decrease and equivalent to $2.5 \text{ g fat} \cdot \text{day}^{-1} \cdot ^\circ\text{C}^{-1}$. When the entrance was about two-thirds blocked and daily mean temperature rose from -33 to -18°C over a 4-day period, the metabolic rate decreased from 138 to 118 g fat/day, a 15% decrease and equivalent to $1.33 \text{ g fat} \cdot \text{day}^{-1} \cdot ^\circ\text{C}^{-1}$. Irrespective of outside air temperature, the maximum daily variation in metabolic rate was about 3% when the entrance was sealed by snow and could be as high as 10% after an air hole (5–8 cm in diameter) developed.

Metabolic rates (1974–1975)

During the 1974–1975 field season, a live bear – den system was installed for comparative purposes, and the method of supplying heat to the simulated bear was changed to prevent thermal stratification during the off time.

Figure 3 summarizes the outside and den air temperatures, and metabolic rates of the simulated and live bears over winter, for both periods when the entrance was open and those when it was sealed.

Although the dens of the simulated bear and live bear were identical, the masses of the bears were not. We had hoped to obtain an animal of about 75 kg (the size of the simulated bear), but the animal we obtained weighed only 42 kg at the

beginning of the dormancy period. As a means of comparing the energy requirements of the simulated and live bears, the metabolic data were first normalized to remove the effect of size difference by using the standard relationship discussed by Kleiber (1961):

$$\text{Metabolic rate}/(\text{mass})^{3/4} = 70 \text{ kcal} \cdot \text{day}^{-1} \cdot \text{kg}^{-3/4}$$

Assuming that the heat of combustion of fat is 9.5 kcal/g, the specific metabolic rate for fasting homeotherms under standard conditions^b is $7.37 \text{ g fat} \cdot \text{day}^{-1} \cdot \text{kg}^{-3/4}$. The average mass of the bear was estimated for each analysis period, and the measured metabolic rate per unit mass to the $3/4$ power computed; these data were again normalized by dividing by $7.37 \text{ g fat} \cdot \text{day}^{-1} \cdot \text{kg}^{-3/4}$ to obtain a metabolic rate expressed as a percentage of a fasting homeotherm under standard conditions. These results, as well as those for the model bear, are presented in Fig. 4 as a function of "environmental temperature" with the entrance open.

Heat transport and environmental temperatures

Table 3 presents the effect of location of the fur surface on rate of heat loss from the simulated bear, and how heat was dissipated from the den as a result of entrance opening and outside air temperature. The results for analysis period 3 (A-3) were used to compute the environmental temperature for an open den.

The definition of "environmental temperature" is based on the temperature difference between an animal's surface and its surroundings such that heat loss follows Newton's law of cooling. Because "surroundings" include solid surfaces and fluids at various distances from the animal, the magnitude of this term is more of hypothetical than of practical value; nonetheless the simplicity of a concept operating in a complicated heat transfer situation endears its use. We have taken the environmental temperature for an open-entrance den to be $0.58(\text{den air temperature}) + 0.24(\text{soil temperature}) + 0.18(\text{den wall temperature})$. The "weights" for the temperatures were taken as the fractional heat lost by convection out the den entrance affected by den air temperature (= 0.58 for period A-3), by conduction through the nest driven by soil temperature at 50 cm (= 0.24), and by radiation driven by den wall and ceiling temperatures above the bear (0.12 + 0.06). Because den air mixes with outside air, a line of regression and a coefficient of determination were computed between environmental temperature for an open den and the mean daily air temperature at the Winton station (Fig. 5). These calculations showed that the den was about 4°C colder and that the data are more scattered for the live bear ($R^2 = 0.59$) than for the model ($R^2 = 0.81$)

^bAssumes a resting, fasting, unstressed animal.

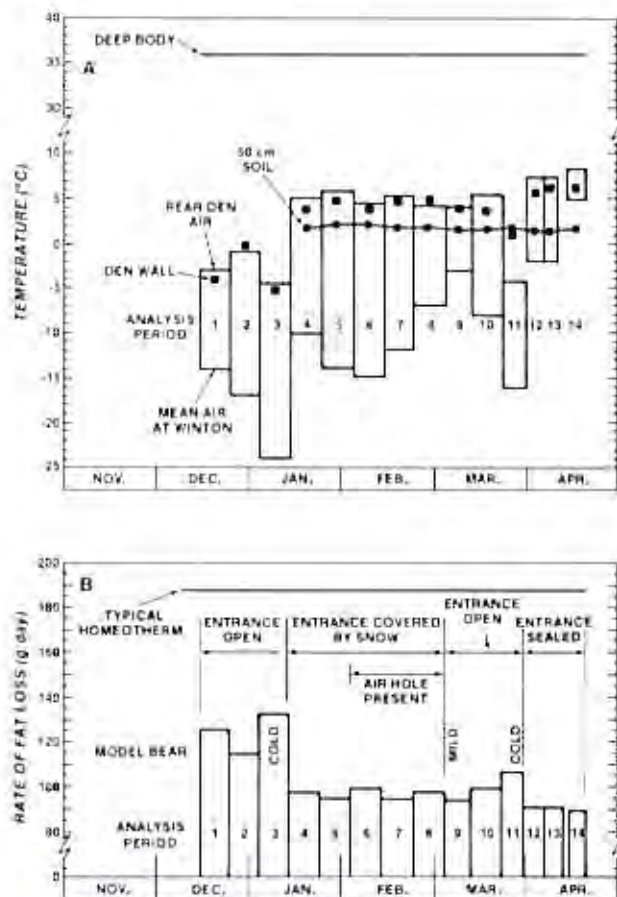


FIG. 2. Temperature distribution and metabolic rate of the simulated bear, 1973–1974. The bars in (A) represent the difference between average air temperature outside and inside the den; the solid squares represent the average den wall surface temperature for the period; the connected solid circles represent the average soil temperature beneath the den. In (B) the height of each bar represents the average electrical power consumption of the model bear converted to rate of mass loss. For the typical homeotherm, metabolic rate equals $70(\text{mass})^{0.75}$ kcal/day, where mass is in kilograms.

because there was a smaller animal in a den of the same size. The colder the outside air temperature, the higher the environmental temperature inside the den was above it. When air temperature at Winton was 0°C , the den for the model bear was about 7°C warmer; when it was -20°C , the den was about 18° warmer.

Discussion

Initial field study

Given the degree of difficulty in taking the field measurements used in the heat budget and the approximations involved in its calculation, the close agreement (within 16%) between the area that balanced the budget and that of an oblate spheroid lends confidence to the assumptions and to the use of a simple geometric shape to approximate a complex surface area.

The pathway of greatest heat loss (Table 2) was by conduction through the ground ($A_g K$). The litter in the bear dens was about 5 cm thick on January 8, but was reduced to less than 2 cm or bare ground by March. As a result, the 49% heat loss in January increased to 65% in March for the 5-year-old bear. The loss by convection ($A_s C$) was low because we assumed free convection only with the den sealed by snow. The sensible

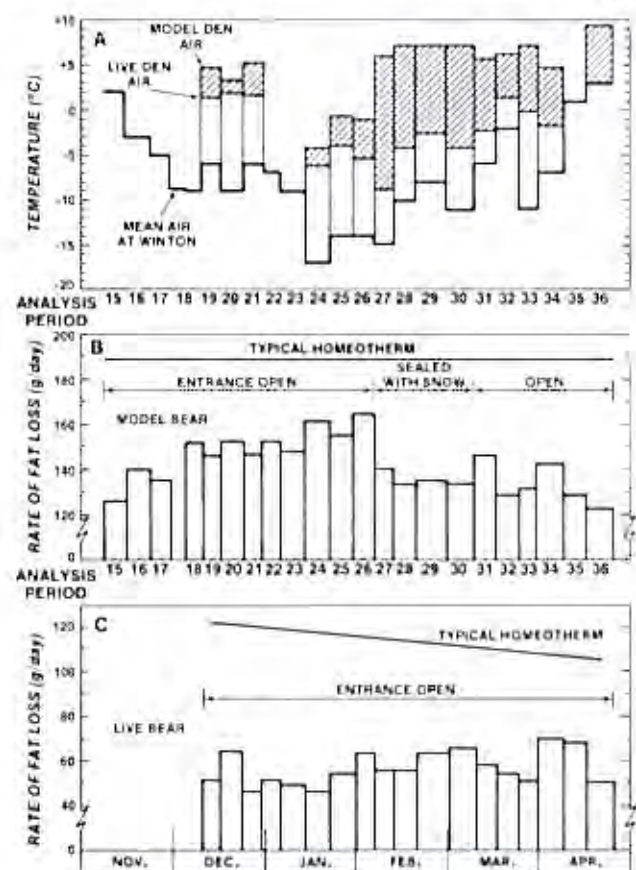


FIG. 3. Air temperature and the metabolic rates of the simulated and live bears, 1974–1975. In (A), the height of each bar represents the average air temperature difference between outside and inside the model bear den; the cross-hatched segments represent the average temperature difference between the model bear and the live bear for den air. In (B) and (C), the height of each bar is the rate of fat loss, converted from average electrical power consumption of the model bear and oxygen consumption of the live bear. For the typical homeotherm in (B) and (C), metabolic rate equals $70(\text{mass})^{0.75}$ kcal/day, where mass is in kilograms.

(C_b) and latent heat (E_b) losses due to breathing, computed using the oxygen requirement and the dissipation of water from respiration, respectively, agree closely with empirical equations used in physiological studies with breathing rate and animal mass as the variables. The assumption that water storage remains nearly constant during dormancy was found to be the case by Nelson et al. (1973). The computed E_b was more than 80% of the maximum loss that could occur if all exhaled air was saturated at deep-body temperature. Because the temperature of exhaled air is probably less than deep-body temperature, these calculations suggest that the problem of dissipating water fast enough to maintain constant body water is greater than the problem of dehydration from lack of drinking.

The metabolic rates determined by the amount of mass lost were means for the periods of approximately 2.5 months preceding the heat budget measurements made in January and March. The assumption that permits combining these data is that the fluxes change relatively slowly with time because of the overlying mantle of soil and snow. More frequent measurements were not taken because of the difficulties with field instrumentation, the problems associated with frequent tranquilization, and our unwillingness to alter the animal's surroundings.

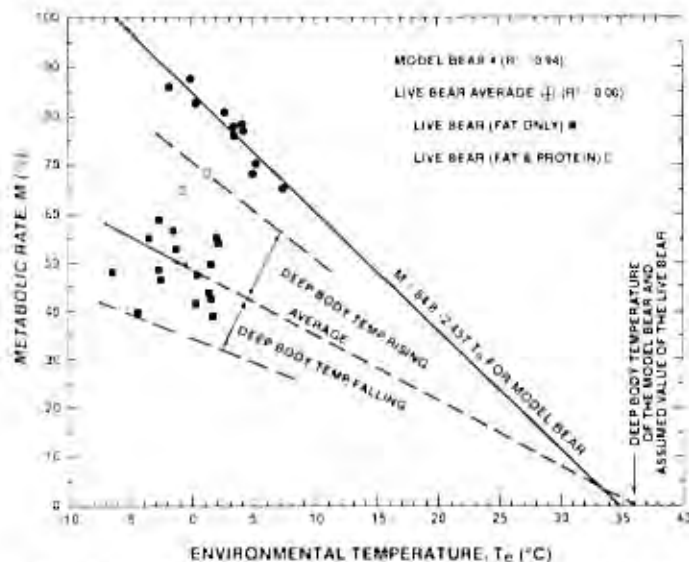


FIG. 4. Metabolic rate expressed as a percentage of that of a fasting homeotherm under standard conditions and as a function of the temperature field of the bear's surroundings.

Model bear—den system (1973–1974)

The air temperature and degree of entrance opening greatly affected the model bear's energy demand (Fig. 2). For analysis period 1 (A-1), the entrance was completely open, the mean daily air temperature was about -14°C , and the energy demand was about 126 g fat/day. This energy demand may be compared with 188 g fat/day, the calculated basal metabolic rate for a fasting homeothermic animal of the same mass under standard conditions (Kleiber 1961). During A-2, the air temperature dropped several degrees, but snow blocked more than half the entrance and decreased the metabolic rate by 10%. During A-3, the weather was colder with no addition of snow, and the metabolic rate increased by 16%.

During A-4 through A-8, the entrance was sealed by snow which decreased the metabolic rate by almost 30% to about 96 g fat/day, irrespective of outside air temperature. When an air hole developed, as almost always occurs with bear dens in the wild, the effect on average metabolic rate was negligible.

During A-9, the weather was mild and the entrance opened slightly, so air temperature again affected energy requirement during A-10 and A-11. For A-12 through A-14, the entrance was sealed with fiber glass insulation to calibrate the system and the metabolic rate decreased to about 90 g fat/day, about 5% less than when the seal was snow.

Metabolic rates (1974–1975)

Simulated bear

The effect of continuous mixing of the liquid in the simulated bear can be seen by comparing its "metabolic rate" in Fig. 2 with that in Fig. 3. With the entrance sealed, the average metabolic rate increased from 95 g fat/day in 1973–1974 to over 130 g fat/day the following year; and when the entrance was open during periods of cold weather, the rate increased from 130 to over 160 g fat/day from one year to the next. The continuous mixing also increased the proportion of the total metabolic heat that passed through the bottom of the bear in contact with the nest. During 1973–1974, an average of 43% of the total flux passed through the nest; in 1974–1975, it increased to 56%.

The stratification in the simulated bear is analogous to the

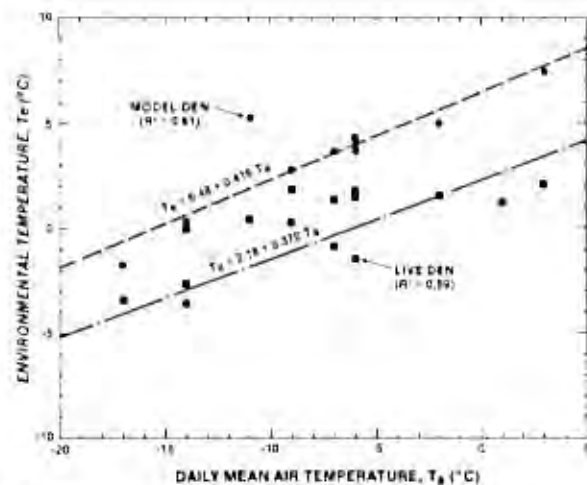


FIG. 5. Environmental temperature in a den with open entrance as a function of daily mean air temperature at Winton, MN.

"hot spots" (e.g., the head) and "cold spots" (e.g., the fat layer of haunches) of live animals. When the pump was off, the liquid in the bottom of the bear was cooler, so less heat was lost through the bottom than would have occurred if the liquid had been mixed well. The result was a reduction in the total energy requirement of the bear. It should be emphasized that a major difference between the simulated bear and a real bear is the uniformity by which internal metabolic heat is supplied to the outer skin. The heat supply in the simulated bear is designed to be uniform so that only the thermal resistances between the skin surface and the den walls limit heat flux through a particular area of interest. The 1974–1975 model bear is a uniform hot spot. In contrast, the cold spot regions of a live bear reduce the rate of heat transfer through an area. Thus, the heat requirement of the simulated bear represents a maximum for a 75-kg animal.

The energy requirement of the simulated bear increased steadily from about 125 g fat/day in late fall to 160 g fat/day over a 30-day period in midwinter when outside air temperature averaged -15°C (Fig. 3). The entrance was kept open to coincide with the open entrance of the live animal. In February the entrance was sealed with snow (A-27 through A-30) to offer a contrast with the open-den data. During that period, mass loss was 135 g/day, a decrease of 15% from the previous 30-day period with the entrance open. Extended to a 180-day denning period, the simulated bear would have lost 35% of its mass if the entrance had been open all winter, and 30% if the entrance had been sealed with snow. These data may be compared with a range of 15–30%, averaging 23%, for 18 bears in the wild (L. L. Rogers, unpublished data), and 26% for the 72-kg bear used in our initial field study.

In Fig. 4, the data from the model bear data illustrate the thermostatic heat requirement for a constant deep-body temperature of 36°C . Linear regression ($M = 84.81 - 2.457T_e$) yields a metabolic rate, M , of $100\% \pm 3\%$ (1 SD) of a typical homeotherm under standard conditions when the environmental temperature around the bear, T_e , is -6°C ; the rate declines to 85% at 0°C , and to 65% at 7.5°C , the warmest temperature recorded. Ideally, the extrapolation of the line of decreasing metabolism with increasing environmental temperature (when below the critical temperature of thermal neutrality) passes through the deep-body temperature of the animal at zero metabolism; that is, if no heat is being produced, the mass

TABLE 3. Partitioning of the heat transport from the simulated bear

	Den open		Den closed	
	-24°C*	-8°C*	Sealed with snow	Sealed but vapor hole present
	(from A-3)	(from A-10)	(from A-4)	(from A-6)
Bear				
Metabolic rate, <i>M</i> (W)	59.7	44.5	44.1	44.4
Loss through top half of bear in contact with air (% of <i>M</i>)	64	56	57	58
Loss through bottom half of bear in contact with nest (% of <i>M</i>)	36	44	43	42
Den				
Loss through nest to ground (% of <i>M</i>)	24	33	37	34
Loss through nest to den air (% of <i>M</i>)	12	11	6	8
Loss through walls (% of <i>M</i>)	12	34	45	28
Loss through ceiling (% of <i>M</i>)	6	10	12	8
Loss out of entrance (% of <i>M</i>)	58	23	6	30

*Mean outside air temperature.

takes on the temperature of its surroundings. In this case the extrapolation is to 34.5°C, only 1.5°C away from the actual deep-body temperature. These data represent a maximum energy requirement for a curled-up bear in a secure den with an open entrance, and illustrate the reduced energy demand of dormant black bears relative to most homeotherms.

Live bear

In Fig. 4, the metabolic data for the live bear are scattered ($R^2 = 0.00$) below those of the model ($R^2 = 0.94$). The degree of scatter masks the linear relationship between metabolic rate and environmental temperature found with the model bear, because the model bear had no change in heat storage over time since it had a constant and uniform deep-body temperature. In comparison, the heat supply of the live bear was sporadic and variable, primarily as a result of the degree of shivering, and was unevenly distributed. Because of the high heat capacity of the bear (32 kcal/°C assuming 70% water and a dry-matter specific heat of 0.4 cal/g°C), a change of 0.5°C in its average internal temperature over a 2-h measurement period of oxygen consumption would cause the maximum displacement from the average metabolic rate when extended to a 24-h period. The average percent metabolism of the live bear over its 145-day denning period was 50% (55 g fat/day) at an average environmental temperature of -0.9°C. Assuming an average deep-body temperature of 36°C (a typical value for denning bears and the temperature of the model), the average percent metabolism for other environmental temperatures may be estimated by the line through these two points as shown in Fig. 4. For metabolic rates above the average, deep-body temperature rises during the measurement period; for rates below, the temperature falls. (Regrettably, deep-body temperature was not monitored continuously.) In the case of the greatest displacement above the average (67% *M* at 1.2°C), 65 g fat/day was measured by oxygen consumption, of which 20 units of heat went into storage, causing body temperature to rise, and 45

units of heat were transferred to the bear's surroundings. In the case of greatest displacement below the average (39% *M* at -4.5°C), the measured rate was 45 g fat/day but body temperature was falling and storage released 18 units; as a result, 63 units were transferred to the bear's surrounding.

Watts et al. (1981) monitored the metabolism and deep-body temperature of a bear averaging 74 kg over a 128-day denning period. Metabolism relative to a fasting homeotherm (under standard conditions) ranged from 22 to 70%, and averaged 37% over a range of deep-body (abdominal cavity) temperatures between 32 and 36°C, averaging 35°C. The den in this case was a metal cylindrical chamber, 0.9 m (diam.) × 1.5 m, and the den air temperature ranged from 1 to -17°C. The average body temperature probably was lower than the 35°C of the abdominal cavity because of the resistance to heat flow between the metabolic sources and the skin. The causes of resistance would be reduced circulation and fat layers in the peripheral regions of the animal. The effect of internal thermal resistance is considerable because the metal den itself is a much better conductor than the model den, and the average air temperature was about 12°C colder; yet the metabolic rate averaged only 37% of the typical homeotherm, compared with more than 75% for the simulated bear of the same size.

On a 180-day basis, the bear studied by Watts and co-workers would have lost about 21% of its fall mass using their predictive mass loss equation (Watts et al. 1981). This is comparable to the 23% average loss found by Rogers but much less than the more than 30% "mass loss" of the simulated bear. Again, the data for the simulated bear represent a maximum energy requirement for the environmental conditions at hand.

It is presumed that bears catabolize fat as their main energy source during dormancy, that they do not urinate or defecate, and that their body water storage is constant, as was found by Nelson et al. (1973). Using these assumptions and the measured oxygen consumed, the metabolic rate averaged 55 g fat/day, which would be a total loss of 7.97 kg (19%) over the

145-day measurement period. However, the actual mass lost by the live bear was 13.1 kg (31%), and it did urinate. Therefore, the bear did not have sufficient fat available for catabolism and additional protein was required as an energy source. When protein catabolism exceeded the bear's ability to recycle urea back into protein (Nelson et al. 1983), urination occurred.

The rate of oxygen consumption over the denning period is presented in Fig. 3 using the equivalent units of grams of fat per day. Then the rate of energy demand is also the mass lost per day if fat is the substrate for catabolism. From early December through March this assumption was essentially the case as the bear did not urinate or defecate. Mass loss ranged from 45 g/day in late December to 63 g/day in early March. During the remainder of March, metabolic rate steadily decreased to 54 g/day, the average for the initial 114 days of denning.

On March 29, an arctic air mass moved into the area and daily minimum temperature fell 23°C to -28°C on March 31. Cold temperatures persisted throughout the 1st week of April. From April 1 to 15, the bear excreted urine and some fecal material in the den entrance, and oxygen consumption increased by 34%. Nelson et al. (1983) have found that protein is continuously broken down during denning, but the nitrogen from urea is immediately recycled back into plasma proteins. As a result, mass loss is restricted to fat loss. We presume that during the period the bear urinated, its reduced fat reserves could not provide for the energy demand, additional protein was catabolized, exceeding the bear's ability to recycle urea nitrogen, urination resulted, and mass loss escalated from 54 to 409 g/day. The latter value was computed using an average of 20 g urea/L urine (Nelson et al. 1973). Given 0.16 g N/g protein, 17 g of urine (with water from storage) are eliminated per gram of protein catabolized. However, water storage is affected by protein catabolism in two other ways: protein catabolism produces 0.7 g H₂O/g less than fat catabolism,⁷ and lean body mass is about 75% water⁸ such that 1 g of protein releases an additional 3 g of water that fat does not. Assuming that the extra water released by protein is used internally to replace the catabolic water deficit and minimize the water lost by urination because of urea formation, the net water storage decrease (and mass lost by the bear) becomes 14.7 g H₂O/g protein catabolized. From April 1 to 15, 2010 L O₂ were consumed and the mass of the bear decreased by 6.1 kg. The mass loss was estimated by using fat as the only catabolic substrate before and after that period. In terms of energy demand, the oxygen consumption represents 995 g of fat or 1884 g of protein. To determine the fraction of each, a mass budget may be written as:

$$(995 \text{ g} \times f_f) + (1884 \text{ g} \times f_p \times (1 + 14.7 \text{ g H}_2\text{O/g protein})) = 6100 \text{ g}$$

and

$$f_f + f_p = 1$$

where f_f and f_p are the fractions of catabolic substrate that are fat and protein, respectively. These equations yield $f_f = 82\%$ and $f_p = 18\%$. The mass lost during the 15-day period aver-

⁷One gram of fat produces 1.1 g of water; 1 g of protein produces 0.4 g of water (Nelson 1973).

⁸Assuming muscle water concentration is similar to blood cell water concentration (Nelson et al. 1973).

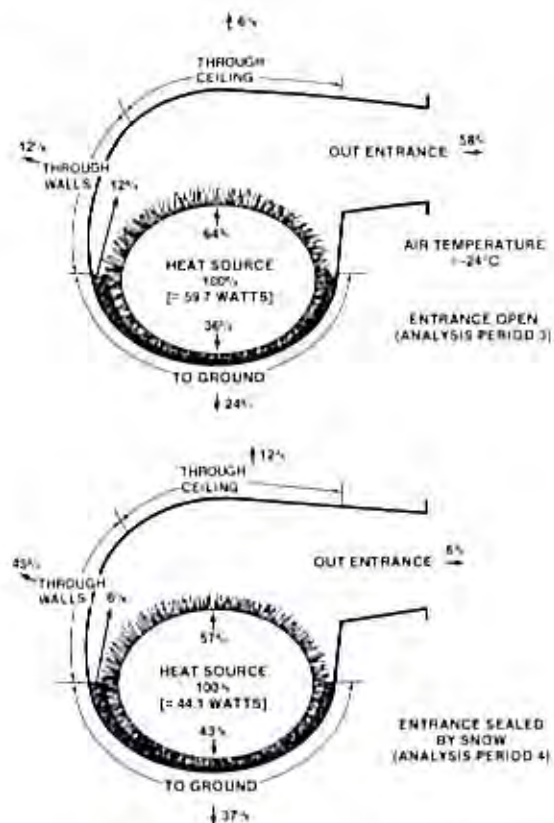


Fig. 6. Heat budget of open and sealed simulated bear-den systems.

aged 54 g fat/day, 23 g protein/day, and 332 g/day of net H₂O storage decrease.

The key point is that once fat reserves have been sufficiently reduced to cause net protein catabolism, urination causes mass loss to cascade, and dehydration, not starvation, is the problem. Kangaroo rats can survive indefinitely on their dry natural diet without an external supply of water (Schmidt-Nielsen et al. 1948). However, when they were given a soybean (40% protein) diet, extra water for urine was required, death occurred in 2–3 weeks, and the mass loss was about 34%. The bear lost 31% of its fall mass during the entire denning period. Using urine concentrations for bears, 41% of the loss was the result of protein catabolism causing water storage to decrease by about 20% in 15 days.

Partitioning the heat transport

Besides determining metabolic heat requirement, a primary reason for building the simulated bear was to determine the magnitude of the heat transfer pathways from the animal as a function of entrance opening and outside weather (Table 3). The greatest difference in rate of heat loss between the top half of the bear in contact with air and the bottom half in contact with the nest occurred, as would be expected, when the den entrance was open with the coldest outside temperatures: 64% of the metabolic heat went through the top and 36% through the bottom. The results for the other times show little variability. The 24–37% loss of metabolic heat through the nest to the ground from the simulated bear may be compared with the 45–65% loss for bears in the wild (Table 2). The causal factor is a uniform, fluffy nest of leaves and small twigs (at least 5 cm thick) for the simulated bear, compared with a thin nest and

bare ground for the wild bear. In other words, the loss through the nest of the simulated bear represents a minimum amount.

Another difference between the simulated and live bears is the neglect of heat loss by breathing in the model. About 11% of a live animal's heat is lost through breathing. This pathway is not present in the model; if it were, heat loss through the skin would be reduced.

The effect of opening the entrance on the heat budget of the den is considerable. Natural sealing of the entrance by snow decreased the flux out the entrance from 58 to 6% of the metabolic heat produced, and decreased the energy requirement of the bear by 27% (Fig. 6). With the entrance pathway removed, the percent of metabolic flux through the ceiling doubled and through the walls, quadrupled, and the percentage of metabolic heat lost from the nest to the ground increased by more than 50%. When the vapor hole formed, metabolic heat lost out the entrance increased from 6 to 30%.

In conclusion, the determination of the transfer coefficients necessary to compute the heat budget of a denning bear can only be obtained through a simulated model; however, the results are only as good as the degree to which simulation represents the actual situation. A simulated bear-den system can remain stationary, permit careful measurement of variables, provide the opportunity for manipulation and control of variables, provide symmetry for averaging, permit repetition of the experiment, and yield quantitative results for heat transfer pathways. It cannot build a "natural" nest, breathe, sweat, and urinate, and supply metabolic heat to the skin with the same inefficiency and variability of a live animal.

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BARTLETT, P. N., and GATES, D. M. 1967. The energy budget of a lizard on a tree trunk. *Ecology*, **48**: 315-322.

- BIRKEBAK, R. C. 1966. Heat transfer in biological systems. *Int. Rev. Gen. Exp. Zool.* **2**: 269-344.
- DEACON, E. L. 1950. The measurement and recording of the heat flux into the soil. *Q. J. R. Meteorol. Soc.* **76**: 479-483.
- FUCHS, M., and TANNER, C. B. 1968. Calibration and field test of soil heat flux plates. *Soil Sci. Soc. Am. Proc.* **32**: 326-328.
- FUNK, J. P. 1962. A net radiometer designed for optimum field sensitivity and a ribbon thermopile used in a miniaturized version. *J. Geophys. Res.* **67**: 2753-2760.
- GATES, D. M. 1962. Energy exchange in the biosphere. Harper and Row, New York.
- . 1970. Animal climates (where animals must live). *Environ. Res.* **3**: 132-144.
- HOCK, R. J. 1957. Metabolic rates and rectal temperatures of active and "hibernating" black bears. *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **16**: 440.
- KLEIBER, M. 1961. *The fire of life*. John Wiley & Sons, New York.
- KREITH, F. 1959. Principles of heat transfer. International Textbook, Scranton.
- NELSON, R. A. 1973. Winter sleep in the black bear, a physiologic and metabolic marvel. *Mayo Clin. Proc.* **48**: 733-737.
- . 1980. Protein and fat metabolism in hibernating bears. *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **39**: 2955-2958.
- NELSON, R. A., WAHNER, H. W., JONES, J. D., ELLEFSON, R. D., and ZOLLMAN, P. E. 1973. Metabolism of bears before, during, and after winter sleep. *Am. J. Physiol.* **224**: 491-496.
- NELSON, R. A., STEIGER, D. L., and BECK, T. D. I. 1983. Neuroendocrine and metabolic interactions in the hibernating black bear. *Acta Zool. Fenn.* **174**: 137-141.
- PORTER, W. P., and GATES, D. M. 1969. Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* **39**: 227-244.
- ROGERS, L. 1977a. Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. Ph.D. thesis, University of Minnesota, Minneapolis.
- . 1977b. The ubiquitous American black bear. In *North American big game*. Edited by W. H. Nesbitt and J. S. Parker. The Boone and Crockett Club and National Rifle Association, Washington, DC, pp. 28-33.
- SCHMIDT-NIELSEN, K., SCHMIDT-NIELSEN, B., and BROKAW, A. 1948. Urea excretion in desert rodents exposed to high protein diets. *J. Cell. Comp. Physiol.* **32**: 361-379.
- SUOMI, V. E., and TANNER, C. B. 1958. Evapotranspiration estimates from heat budget measurements over a field crop. *Trans. Am. Geophys. Union*, **39**: 298-304.
- THORKELOSON, J., and MAXWELL, R. K. 1974. Design and testing of a heat transfer model of a raccoon (*Procyon lotor*) in a closed tree den. *Ecology*, **55**: 29-39.
- WATTS, P. D., ORITSLAND, N. A., JONKEL, C., and RONALD, K. 1981. Mammalian hibernation and the oxygen consumption of a denning black bear (*Ursus americanus*). *Comp. Biochem. Physiol.* **A**, **69**: 121-123.