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ABSTRACT.—Thermal energetics for shrews, weasels, and lemmings from arctic environments were evaluated by using physical and physiological energy exchange data in an energy budget equation. This approach allowed quantification of the effects of different temperature and radiative and convective regimes on metabolic heat production requirements. Tests of the predictive accuracy of the technique were carried out by placing fur-covered, internally heated metal casts of the animals in natural settings and comparing predicted with actual power input requirements. Test results were good, confirming the accuracy of the energy budget model. Thermoregulatory energy requirements were computed for small mammals in several microclimate regimes typical of the Alaskan North Slope region. Estimations were also made of daily and yearly metabolic expenditures by integrating energy budget information with climatic data and the behavior patterns of the animals. The energy requirements of these animals are high throughout the year, but differ significantly between the various available microhabitats. Maintenance of a positive energy balance depends heavily on efficient foraging strategies, selection of the most energetically favorable microhabitats, and the use of winter nests.

The bioenergetic problems of small mammals living in arctic environments have been of considerable interest to ecologists and physiologists. Metabolic and thermoregulatory adaptations to cold climates have been intensively studied since the early work of Scholander et al. (1950). Unfortunately, many of these studies could not fully take into account the effects of wind, radiation, sky conditions, and other thermal factors aside from ambient air temperature. Techniques are now available that simplify the evaluation of all important avenues of energy exchange (Porter and Gates, 1969; Bakken, 1976; Campbell, 1977; Robinson et al., 1976). Through these approaches, the thermal significance of any one adaptation to stressful environmental conditions can be assessed, the effects of changes in important climatic parameters other than temperature may be determined quantitatively, and the energetic costs of survival in natural environmental settings can be estimated.

This paper utilizes a total energy budget approach to the bioenergetics of arctic weasels, lemmings, and shrews. All of these animals are active throughout the year. They must maintain high body temperatures in severe winter conditions, despite small size and relatively poor insulation. Lemmings are important primary consumers in many tundra habitats, and weasels are major predators on lemmings. A thorough understanding of the energetics of these species is crucial for evaluating many aspects of the dynamics of arctic ecosystems.

MATERIALS AND METHODS

Five species of small mammals collected from the North Slope of Alaska were used in this study: ermine (*Mustela erminea*), least weasel (*Mustela nivalis*), masked shrew (*Sorex cinereus*), brown lemming (*Lemmus sibiricus*), and varying lemming (*Dicrostonyx torquatus*). Specimens were prepared for experimentation as fur-covered, internally heated metal casts (Morrison and Tietz, 1957; Heller, 1972). This technique allowed measurements to be made directly under thermal steady-state conditions. The construction and use of the casts to derive basic data on physical energy exchange parameters (insulation, surface areas, radiation surface areas, and convection coefficients) are fully described by Chappell (1980). In addition to the solid casts, several fur-covered hollow copper casts were also fabricated as described in Bakken and Gates (1975). These were used to measure the effective environmental temperature, which is functionally an

TABLE 1.—*Physical energy exchange parameters. A = surface area, I = pelt insulation, C is a multiplicative factor correcting for conductance differences between live animals and casts, ABS = pelt absorptivity, h_c = convection coefficient, sp = summer pelage, wp = winter pelage.*

Species	$A^{1,2}$	$Isp^{1,3}$	$Iwp^{1,3}$	Csp	Cwp	ABSsp	ABSsp	$h_c^{1,4}$ V = 0.1	$h_c^{1,4}$ V = 1.0
Ermine	0.0270	70	70	1	1	0.75	0.3–0.4	0.0028	0.0062
Least weasel female	0.0130	53	53	1	1	0.75	0.3–0.4	0.0068	0.0095
Masked shrew	0.0026	60	60	1	1	0.8	0.8	0.007	0.014
Varying lemming	0.0185	109	133	1.3	1.9	0.75	0.45	0.0037	0.0060
Brown lemming	0.0170	98	119	1.3	1.9	0.8	0.8	0.0039	0.0064
Brown lemming (6 g neonate)	0.0037	62	62	1.5	1.5	0.8	0.8	0.0049	0.0084

[1] Values from Chappell (1980). [2](m^2); [3]$[(m^2 \ °C)/kW]$; [4]$[kW/(m^2 \ °C)]$.

integration of the effects of wind, solar radiation, and ambient temperature (Morhardt and Gates, 1974; Bakken, 1976). Physiological data on body temperatures, metabolic rates, and rates of evaporative water loss were obtained from the literature (Tables 1 and 2). When necessary data were not available, reasonable estimates were used, based on knowledge of similar species. Appropriate derivations of the metabolic variables are discussed under Results.

Most calculations were based on an energy budget equation (Porter and Gates, 1969) which contains terms for the important pathways of heat flow to and from an organism:

$$Q_{abs} + M - \lambda E = \epsilon \sigma (T_r^4) + h_c(T_r - T_a) + C + W + S \qquad (1)$$

where Q_{abs} is absorbed radiation, M is metabolic heat production, ϵ is pelt emissivity, σ is the Stephan-Boltzmann constant, T_r is pelage surface temperature (K), h_c is the convection coefficient, T_a is ambient temperature, λE is evaporative water loss, C is conduction to the ground, W is work, and S is the rate of energy storage. In most situations, C, W, and S are unimportant and can be deleted. All terms are expressed in surface-area specific units for convenience of calcuations. Surface temperature (T_r) can be expressed as a function of body temperature (T_b) and insulation (I):

$$T_r = T_b - I(M - \lambda E). \qquad (2)$$

Insulation varies somewhat with incident radiation and with wind speed (Cena and Monteith, 1975; Robinson et al., 1976; Walsberg et al., 1978; Chappell, 1980). For these calculations, it was assumed that I decreased by 10% at high wind speeds (>5 m s^{-1}) for shrews and weasels, and by 20% for the longer-furred lemmings (Chappell, 1980). The overall thermal conductances of casts are not necessarily equivalent to those of live animals, as casts cannot duplicate the effects of peripheral cooling, piloerection, or vascular adjustments. However, casts will respond pro-

TABLE 2.—*Physiological parameters used in energy budget predictions. Sources: 1) Casey and Casey, 1979; 2) Casey et al., 1979; 3) Withers et al., 1979; 4) Brown and Lasiewski, 1972; 5) Scholander et al., 1950; 6) Folk et al., 1977; 7) Moors, 1977; 8) Morrison et al., 1959; 9) Porter and Gates, 1969; 10) Coady, 1975; 11) Peterson et al., 1976; 12) Hart and Heroux, 1955.*

Species	T_b °C normal	T_b °C min.	BMR (KW m^{-2})	EWL (% MR)	Sources
Ermine	37.5	36.5	0.056	10	1, 2, 3, 4, 6, 7
Least weasel	37.5	36.5	0.050	10	same as above
Masked shrew	38.0	37.5	0.093	10	8, 9
Varying lemming	37.5	37.0	0.038	5	2, 3, 5, 12
Brown lemming	37.5	37.0	0.038	5	2, 3, 10, 11
Brown lemming (6 g neonate)	37.5	37.0	0.032	5	same as above

portionally to wind and radiation, and cast readings can be equilibrated for live animals with a simple correction factor (G. S. Bakken, in litt.). This was obtained by comparing thermal conductances of casts to those of living animals (published in the literature), and applied (when necessary) to the insulation parameter of Eq. 2 (Table 1). An additional correction is necessary to account for surface area differences between live animals (in curled posture) and casts (usually in extended posture). This was accomplished by multiplying the calculated conductance by the value: (curled area)/(extended area) when making these calculations.

Incident radiation intensities were measured at ground level with a silicon-cell pyranometer. This instrument was used to estimate changes in radiation flux during test runs; it does not give correct values for absorbed radiation on the curved, multicolored surfaces of animals. An estimation of Q_{abs} for cylinders of different absorptivities as a function of air temperature is given by Porter and Gates (1969). Minimum Q_{abs} occurs at night when the sky is clear. Blackbody conditions occur inside cavities or when the sky is overcast and cloud temperature approximates near-ground air temperature. Maximum Q_{abs} occurs in full sunlight, and is determined by the average short-wave absorptivity of the integument. Pelage absorptivities were obtained from the literature (*Sorex*—Porter and Gates, 1969), or measured on an integrating spectrophotometer (Table 1).

Tests of energy budget predictions were conducted by placing casts in the natural tundra environment, measuring microclimate conditions, heating the cast until a constant internal cast temperature (T_c) was attained, and comparing predicted power requirements with the actual power supplied to the cast (uncorrected I values were used for this calculation). Tests were carried out under four basic microenvironmental conditions: inside snow caves, on the snow surface on clear nights, on the snow surface on clear days, and on the summer tundra surface on clear days. Measurements attempted on partly cloudy days were not successful because incident radiation tended to change faster than the casts could equilibrate. Radiation intensities on heavily overcast days (the most common sky condition during the summer) were similar to blackbody levels.

The casts were placed on small pieces of styrofoam to insulate them from wet soil surface (in live animals only the feet would touch the ground). Soil or snow surface, air, and internal cast temperatures were monitored on a portable thermocouple thermometer. Power was supplied to cast heaters through a digital power supply with volt-amp readouts (heat lost through cable resistances was taken into account). A hand-held anemometer (Florite) capable of readings at wind speeds above about 0.7 m s^{-1} measured wind velocity (V) near the ground and at 1 m above the surface. When near-ground V was below the minimum resolution of the anemometer, it was calculated from the 1-m measurements (which were almost always >1 m s^{-1}) using the boundary-layer data in Coyne and Kelley (1975). In preliminary trials the casts were oriented facing into the wind. However, in practice, wind orientation seemed to make little difference to the energy balance (Mitchell, 1976). Therefore, during experiments, the long axes of the casts were oriented perpendicular to incoming solar radiation (if present). In all test conditions except snow caves, the calculated convective heat loss was increased by 50% to account for the effects of turbulence (Nobel, 1974; Mitchell, 1976).

Because of the probable importance of nests to these animals (MacLean et al., 1974; Casey, in litt.), the insulative value of nests was estimated in a simple manner. Casts were placed in typical lemming nests found on the tundra, or in artificial cotton nests, and the nest and cast were placed in a temperature controlled chamber. The power necessary to maintain normal T_b at typical subnivian winter T_a's was then compared to that needed without the nest. All nests (real and artificial) were 15 to 20 cm in diameter (as described in MacLean et al., 1974).

Estimation of daily, monthly, and yearly energy requirements were derived from the physical and physiological energy exchange data and from information on local microclimates. General meteorological data were obtained from the U.S. Environmental Data Service (1977 Local Climatological Data: annual summary with comparative data, Barrow, Alaska). Ground temperatures for a nearly average year came from Kelley and Weaver (1969). For all above-ground calculations a wind speed of 1 m s^{-1} was used, because this is close to the average near-ground air velocity near Barrow (Coyne and Kelley, 1975). The amount of ground-surface shade during the summer was estimated from transects. On sunny days the proportion of a 10-m transect line covering shaded ground was measured hourly, and the hourly readings were averaged. This was done in mid-month for May through September. Shading is caused by tundra vegetation; snow cover reduces surface shade to nil in the winter months. Blackbody conditions were assumed for shade

TABLE 3.—*Field tests of energy exchange predictions. Microclimate types are abbreviated as SC (snow cave), SSS (snow surface in sunlight), SSN (snow surface on a clear night), and TSS (summer tundra surface in sunlight). Wp = winter pelage, Sp = summer pelage.*

Cast	Microclimate type	V (m s⁻¹)	T_a (°C)	T_b (°C)	Predicted power (W)	Actual power (W)	% error
Least weasel F2	SC	0.1	−8.0	36.8	3.09	3.23	−4
(40 g, sp)	SSS	1.4	−7.2	39.4	4.01	3.90	+3
	TSS	1.3	16.3	37.8	1.20	1.24	−3
	SSN	0.2	−24.6	37.0	4.93	5.11	−4
Ermine F1	SSN	0.2	−25.0	37.0	7.94	7.55	+5
(131 g, sp)	TSS	0.3	3.4	38.8	2.91	3.04	−4
	SC	0.1	−6.7	37.4	4.53	4.90	−7
	SSS	1.0	−9.2	36.9	5.32	5.59	−5
Masked shrew 2	SSN	0.2	−24.5	37.0	1.07	1.03	+3
(3.7 g, wp)	TSS	0.7	7.8	37.7	0.38	0.4	−6
	SC	0.1	−11.4	37.9	0.75	0.83	−10
Varying lemming W2	SC	0.1	−5.3	37.1	2.34	2.09	+12
(52 g, wp)	SSS	1.3	−5.8	40.4	2.52	2.36	+7
	TSS	0.2	21.4	44.7	0.83	0.8	+3
	SSN	0.4	−25.0	37.0	4.32	4.15	+4
Brown lemming W2	SSN	0.2	−24.0	37.0	2.63	2.46	+7
(37 g, wp)	TSS	0.3	5.8	42.9	0.77	0.70	+10
	SC	0.1	−5.3	37.5	2.34	2.09	+12
Brown lemming B	TSS	0.8	11.2	38.3	0.28	0.25	+11
(6 g)	SC	0.1	−7.8	38.0	0.85	0.78	+10

or periods of overcast skies. The physical, physiological, and microclimate data were used in the energy budget equation to predict the cost of thermoregulation for each set of conditions (here, I values were corrected for conductance differences between casts and live animals).

The energy budget predictions for costs in various microclimates were then integrated with information on activity levels and behavior of the animals. Derivation of behavioral data is explained in more detail under Discussion. All calculations were done on a monthly basis, assuming constant conditions during the month. Each environmental variable was treated independently; for example, the proportion of time spent in sunlight during a given month would be calculated as:

(percent of total time active) × (percent of activity time spent above surface) × (percent of time during month the sun is above the horizon) × (percent of time in month sky is clear) × (percent of ground surface shaded).

The cost of locomotory activity was assumed to be 3 times the basal metabolic rate; this cost was added to thermoregulatory energy requirements for those times the animals were active (Hart, 1971; Wunder, 1970; W. Karasov, pers. comm.).

RESULTS

Correction factors for differences in thermal conductance between live animals and casts were necessary only for lemmings; there was little or no difference in weasels and shrews. Live lemmings in winter pelage have thermal conductances about one-half as large as those measured from casts (Scholander et al., 1950; Casey et al., 1979). The conductance of summer animals is about 20–30% less than that of casts (Hart and Heroux, 1955). The long fur of lemmings apparently requires careful grooming and pilomotor control to reach maximum insulative value; adjustments that are difficult for the experimenter to duplicate.

Results from field-testing of the energy budget parameters are shown in Table 3. Because of space limitations and for convenience of presentation, data are shown for
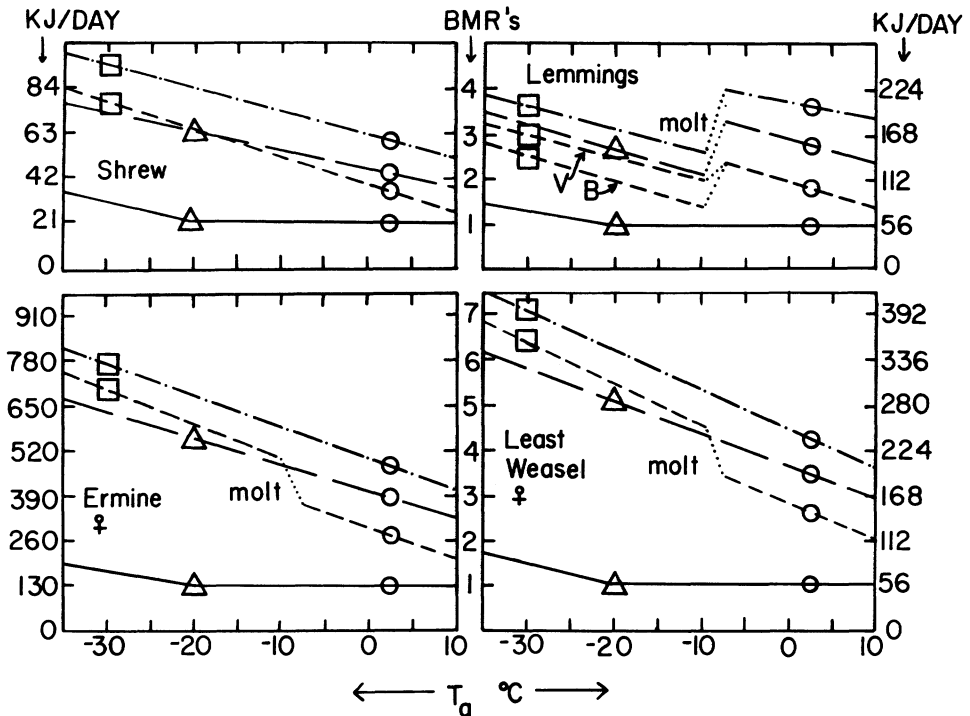
FIG. 1.—Costs of thermoregulation in representative microhabitats for masked shrews, least weasels, ermines, and lemmings. Costs are given in absolute units (KJ/day) and as relative increases above BMR. Solid line = nest, short dashes = surface in sunlight, long dashes = burrow or subnivian space, and dashes + dots = surface on a clear night. Average winter temperatures are indicated by triangles for subnivian microhabitats and squares for the surface; average summer temperatures are indicated by circles. For lemmings, "B" and "V" denote brown and varying lemming, respectively. Dotted lines indicate pelage changes (color and/or insulation) caused by molting. The T_a is an average value; this axis can be converted into approximate time of year by consulting Table 4.

only six casts (a small portion of the tests). Whenever possible, several (up to four) tests were run for each cast in each microclimate on different days. The results in Table 3 are runs that yielded errors of estimation that were about average for the cast in question; i.e., if four runs of a particular cast in a particular microclimate had average errors of 5%, the run with an error closest to 5% was chosen for use in the table. The average error of estimation from acceptable runs of all casts in all conditions was 6.3% (n = 72; SD= 4.3%; maximum error 18.6%). There was no perceptible tendency for larger errors in any one microclimate condition, but estimates tended to be less accurate at higher wind speeds, perhaps because there was more gusting at high than at low V. In short-furred casts (weasels, shrews) there was no tendency to either over- or underestimate power requirements (19 overestimates, 22 underestimates). In the longer-furred lemmings there was a trend towards overestimation (24 of 31 runs), but the overestimates were slight in most cases.

Tests of the insulative value of lemming nests were run at ambient temperatures of −20 and −35°C to simulate both average subnivian T_a's during the coldest month, and also the worst conditions likely to be encountered (MacLean et al., 1974). With

TABLE 4.—*Weather data for the Barrow, Alaska, region. Air temperatures and cloud cover data are from the U.S. National Weather Service. Ground temperatures are from a single year that had air temperatures close to the average (Kelley and Weaver, 1969). Near-ground wind speed was extrapolated from Weather Service data using information in Coyne and Kelley (1975).*

Month	T_a (°C)	T_{ground} (°C)	Approximate V near ground (m s^{-1})	Percent overcast	Percent of time sun above horizon
January	−25.9	−16.8	1.0	32	6.2
February	−28.1	−19.3	1.0	52	22.5
March	−26.2	−20.4	1.0	48	43.4
April	−18.2	−20.4	1.0	56	65.5
May	−7.2	−17.7	1.0	84	94.8
June	0.6	0	1.0	80	100
July	3.7	5.4	1.0	79	100
August	3.1	2.8	1.0	89	75.5
September	−1.0	−1.3	1.0	92	53.1
October	−9.3	−8.3	1.0	87	34.3
November	−17.9	−9.3	1.0	84	9.0
December	−24.7	−14.3	1.0	65	0

both real and simulated (cotton) nests, casts of adults of all species tested could be maintained at normal T_b's at $T_a = -20$°C with a power input roughly equal to thermoneutral resting metabolic rates. These results are in agreement with data from live lemmings (Casey, in litt.). Casts of 6-g lemming pups could not be kept at normal T_b at T_a's below about −5°C unless the power input was increased to well above basal metabolic rates. At −35°C, some increase in power input above thermoneutral levels was necessary for all casts. This increase varied from about 50% in ermine and winter-pelaged lemmings to about 100% for least weasels and small (<40 g) brown lemmings. Nevertheless, the insulation of the nest decreased energy requirements dramatically in all circumstances.

Daily energy requirements for thermoregulation in five representative microclimates are shown in Fig. 1. Parameters used in computing daily requirements are available in Table 1 and estimates of total energy requirements of free-living animals are given in Table 5; average daily metabolic requirements (ADMR) for each month are given as well as the total energy expenditures for the entire year. Two estimations (a maximum and a minimum) were made for each species because of the lack of detailed information on activity levels and habitat selection in the wild. Data used for calculating these estimates are available in Tables 1, 2, and 4, and Appendix I.

TABLE 5.—*Daily energy requirement for each month (kJ) and yearly total (kJ × 10^3), predicted with data in Tables 1, 2, and 4, and Appendix I.*

Species		Jan.	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Ermine	max	702	718	723	709	649	620	586	603	613	643	650	681	240
	min	374	381	383	375	501	479	452	465	476	349	352	367	151
Least	max	364	373	377	369	346	351	327	348	332	330	335	354	128
weasel	min	194	198	199	195	261	249	234	241	247	179	181	189	78
Masked	max	93	95	96	94	88	85	81	83	84	87	88	91	32.4
shrew	min	72	73	74	72	69	66	63	65	66	67	68	71	25.1
Brown	max	231	235	237	231	258	248	235	240	245	215	219	226	85.7
lemming	min	131	132	134	131	200	193	183	187	191	124	126	129	56.6
Varying	max	235	240	241	236	268	255	241	248	253	219	222	230	87.9
lemming	min	132	134	135	133	207	198	187	192	197	125	127	130	57.8

DISCUSSION

Estimates of Short-term Energy Requirements

Field tests.—The energy budget equations used in this study are based on simple relationships derived in large part from heat transfer theory (Gates, 1962; Porter and Gates, 1969; Bakken, 1976). Recent empirical data from carefully controlled laboratory experiments have revealed that some relationships between energy exchange parameters may be more complex than previously assumed (Wathen et al., 1971, 1974; Kowalski and Mitchell, 1976; Mitchell, 1976; Walsberg et al., 1978). Because of these uncertainties, the field tests were conducted to see how much confidence could be placed in calculations based on simple assumptions. Specifically, the tests were designed to reveal if the values of energy exchange parameters obtained in the laboratory (Chappell, 1980) could accurately predict energy requirements in natural situations, which may be very different from the laboratory environment. All of these laboratory measurements were made in blackbody conditions at T_a's in the 15 to 25°C range; field tests encompassed radiant environments ranging from clear nights to sunny days, and T_a's from 15 to −25°C. Ideally, the tests would have been performed with living animals, but technical considerations would have made this extremely difficult. However, the major pathways of energy flux are across the animals' surfaces, and therefore the casts should approximate living animals because their sizes, shapes, and surface characteristics are similar.

The tests demonstrated that predictions of necessary metabolic rate based on Eq. 1 and 2 are satisfactory (Table 3), at least within the range of microclimates utilized. The small average error (about 6%) suggests that the basic equations and the empirically obtained values for physical energy exchange parameters (Table 1) are sufficiently accurate for most purposes. In addition, the estimations of absorbed radiation loads under different regimes of sky conditions and T_a also appear satisfactory.

Effects of microclimate and coat color.—Results from field tests lend confidence to more general applications of energy budget analysis. These can yield many insights into a species' bioenergetic problems and the success of adaptations to them. The severe cold of winter is the most obvious stress that must be met by small arctic mammals. Assuming that maximum sustainable metabolism is about 5 to 8 times the basal rate (Wunder, 1970; Bartholomew, 1977), adults of all the species studied here can tolerate typical subnivian conditions during the coldest months of an average year (T_a and T_{ground} about −20°C). MacLean et al. (1974) reported subnivian temperatures in the Barrow region as low as −35°C for periods of a few days. Under these conditions, shrews and the small female least weasels will be severely stressed and might have to restrict their activities to a well-insulated nest. Larger weasels and adult lemmings should still be able to maintain heat balance outside of the nest, albeit at a high energy cost. Temperatures often reach −40 to −50°C on the snow surface. These conditions certainly exceed the thermoregulatory capabilities of weasels and are near the upper limits for lemmings. Presumably the animals normally avoid such severe cold by remaining in the subnivian space.

Energy budget analysis can also reveal more subtle details of the relative importance of various heat exchange pathways. Small mammals do not support the thick boundary layers characteristic of bulky objects, and hence are subject to large convective heat losses. The wind speed (V) is critically important because convective heat transfer increases with increasing V. For example, shrews maintaining a metabolic rate 5 × basal in blackbody radiant conditions can tolerate (i.e., maintain constant T_b at) a T_a of about −30°C in unstirred air, −18°C in a modest wind (V = 1 m s⁻¹), and around −10°C in the highest winds they are likely to experience (V = 5 to 10 m s⁻¹). The effect of wind is noticeably less severe in the lemmings and ermines;

energy balance of these larger animals is more strongly coupled to environmental radiation loads. In unstirred air the tolerable T_a (at any metabolic rate) is about 32°C higher on a clear night than in sunlight for an ermine in summer pelage, but the difference is only 20°C for a shrew. At higher wind velocities, proportionally more heat is exchanged convectively and the importance of radiant heat exchange decreases. At $V = 10$ m s^{-1} the tolerable T_a of ermines is only about 6°C higher at night than in sunlight.

The costs and benefits of seasonal changes in pelage color are of special interest. White coats absorb less short-wave radiation than dark coats, and are usually depicted as decreasing the radiant heat load on an animal. Walsberg et al. (1978) have presented theoretical arguments and empirical evidence that, under certain conditions, a white pelage may transfer more of an incident radiation load to the skin than will a dark coat. This effect arises from a greater penetration of short-wave radiation into the more transparent white pelages. Radiant heat is therefore distributed deep within a white coat, rather than near the surface, resulting in a lower percentage of absorbed energy being removed by convection. Thus, white winter coats of weasels and varying lemmings may conceivably offer distinct thermal advantages over dark coats for animals active on the surface in sunny weather. However, the effect described by Walsberg et al. (1978) is highly dependent on the thickness and thermal conductance of the pelage, and the rate of convective heat loss. In cold conditions, a white coat will be thermally advantageous only if wind speeds are high (above a minimum "crossover" velocity) and the coat is thick, with low thermal conductivity. Convective heat loss is high in weasels and lemmings because of small body size, but these animals have relatively thin coats. Walsberg et al. (1978), using preparations of pigeon plumage, demonstrated that dark coats $\sim$ 10 mm thick always transferred significantly more incident energy to the skin than white coats of similar thickness, regardless of wind speed (up to 9 m s^{-1}). Significantly, all of the small mammals studied here have pelage thicknesses of 15 mm or less; in weasels the coat is usually under 8 mm thick. Also, most wind velocities encountered by these animals are low, around 1 m s^{-1}. In Walsberg et al.'s (1978) experiments, the crossover wind velocity for 30-mm thick coats was 3 m s^{-1}; for thinner pelages the crossover velocity will presumably be higher. Finally, at high latitudes there is little sunlight available during the winter when cold stresses are greatest.

For the above reasons, it seems unlikely that the white coloration of weasels and varying lemmings will be thermally beneficial to cold-stressed animals. Experimental evidence from the field tests, though limited, supports this view. In sunlight, casts of white ermines always required more energy to maintain a particular T_b than did summer pelaged casts. Winter and summer ermine pelts have approximately equal insulative properties in blackbody conditions. This was true at wind speeds up to about 2 m s^{-1}, the highest encountered in field tests. Further, casts of winter-pelaged ermines and varying lemmings did not require less energy input than predicted from simple measurements of pelage absorptivity. Finally, sunny-day field measurements of effective temperature (made with thin copper casts) were always lower for winter-pelaged animals than for summer-pelaged individuals (often by 5 to 10°C). There data suggest that weasels and lemmings could decrease cold stress somewhat (on sunny days) if they had dark, rather than white, coats in winter. However, as Walsberg et al. (1978) pointed out, thermoregulatory considerations can be overridden by other selective pressures in the evolution of coat color. Apparently the concealment and crypticity offered by a white coat is more important to weasels and lemmings than the thermal tradeoffs. It should be stressed that for larger arctic species with thicker coats, such as ptarmigan, snowy owls, white-phase gyrfalcons, hares, foxes, and polar bears, white coloration may indeed offer definite thermal advantages.

In general, the calculations emphasize the importance of staying within the sub-nivian space in winter. This would be the case even if outside air temperature was not colder than ground temperature (Table 4), for two reasons: 1) wind speeds are much lower under the snow; 2) the subnivian radiation environment approximates a blackbody cavity, whereas on the surface an animal may be exposed to the clear night sky.

The magnitude of these effects is apparent from Fig. 1, which shows the energy requirements for maintaining constant, normal T_b in several typical tundra microenvironments. In midwinter ($T_a = -30°C$, $T_{ground} = -20°C$, $V = 1$ m s^{-1}), the energetic costs of living on the snow surface are usually about 15 to 25% greater than the costs of remaining in the subnivian space, even if the sun is shining. The one exception is the dark, heavily insulated brown lemming, which can slightly lower costs by sunning. On clear nights the cost of being on the surface is 40 to 50% greater than the costs of staying under the snow.

In summer, most animals can save 10 to 20% on thermoregulatory expenses if they remain in burrows on cloudy days. This is due to the different wind speed regimes, as T_a and T_{burrow} are similar in summer. If the sun is out, animals will save an average of 30% of thermoregulatory costs if they emerge from burrows and take advantage of increased Q_{abs}, despite higher convective losses.

In any season the nest is a far more equitable thermal environment than anything to be found outside of it (Fig. 1). Adults of all species can maintain normal T_b with thermoneutral metabolic rates in nests at ambient temperatures to $-20°C$. Even at lower T_a's, the necessary increases in heat production are relatively small. In some years lemmings breed during the winter, and the thermoregulatory problems of neonates may be severe (Casey, in litt.). Single young lemmings cannot maintain thermoneutral MR in nests at T_a's lower than about 0 to $-10°C$, but in nature there will be several pups in each nest. The increased mass, decreased mass-specific surface area, and increased area-specific heat production that result from huddling may significantly lower the T_a limits for thermoneutrality (Pearson, 1947; Casey, in litt.). On the other hand, single shrews can probably maintain thermoneutral metabolism in nests at low T_a's because of their very high area-specific metabolic rates.

Estimates of Long-term Energy Requirements

A logical extension of energy budget calculations is predicting long-term metabolic costs for animals living in natural situations. Accurate estimates of food requirements are important for studies of natural history, population ecology, and ecosystem dynamics. Often these estimates are extrapolations of average daily metabolic rates (ADMR) obtained in simple laboratory conditions. Predictions based on energy budgets are more flexible for these purposes because they can easily incorporate a wide range of climatic conditions that pose problems for other methods. However, the accuracy of this or any other approach is dependent on knowledge of the behavior patterns of the animals, especially for the arctic species studied here. Habitat selection is crucially important because the energetic requirements of the various available microhabitats differ so much. The amount of time spent active is also of vital importance. An active, foraging animal is outside of its insulated nest and exposed to harsh ambient conditions. Also, exercise itself may be costly.

Assumptions.—Unfortunately, information on habitat selection and activity patterns of small arctic mammals is incomplete or totally lacking, especially for the winter months when most activities are subnivian. Precise estimates of energy requirements therefore are impossible, but by using such data that are available, reasonable predictions of maximum and minimum probable costs can be obtained. These calculations

are rough and of necessity based on assumptions and educated guesses, but they can be refined as more behavioral information accumulates. The assumptions used for these estimates are discussed below.

For the most part, the proportion of time overwintering animals spend outside of nests can only be guessed. Obviously they should attempt to maximize the time spent in the essentially thermoneutral nest. However, weasels, lemmings, and shrews do not store large quantities of food or fat, and therefore must routinely engage in some foraging activity. Social interactions and reproductive behavior may also require leaving the nest. The only species for which activity data are available is the brown lemming. The estimates range from 70% of time active in summer (Banks et al., 1975; Peterson et al., 1976) to 30% of time active in winter (S. F. MacLean, pers. comm.). The 30 and 70% values for activity in winter were used as upper and lower bounds for brown and varying lemmings and for weasels. Shrews are usually depicted as spending much more time active than at rest (Crowcroft, 1954; Ingles, 1960; Pearson, 1947; Morrison et al., 1959). Further, shrews have high metabolic rates, which they probably sustain in the arctic winter by feeding on dormant or pupating insects or other soil arthropods. Because foraging in frozen soil is no doubt difficult and time consuming (Vleck, 1979), shrews were assumed to spend 50 to 70% of their time active. Activity levels of all species were assumed to be 50 to 70% in summer, because of high reproductive effort, social interactions, and other factors.

The problem of determining habitat selection is simplified by the small number of microhabitats available. In winter the animals can choose between the nest, the subnivian environment, and the snow surface. In the first two, wind speeds are constant and low, and radiant energy loads approximate blackbody conditions. Only on the surface do variations in wind and radiant environment have to be considered. In summer, animals may select the nest, burrow systems, or tundra surface. Again, wind and radiation will only fluctuate significantly in the above-ground microhabitats. For this study, animals were assumed not to select for particular weather or shade conditions during surface excursions. This assumption is open to question (Peterson and Batzli, 1975). However, even if incorrect it is not likely to result in large errors because wind and sky conditions are fairly constant during the summer (Table 4; Myers and Pitelka, in press), and because only a small portion of time in winter is spent on the snow surface (here assumed to be 1–5% of activity time). In summer the time spent above ground is much higher. Above-ground activity was assumed to comprise 30 to 50% of total activity time. For much of the summer, above-ground conditions will approximate the burrow microclimate, except for wind speed. Temperatures are similar and the prevalence of heavy overcast results in blackbody-like radiant conditions. A summary of the month-by-month activity patterns, habitat selection, and other factors is given in the appendix.

Daily metabolic costs.—Results from these calculations (Table 5) indicate that metabolic costs are high for small arctic mammals during all seasons of the year. The average of minimum estimates of ADMR over the entire year for all five species is about 2.9 times the basal metabolic rates; the average of maximum ADMR estimates is about 4.0 times basal levels. Actual values are presumably intermediate.

There does not seem to be a striking seasonal difference in daily energy requirements. Maximum cost estimates suggest that ADMR averages only 11% larger in March (coldest month) than in July (warmest month), and minimum estimates predict that summer ADMR should exceed winter ADMR by about 15% for all species except shrews. This apparent paradox results from assuming that a larger portion of time is spent inactive, inside the nest, in winter than in summer. Also, even though temperatures are some 30°C warmer in summer than in winter, they are still well below the

animals' thermoneutral zones. If the high and low estimates for each species are averaged, ADMR is predicted to be roughly four times basal metabolism in both summer and winter.

Field ADMR of brown lemmings in summer has been estimated with radiotelemetry and the D_2O^{18} isotope technique by Peterson et al. (1976). While their results were limited, they obtained 24 to 48 h field metabolic rates from three animals, with ADMR's averaging 201 kJ/day. The 190–230 kJ/day figure predicted in the present study compares favorably with this direct measurement.

As expected, the highest ADMR values relative to basal metabolism (or "functional scope") occur in least weasels, a species with poor insulation and small body size. The larger ermines and the better insulated lemmings require smaller functional scopes. For their size, shrews have large absolute ADMR's, but their basal metabolism is so high that their functional scope is similar to that of lemmings. In no case is the predicted increase above basal metabolism unrealistically large, although the highest estimate for least weasels (6 times basal rates) approaches the maximum metabolic scope for small mammals (Wunder, 1970; Bartholomew, 1977). Weasels may counter-act this potential problem by increasing basal metabolic rates during the winter. This strategy will not change the absolute thermoregulatory energy requirement, but would reduce the necessary increase relative to BMR (Casey and Casey, 1979). It is also possible that metabolic requirements for weasels in years of high lemming populations might be lower than the minimum estimates given here. Weasels apparently hunt lemmings by investigating their nests (MacLean et al., 1974). If inhabited lemming nests are very abundant, foraging time for weasels, and its concomitant high ther-moregulatory and exercise costs, might be greatly reduced.

Exercise costs.—The importance of exercise for the energy budgets of animals is of considerable interest (McNab, 1963; Pearson, 1960; Martinsen, 1969; Chew and Chew, 1970); in some species exercise metabolism forms a major part of ADMR (Wun-der, 1970). For the small arctic mammals studied here, the cost of exercise is appar-ently minor relative to the costs of thermoregulation. In this study exercise was as-sumed to require a metabolic output equivalent to about three times basal metabolism, a cost similar to that noted in field experiments on small rodents in thermoneutral environments (W. Karasov, in litt.). Despite this rather high cost relative to BMR, exercise costs form at most about 48% of the predicted ADMR in both winter and summer conditions; in most species exercise comprises roughly one-third of ADMR. The highest exercise costs relative to ADMR occur in lemmings, which are well insulated and have relatively low thermoregulatory costs. Because exercise costs are modest, errors in their estimation will not markedly affect the accuracy of ADMR predictions; for example, reducing the estimated exercise cost from $3 \times$ BMR to $1 \times$ BMR changes predicted ADMR by only about 22% in most species. The fraction of ADMR made up by exercise costs does not change appreciably with changes in ac-tivity time, as thermoregulatory costs are also linked to activity.

Food requirements.—If the caloric requirements, assimilation efficiency, and caloric content of food items are known, the amount of food needed by an animal can be calculated. Using Gessaman's (1972) estimate of the caloric content of lemmings and Moors' (1977) values for the assimilation efficiency of weasels, I estimate that a 40-g female least weasel living in the Barrow area would require almost exactly one av-erage-sized lemming per day (373 total) during an average year. A 130-g ermine would need roughly 700 lemmings (two a day) for the same period. These figures are similar to those derived by MacLean et al. (1974), using a simpler approach. If a masked shrew has a similar assimilation efficiency, it will require some 5.7 kg of food per year—about 1,600 times its body mass. This is particularly impressive when one con-

siders that shrews probably feed on overwintering insects or other soil arthropods that must be dug out of the frozen ground. Possibly shrews are dependent on "refuges," such as large carcasses, which could provide not only meat but also quantities of insect larvae. Lemmings also have rather dramatic food requirements. Several authors have commented on the very low assimilation efficiencies of lemmings (Coady, 1975; Batzli et al., in press). When eating natural food items the assimilation efficiency is between 31 and 36%, as compared to 55 to 75% in other microtines. This, coupled with the high water content of tundra vegetation (80–90%, G. Laursen, pers. comm.) and probable low nutrient content of dormant, overwintering plants, leads to a high rate of food intake. Calculations from the present study predict an annual requirement for a 55-g lemming of about 70 kg of plants (wet mass). This is 1,300 times the animals' body mass, or about 3.5 times body mass of food consumed daily (53% of body mass in dry forage). This figure is similar to food consumption rates obtained in feeding experiments. Coady (1975), Batzli et al. (in press), and Schultz (1964) found that the total dry mass of food ingested daily represented 32 to 61% of body mass. The importance of lemmings as primary consumers is obvious from these figures. Their impact on the slow-growing tundra vegetation can be severe, especially during peak years when they reach high population densities. Extensively grazed areas around nests are often visible after snowmelt in years of lemming abundance.

The above calculations do not take into account the energy necessary to heat ingested food from ambient to body temperature. Low ambient temperatures, high water content and low energy content of food, and low assimilation efficiencies increase the proportion of assimilated energy that must be diverted to heating food. Preliminary calculations indicate that this factor is unimportant in shrews because of the high energy content of prey and efficient assimilation. The prey of weasels is already at their body temperature when captured. However, in lemmings it may increase heat production and food requirements significantly (20 to 30% or more at $T_a = -20°C$, depending on food water content). Whether or not forage is frozen is very important, because the heat of fusion is large compared to the energy necessary to heat water the required amount. The energetic costs of consuming cold food have been overlooked in many investigations, and the problem warrants further study.

In general, the estimates of food consumption lead to the conclusion that foraging will require a large portion of a small arctic mammal's time, even in the best of circumstances. The sheer bulk of forage needed by a lemming must force it to spend substantial periods simply handling and chewing food items, above and beyond the time necessary for searching out and traveling to and from feeding areas. Even if a lemming does not leave its nest at all, it must process 63 g of plants daily. Every excursion out of the nest results in heat losses, which dramatically increase energy requirements. At $T_a = -20°C$, a lemming needs at least 160 g of food daily if it spends 30% of its time foraging; this rises to almost 300 g if it spends 70% of its time foraging. In the face of economics as severe as these, selection for efficient foraging must be very strong.

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APPENDIX I.—*Values used for computing daily and yearly energy requirements are given below in tabular form. Abbreviations are: Abs = pelt absorptivity; %A = percent of time active; %AG = percent of activity above ground; I = pelt insulation [(m² °C)/kW]. Where two values are given (e.g., 70, 30) the first was used for maximum requirements and the second for minimum requirements. "%GS" (in parentheses) gives the percentage of ground or snow surface shaded on clear, sunny days.*

Species		Month (%GS)											
		Jan. (0)	Feb. (0)	Mar. (0)	Apr. (0)	May (30)	Jun. (60)	July (60)	Aug. (60)	Sept. (50)	Oct. (0)	Nov. (0)	Dec. (0)
Ermine	Abs	0.4	0.4	0.4	0.4	0.75	0.75	0.75	0.75	0.75	0.4	0.4	0.4
	%A	70, 30	70, 30	70, 30	70, 30	70, 50	70, 50	70, 50	70, 50	70, 50	70, 30	70, 30	70, 30
	%AG	5, 1	5, 1	5, 1	20, 1	30	50, 30	50, 30	50, 30	30	10, 1	5, 1	5, 1
	I	70	70	70	70	70	70	70	70	70	70	70	70
Least weasel	Abs	0.4	0.4	0.4	0.4	0.75	0.75	0.75	0.75	0.75	0.4	0.4	0.4
	%A	70, 30	70, 30	70, 30	70, 30	70, 50	70, 50	70, 50	70, 50	70, 50	70, 30	70, 30	70, 30
	%AG	5, 1	5, 1	5, 1	20, 1	30	50, 30	50, 30	50, 30	30	10, 1	5, 1	5, 1
	I	53	53	53	53	53	53	53	53	53	53	53	53
Masked shrew	Abs	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
	%A	70, 50	70, 50	70, 50	70, 50	70, 50	70, 50	70, 50	70, 50	70, 50	70, 50	70, 50	70, 50
	%AG	5, 1	5, 1	5, 1	20, 1	50, 30	50, 30	50, 30	50, 30	30, 1	10, 1	5, 1	5, 1
	I	60	60	60	60	60	60	60	60	60	60	60	60
Brown lemming	Abs	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75	0.75
	%A	70, 30	70, 30	70, 30	70, 30	70, 50	70, 50	70, 50	70, 50	70, 50	70, 30	70, 30	70, 30
	%AG	5, 1	5, 1	5, 1	20, 1	30	50, 30	50, 30	50, 30	30	10, 1	5, 1	5, 1
	I	226	226	226	226	130	130	130	130	130	226	226	226
Varying lemming	Abs	0.45	0.45	0.45	0.45	0.75	0.75	0.75	0.75	0.75	0.45	0.45	0.45
	%A	70, 30	70, 30	70, 30	70, 30	70, 50	70, 50	70, 50	70, 50	70, 50	70, 30	70, 30	70, 30
	%AG	5, 1	5, 1	5, 1	20, 1	30	50, 30	50, 30	50, 30	30	10, 1	5, 1	5, 1
	I	250	250	250	250	140	140	140	140	140	250	250	250