Journal of Mammalogy, 81(3):683–690, 2000

ENERGETIC COST OF HEATING INGESTED FOOD IN MAMMALIAN HERBIVORES

DOMINIQUE BERTEAUX*

Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec J1K 2R1, Canada
Present address: Department of Natural Resource Sciences, McGill University, Macdonald Campus, 21, 111 Lakeshore, Ste-Anne-de-Bellvue, Quebec H9X 3V9, Canada

Many mammalian herbivores remain active throughout winter. To satisfy daily energy needs, they ingest large quantities of cold food that subsequently must be warmed to body temperature. Some energy is inevitably lost during this process. Because the specific heat capacity of cellulose is only one-third that of liquid water, the quantity of energy that is lost depends primarily on the temperature and amount of water (free or contained in plants) that is ingested. Using the doubly labeled water method with meadow voles (*Microtus pennsylvanicus*) studied under field conditions, I show that the cost of heating ingested water represents 4.7–12.9% of the daily energy budget of nonreproductive individuals. Whether ingested water is liquid or frozen is critical because of the high cost of melting ice. I show that the fraction of individual energy budgets diverted to heating ingested food should be similar for small and large herbivores, and I explore some consequences of this result for our understanding of the winter ecology of mammalian herbivores.

Key words: Canada, doubly labeled water, energy, herbivores, *Microtus,* water metabolism, winter

Food that homeotherms ingest usually must be heated from ambient to body temperature (hereafter, ''ingested food'' includes both solid food and drinking water). In winter, some energy is inevitably lost during this process. How much energy is lost depends on 3 factors. First, it depends on the difference in temperature between food eaten and the body of the consumer. This difference can be negligible (e.g., a carnivore eating a freshly killed prey), or it can be as high as 80°C (e.g., an ungulate feeding on frozen vegetation at −40°C). Second, the amount of energy lost depends on the quantity of food that is ingested. Species relying on foods low in energy are expected to eat more and should suffer higher costs. Finally, the cost of warming food depends on the quantity of energy required to heat 1 g of food by 1°C (the specific heat capacity of the food). Because water has a very high specific heat capacity compared with other constituents of food (Schmidt-Nielsen 1990), foods containing a high proportion of water are the most costly to warm.

The necessity of heating ingested food from ambient to body temperature should be most costly for animals active at low ambient temperatures that rely on large quantities of food low in energy content. Mammalian herbivores that live in temperate or arctic climates and that do not hibernate form the majority of species in this category. Accordingly, the possible importance of the ingestion of cold food for winter energetics of mammalian herbivores has been suggested by several authors (Berteaux et al. 1998; Chappell 1980; Doenier et al. 1997; Feist 1984; Holleman et al. 1982; Sopella et al. 1992; White 1975;

---

* Correspondent: d.berteaux@nrs.mcgill.ca

Whitney 1977). However, few detailed estimates of this energetic cost exist, and the rare estimates available in the literature (e.g., Chappell 1980; Holleman et al. 1982) vary by more than 10-fold. It is thus extremely difficult to evaluate the impact that the cost of warming ingested food has on physiology, behavior, and ecology of a species.

Using meadow voles (*Microtus pennsylvanicus*), 40-g herbivorous rodents of North America that remain active under the snow throughout winter, I asked 3 questions. First, how much energy do individuals lose every day from warming ingested food to body temperature? Second, is this a trivial or important cost when compared with the daily energy budget of individuals. Finally, could this energetic cost have any implication for our understanding of the winter ecology of mammalian herbivores?

MATERIALS AND METHODS

Field procedures.—Individuals were adult, nonreproductive, female meadow voles from a captive colony that was periodically outbred with wild voles (Berteaux et al. 1994). I studied individuals in predator-free enclosures that were built in an old-field community on the grounds of the Université de Sherbrooke, Québec, Canada (45°15′N, 27°00′W). The same enclosures were used in winter and summer, but experimental animals were different. Animals fed on natural vegetation (forbs and grasses), and no supplementary food was added to the enclosures. Plants present in the enclosures and known to be preferred by meadow voles were *Festuca rubra*, *Agropyron repens*, *Carex*, *Fragaria virginiana*, *Phleum pratense*, and *Poa* (Bergeron and Jodoin 1989; Bergeron et al. 1990).

For the winter study, I acclimatized voles to natural photoperiod and temperatures for 11–18 weeks before individuals were released in the enclosures (Berteaux 1998). Voles were released either alone in 25-m^2 enclosures or as groups of 4 in 100-m^2 enclosures. Social status did not affect water turnover or energetic expenditures (Berteaux et al. 1996a). Some voles were radiocollared, but this did not influence their physiology (Berteaux et al. 1996c). Individuals were allowed to habituate to the enclosures for 2 weeks before they were captured with Sherman traps baited with slices of apple and protected by shelters (Iverson and Turner 1969). Voles were transported within a few minutes after capture to a building located near the study site, weighed to the nearest 0.1 g, and given an intraperitoneal injection of 4 μl/g body mass of distilled water containing 77.9 atoms of oxygen-18/100 atoms of oxygen and 94 mCi of tritium/ml. After 1 h, a 150-μl sample of blood was taken under light anesthesia (methoxyfluorane) from the suborbital sinus using heparinized glass capillary tubes. I released animals at their point of capture and tried to recapture them at the same time of day 24 or 48 h later for collection of 2nd or 3rd samples of blood. Samples of blood were taken from 5 individuals before isotopic injection for measurement of natural abundance of ^{18}O. Measurements of daily water flux and energetic expenditure were obtained during 6 observation days that were staggered over a 51-day period from 25 January to 16 March 1994.

In summer, animals were acclimatized to natural photoperiod and temperatures for ≥2 weeks before being released singly into 25-m^2 enclosures (Berteaux 1998). Voles were allowed to habituate to the enclosures for 1 week before they were captured with Sherman traps baited with slices of apple. Injection of doubly labeled water was performed as previously described, except that all operations were performed in the field. Measurements of daily water flux and energetic expenditure were obtained during 12 observation days over a 42-day period from 12 July to 22 August 1994.

I could not measure directly the temperature of the water that voles ingested in the field. I thus considered the daily mean temperature (the average value of the nighttime minimum and the daytime maximum temperatures) of air at ground level as a reasonable approximation of the temperature of water ingested by voles. That estimate was realistic because the influence of solar radiation was minimal at ground level because of the 40-cm layer of snow (winter) or the dense cover of vegetation (summer) under which animals lived.

Determination of metabolic and water flux rates.—Samples of blood were refrigerated before being vacuum distilled in Pasteur pipettes to recover the water (Nagy 1983). I analyzed for

TABLE 1.—Body mass, total body water, water influx, and daily field metabolic rate of nonbreeding female meadow voles (*Microtus pennsylvanicus*) maintained in field conditions in winter and summer 1994.

Variable	Winter		Summer			
	Minimum–maximum	$\bar{X} \pm SD$	Minimum–maximum	$\bar{X} \pm SD$	F^a	P
Body mass (g)	28.9–41.0	34.61 ± 3.10	28.7–40.9	35.46 ± 3.47	0.57	0.46
Total body water (%)	65.9–78.0	72.54 ± 2.93	69.8–79.7	75.61 ± 3.12	8.64	0.006
Daily mass change rate (%)	−10.04–8.33	−1.04 ± 4.32	−4.87–3.18	−0.75 ± 2.60	0.05	0.83
Water influx rate (ml H_2O g^{-1} day^{-1})	0.69–1.66	1.00 ± 0.25	0.63–1.03	0.86 ± 0.12	3.97	0.05
Field metabolic rate (kJ g^{-1} day^{-1})	2.82–4.74	3.40 ± 0.43	1.84–3.23	2.77 ± 0.42	17.46	<0.001
n (individuals)	23		13			
n (measurements)	35		47			

[a] *d.f.* = 1, 34.

^3H using a liquid scintillation counter (LS 6000, Beckman Instruments, Fullerton, California) and for ^{18}O using the guanidine hydrochloride method to prepare CO_2 gas (Dugan et al. 1985; Wong et al. 1987) that was analyzed with a isotope ratio mass spectrometer (VG-Isogas Sira 12, VG Isotech, Middlewich, United Kingdom; Thomas et al. 1995). All samples were analyzed in duplicate, and a triplicate sample was run when the coefficient of variation (*CV*) was >2%.

Volume of body water at time of initial capture was estimated from the ^{18}O dilution space following Nagy (1983:appendix 1). I assumed that percentage body water remained constant during the period of measurement. When body mass changed between the 1st and subsequent recaptures, I assumed that the volume of the animal's body increased or decreased linearly. Daily water influx was calculated according to Nagy and Costa (1980:equation 4). I also calculated CO_2 production using equation 1 in Nagy (1983) and estimated energetic expenditure by assuming an equivalence of 21.7 J/ml CO_2 (Nagy 1983). Detailed analyses of water flux and energetic expenditure are presented elsewhere (Berteaux and Thomas 1999; Berteaux et al. 1996a, 1996b).

Statistical analyses.—Parametric tests were performed after verification of normality with Shapiro–Wilk tests (SAS Institute Inc. 1994a). Tests are from Sokal and Rohlf (1981), and analyses were carried out with JMP version 3.0 (SAS Institute Inc. 1994b). Statistical significance was defined as $P < 0.05$, and results are reported as $X \pm SD$, unless otherwise stated.

RESULTS

I obtained 82 measurements from 36 individuals for both daily water influx and daily energetic expenditure. Thirty-five measurements (23 individuals) were obtained in winter, and 47 measurements (13 individuals) were obtained in summer. Thus, 1.5 ± 0.5 and 3.6 ± 1.8 measurements were obtained per individual during winter and summer, respectively.

Water ingestion.—Water influx averaged 1.00 ml H_2O/g/day during winter and 0.86 ml H_2O/g/day during summer (Table 1). Those values were significantly different. Using doubly labeled water, one cannot partition total intake of water among the 4 possible sources: drinking water, preformed water contained in food, water produced during oxidation or assimilation of foodstuffs, and water obtained by diffusion across skin or lungs. Metabolic water, however, can be quantified using the amount of metabolizable energy in the diet and the water yielded on oxidation of foodstuffs (Nagy 1983). Assuming that a diet of plants generated 0.637 μl of metabolic water/ml CO_2 expired and the energetic equivalency is 21.7 J/ml CO_2 (Nagy 1983), my values of field metabolic rates (3.40 and 2.77 kJ/g/day in winter and summer, respectively; Table 1) yield 99.8 and 81.3 μl of metabolic water produced per gram body mass in winter and summer, respectively. Metabolic water thus represented 10.0% of water influx observed in voles during winter and 9.4% during summer.

Exchange of water vapor accounts for a very small fraction of the total input of water (Nagy and Costa 1980). Thus, total amount of water consumed, either as preformed water contained in food or as drinking water, approximately equaled the total gain of water minus the metabolic water produced, which corresponds to 0.89 and 0.78 ml H_2O/g/day for winter and summer, respectively. Voles did not gain or lose mass during the period of measurement (Table 1); thus, calculated amounts of ingested water were for animals in a steady state.

Energy to warm ingested water.—Mean daily ambient temperature at the ground ranged from −3.4°C to 1.7°C and averaged −1.3 ± 1.4°C during the 6 winter days of measurement. Under the snow, temperature was virtually constant across the 24-h cycle. Ingested water thus had to be warmed from −1.3°C to 37°C, the approximate body temperature of a meadow vole (Wunder 1985). Two extreme scenarios were explored, depending on whether water was ingested as ice. If water was entirely consumed as ice in frozen vegetation or as snow, the amount of heat needed to raise the temperature of 1 ml of water by 1°C was 2.100 J when it was frozen and 4.184 J when it was liquid (Weast 1973; Fig. 1), and an additional expenditure of 335 J/g was required to melt ice (Weast 1973; Fig. 1). Thus, 492.5 J were needed to warm 1 ml of water from −1.3°C to 37°C. Because 0.89 ml H_2O were consumed per day per gram of body mass in winter, a total of 438 J/g/day were devoted to warming consumed water if it were all frozen when ingested. In a 2nd scenario, water was consumed completely in a liquid form. That may have been the case if voles satisfied their need for water only with preformed water contained in plants. Water contained in shoots of herbaceous plants may not be frozen, even at temperatures of about −2°C, mainly because of the presence of soluble carbohydrates in cellular and extracellular fluids and various attractive forces with which water is held in plant tissues (Marchand 1991; Sakai and Larcher 1987). In this case, the amount of heat necessary to warm ingested water was only 160.2 J/ml ingested, or 160 J/g/day for an individual.

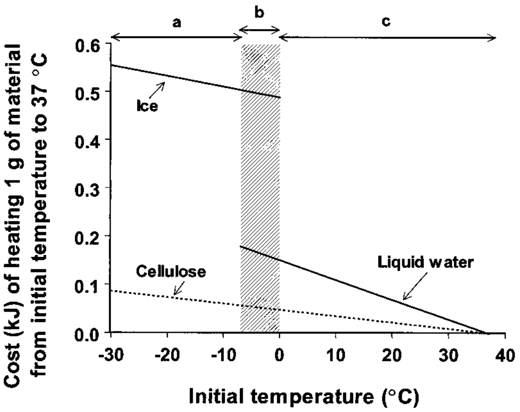

FIG. 1.—Energetic cost of heating 1 g of liquid water and ice (solid line) or cellulose (dashed line) from ambient to body temperature (37°C). Water available to herbivores is frozen in zone a. In zone b, free water is frozen, but water contained in herbaceous plants can be liquid. In zone c, water available to herbivores is liquid. The specific heat capacity of frozen water is about one-half that of liquid water, which explains the difference in slope between the 2 solid lines. Note the high cost of melting ice because of the latent heat of fusion of water.

During the 12 summer days of measurement, mean daily temperature ranged from 9.2°C to 32.0°C and averaged 19.7 ± 2.3°C. Because voles ingested 0.78 ml of water per day per gram of body mass, a total of 56.5 J/g/day were devoted to warming absorbed water in summer.

Proportion of energy budget to warm ingested water.—Average field metabolic rate of voles was 3.40 and 2.77 kJ/g/day in winter and summer, respectively. Thus, the energetic cost of warming ingested water to body temperature represented 12.9% of the winter budget of a vole if water was frozen when ingested. If water was liquid, the figure drops to 4.7%. In summer, only 2.0% of the daily energy budget was spent to heat ingested water from ambient temperature to 37°C.

Daily energetic expenditures (kJ/g/day) of voles were 22.7% higher in winter than summer, and I calculate that 60.6% (cost of warming water consumed in winter minus cost of warming water consumed in summer divided by winter energetic expenditure minus summer energetic expenditure) of that seasonal increase was due solely to the necessity of warming ingested water to body temperature if all water was frozen when consumed during winter. Only 16.5% of that increase, however, was caused by the cost of heating ingested water if it was liquid when ingested during winter.

DISCUSSION

Meadow voles living under snow spent 4.7–12.9% of their daily winter energy budget heating ingested water, depending on whether water was liquid or frozen. Intermediate costs are expected if only a fraction of ingested water was frozen.

I measured the cost of heating ingested water but did not consider the cost of heating dry herbage. The specific heat capacity of cellulose is less than one-third that of liquid water (1.3 versus 4.2 J/g/°C; Perry and Perry 1959), and, more important, there is no latent heat of fusion for cellulose (Fig. 1). Thus, the cost of heating dry herbage likely was very low compared with that of heating water.

Were voles more likely to ingest liquid or frozen water? Ambient temperature under the snow was always $<0°C$ during the study, and all free water was thus in the form of ice or snow. Meadow voles can eat large quantities of ice when maintained on dry food (e.g., rabbit chow) at freezing temperatures (F. Masseboeuf, pers. comm.). They also probably eat some ice when feeding on natural vegetation because it was frequent to hear them gnawing on ice below the snow cover (F. Masseboeuf, pers. comm.). However, water contained in plants likely was liquid, so voles ingested a mixture of liquid and frozen water.

One important aspect regarding the generalization of my results is whether the cost of warming ingested food to body temperature, as a proportion of the daily energy budget, should be related to body size. The following reasoning shows that this cost should be independent of body size. The quantity of energy spent to heat ingested food depends primarily on the amount of food that is ingested, which is directly proportional to individual energetic expenditure. Thus, when expressed as a fraction of total energetic expenditure, the quantity of energy spent to heat ingested food should not vary with body size. Unfortunately, the cost of heating ingested food has been evaluated in so few species that robust interspecific comparisons are not possible. Preliminary evidence, however, suggests that there is no relation between body size and the cost of heating ingested food (Table 2).

The cost of warming ingested water to body temperature has 2 implications for selection of food by herbivores in winter. First, when both frozen and unfrozen plant tissues are available to herbivores, individuals should select unfrozen plant tissues because they are much less costly to warm. Given that species of plants vary in their ability to maintain cellular and extracellular fluids as liquid at low temperature (Sakai and Larcher 1987), this could translate into the preference of herbivores for some species of plants over others. Whether such a differential herbivory pressure may have increased the freezing point of some species of plants through natural selection is unknown. Second, herbivores may avoid ingesting high-protein foods during winter because ingestion of a high-protein diet results in increased water demands for catabolism of protein and renal excretion of urea.

TABLE 2.—Estimation of the energetic cost of heating ingested food and water in several mammalian herbivores.

Species	Body mass (g)	Temperature (°C)	Energetic cost[a]	Reference
Reindeer (*Rangifer tarandus*)	100,000	−30	6–8%[b]	White (1975)
Reindeer	70,000	−23	6.5–13.9%[c]	Soppela et al. (1992)
Lemmings (various species)	55	−20	20–30%[d]	Chappell (1980)
Redback vole (*Clethrionomys rutilus*)	15	−23	2.5%	Holleman et al. (1982)
Redback vole	15	−10	11%[e]	Whitney (1977)

[a] Cost is expressed as a percentage of daily energetic expenditure. Only the estimates of Soppela et al. (1992) and Holleman et al. (1980) are based on actual measurements of water flux and energetic expenditure obtained with isotopic techniques.

[b] The cost was originally expressed as a fraction of fasting metabolic rate; I standardized estimates assuming total energetic expenditure to be 3 times fasting metabolic rate; costs are expressed as a percentage of daily energetic expenditures.

[c] Percentages refer to the sole cost of heating ingested water.

[d] No details were given by the author on how these estimates were reached.

[e] Percentage is derived from raw data on field energetic expenditures and cost of heating food and water provided by Whitney (1977).

Sopella et al. (1992) fed captive reindeer (*Rangifer tarandus*) 4 rations that supplied equal energy but differed in content of protein. Using tritiated water, they showed that daily inflow of water was correlated positively with the dietary supply of protein, and high inflow of water translated into high thermal energetic costs. Similarly, Berteaux et al. (1998) showed that wild white-tailed deer (*Odocoileus virginianus*) avoid excess protein during winter and suggested that the function of this dietary selection was to decrease the need for water and associated energetic costs.

Benefits of living under snow have long been recognized by ecologists (Formozov 1946; Halfpenny and Ozanne 1989; Marchand 1982; Merritt 1984). Snow provides small mammals an environment where convective and conductive losses of heat are reduced, thus decreasing thermoregulatory costs. Snow also may be important in keeping food at a temperature higher than that of the air, which could be especially important if snow prevents plants and free water from freezing. Thus, snow not only provides small mammals with a protecting blanket. It also provides them with relatively ‘‘hot meals.’’

The cost of warming ingested food to body temperature could have other implications. For example, some small mammals sometimes reproduce in winter (Merritt 1984) or very early spring. The increased demand for water by lactating females and the cost of warming ingested water suggests that availability of unfrozen water (free or contained in plants) might be as important as ambient temperature for a balanced energy budget. Thus, availability of unfrozen water may predict occurrence of winter breeding. As another example, when ungulates can choose between different foods located under or above the snow (e.g., when both tree and ground lichens are available), the higher temperature of lichens located under the snow cover could potentially compensate for the cost of digging them out. These are unexplored but exciting directions for future studies on the winter ecology of mammalian herbivores.

RÉSUMÉ

Beaucoup de mammifères herbivores sont actifs en hiver. Afin de satisfaire leurs besoins énergétiques, ils doivent ingérer de grandes quantités de nourriture dont la temperature doit être élevée jusqu’à celle du corps. Cela se traduit inévitablement par une perte d’énergie. La quantité d’énergie dépensée dépend principalement de la quantité d’eau (libre ou contenue dans les plantes) qui est ingérée, ainsi que de sa temperature, puisque la capacité calorifique

spécifique de l'eau liquide est 3 fois plus élevée que celle de la cellulose. L'utilisation de la technique de l'eau doublement marquée sur des Campagnols des champs (*Microtus pennsylvanicus*) étudiés en conditions naturelles m'a permis de montrer que le coût du réchauffement de l'eau ingérée représentait 4.7 à 12.9% du budget énergétique des individus. L'état de l'eau (glacée ou liquide) est critique étant donné le coût important de faire fondre la glace. Je montre que la proportion du budget énergétique allouée au réchauffement de l'eau ingérée devrait être la même pour les petits et les grands herbivores. Je discute certaines conséquences de ces résultats pour notre compréhension de l'écologie hivernale des mammifères herbivores.

ACKNOWLEDGMENTS

I thank P. Albert, J. Bêty, A. Frève, F. Masseboeuf, and E. Rengifo for assistance in the field; P. Albert, J. Bêty, and M. Léonard for assistance in analysis of samples of blood; and B. Mercier and D. Proulx for animal care. Funding was provided by the Natural Sciences and Engineering Research Council of Canada and the Fondation pour la Formation de Chercheurs et l'Aide à la Recherche of Québec through grants to J.-M. Bergeron and D. Thomas.

LITERATURE CITED

BERGERON, J.-M., R. BRUNET, AND L. JODOIN. 1990. Is space management of female meadow voles (*Microtus pennsylvanicus*) related to nutritive quality of plants? Oecologia 82:531–536.

BERGERON, J.-M., AND L. JODOIN. 1989. Patterns of resource use, food quality, and health status of voles (*Microtus pennsylvanicus*) trapped from fluctuating populations. Oecologia 79:306–314.

BERTEAUX, D. 1998. Testing energy expenditure hypotheses: reallocation versus increased demand in *Microtus pennsylvanicus.* Acta Theriologica 43:13–22.

BERTEAUX, D., J.-M. BERGERON, D. W. THOMAS, AND H. LAPIERRE. 1996a. Solitude versus gregariousness: do physical benefits drive the choice in overwintering meadow voles? Oikos 76:330–336.

BERTEAUX, D., J.-M. BERGERON, D. W. THOMAS, AND H. LAPIERRE. 1996b. Repeatability of field metabolic rate in female meadow voles (*Microtus pennsylvanicus*). Functional Ecology 10:751–759.

BERTEAUX, D., M. CRÊTE, J. HUOT, J. MALTAIS, AND J.-P. OUELLET. 1998. Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. Oecologia 115:84–92.

BERTEAUX, D., R. DUHAMEL, AND J.-M. BERGERON. 1994. Can radio collars affect dominance relationships in *Microtus*? Canadian Journal of Zoology 72: 785–789.

BERTEAUX, D., F. MASSEBOEUF, J.-M. BONZOM, J.-M. BERGERON, D. W. THOMAS, AND H. LAPIERRE. 1996c. Effect of carrying a radiocollar on expenditure of energy by meadow voles. Journal of Mammalogy 77:359–363.

BERTEAUX, D., AND D. W. THOMAS. 1999. Intrapopulation variation in field water metabolism of female meadow voles (*Microtus pennsylvanicus*). Physiological and Biochemical Zoology 72:545–554.

CHAPPELL, M. A. 1980. Thermal energetics and thermoregulatory costs of small arctic mammals. Journal of Mammalogy 61:278–291.

DOENIER, P. B., G. D. DELGIUDICE, AND M. R. RIGGS. 1997. Effects of winter supplemental feeding on browse consumption by white-tailed deer. Wildlife Society Bulletin 25:235–243.

DUGAN, J. P., ET AL. 1985. Guanidine hydrochloride method for determination of water oxygen isotope ratios and the oxygen-18 fractionation between carbon dioxide and water at 25°C. Analytical Chemistry 57:1734–1736.

FEIST, D. D. 1984. Metabolic and thermogenic adjustments in winter acclimatization of subarctic Alaskan red-backed voles. Pp. 131–137 in Winter ecology of small mammals (J. F. Merritt, ed.). Carnegie Museum of Natural History, Special Publication 10:1–242.

FORMOZOV, A. N. 1946. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Boreal Institute, University of Alberta, Edmonton, Alberta, Canada.

HALFPENNY, J. C., AND R. D. OZANNE. 1989. Winter: an ecological handbook. Johnson Books, Boulder, Colorado.

HOLLEMAN, D. F., R. G. WHITE, AND D. D. FEIST. 1982. Seasonal energy and water metabolism in free-living Alaskan voles. Journal of Mammalogy 63:293–296.

IVERSON, S. L., AND B. N. TURNER. 1969. Under-snow shelter for small mammal trapping. The Journal of Wildlife Management 33:722–723.

MARCHAND, P. J. 1982. An index for evaluating the temperature stability of a subnivean environment. The Journal of Wildlife Management 46:518–520.

MARCHAND, P. J. 1991. Life in the cold. 2nd ed. University Press of New England, Hanover, New Hampshire.

MERRITT, J. F. (ED.). 1984. Winter ecology of small mammals. Carnegie Museum of Natural History, Special Publication 10:1–242.

NAGY, K. A. 1983. The doubly labeled water ($^3HH^{18}O$) method: a guide to its use. University of California, Los Angeles, Publication 12-1417:1–45.

NAGY, K. A., AND D. P. COSTA. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. American Journal of Physiology 238: R454–R465.

PERRY, J. H., AND R. H. PERRY (EDS.). 1959. Engineering manual. McGraw-Hill, New York.

SAKAI, A., AND W. LARCHER. 1987. Frost survival of plants: responses and adaptation to freezing stress. Ecological Studies 62:1–346.

SAS Institute Inc. 1994a. JMP statistics and graphics guide. Version 3. SAS Institute Inc., Cary, North Carolina.

SAS Institute Inc. 1994b. JMP user's guide. Version 3. SAS Institute Inc., Cary, North Carolina.

Schmidt-Nielsen, K. 1990. Animal physiology: adaptation and environment. 4th ed. Cambridge University Press, Cambridge, Massachusetts.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. 2nd ed. W. H. Freeman and Company, San Francisco, California.

Sopella, P., M. Nieminen, and S. Saarela. 1992. Water intake and its thermal energy cost in reindeer fed lichen or various protein rations during winter. Acta Physiologica Scandinavia 145:65–73.

Thomas, D. W., K. Martin, and H. Lapierre. 1995. Doubly labelled water measurements of field metabolic rate in white-tailed ptarmigan: variation in background isotope abundance and effect on CO_2 production estimates. Canadian Journal of Zoology 72:1967–1972.

Weast, R. C. 1973. Handbook of chemistry and physics. CRC Press, Boca Raton, Florida.

White, R. G. 1975. Some aspects of nutritional adaptations of arctic herbivorous mammals. Pp. 239–268 in Physiological adaptation to the environment (F. J. Vernberg, ed.). Intext Educational Publishers, New York.

Whitney, P. 1977. Seasonal maintenance and net production of two sympatric species of subarctic microtine rodents. Ecology 58:314–325.

Wong, W. W., L. S. Lee, and P. D. Klein. 1987. Oxygen isotope ratio measurements by reaction of microliter quantities of biological fluids with guanidine hydrochloride. Analytical Chemistry 59:690–693.

Wunder, B. A. 1985. Energetics and thermoregulation. Pp. 812–844 in Biology of New World *Microtus* (R. H. Tamarin, ed.). Special Publication, The American Society of Mammalogists 8:1–893.

Submitted 29 March 1999. Accepted 18 October 1999.

Associate Editor was Allen Kurta.