EFFECT OF CARRYING A RADIOCOLLAR ON EXPENDITURE OF ENERGY BY MEADOW VOLES

DOMINIQUE BERTEAUX, FABRICE MASSEBOEUF, JEAN-MARC BONZOM, JEAN-MARIE BERGERON,
DONALD W. THOMAS, AND HÉLÈNE LAPIERRE

Groupe de Recherche en Écologie, Nutritíon, et Énergétique,
Département de Biologie, Université de Sherbrooke,
Sherbrooke, Quebéc J1K 2R1, Canada (DB, FM, J-MB, J-MB, DWT)
Musée du Séminaire de Sherbrooke, Sherbrooke, Québec J1H 1J9, Canada (DWT)
Lennoxville Research Station, Agriculture Canada,
Box 90 Lennoxville, Québec J1M 1Z3, Canada (HL)

We compared the daily expenditure of energy of meadow voles (*Microtus pennsylvanicus*) with and without dummy radiocollars. Daily expenditure of energy was estimated by doubly labelled water, while voles were kept in large outdoor cages. Carrying a radiocollar (6.7–9.0% of body mass) had no effect on daily expenditure of energy. Metabolism of caged animals was not inferior to that of free-ranging ones, suggesting that caging did not reduce locomotory costs and that radiocollars do not influence energy budgets of voles in natural conditions. Subsequently, we remove a potential argument against the use of telemetry on mammals of small size. We also validate the simultaneous use of radiotelemetry and doubly labelled water in small running mammals, which should offer new opportunities to investigate ecological energetics of these species.

Key words: *Microtus pennsylvanicus,* meadow vole, daily energy expenditure, doubly labelled water, radiocollar, telemetry

Radiotelemetry is now used routinely to study mammals in natural environments. Radio packages generally are attached to collars or implanted intraperitoneally (Kenward, 1987). White and Garrott (1990) encouraged researchers to investigate possible impacts of transmitters on individuals, because the value of this technique is compromised if transmitters affect the study animals. Among mammals, species of small size have received the most attention, probably because of the higher body mass:transmitter-mass ratio (White and Garrott, 1990). However, one consequence of this high ratio, namely the energetic cost of carrying a transmitter, has never been investigated, and to date, the only studies devoted to this topic concern birds (Gessaman and Nagy, 1988; Gessaman et al., 1991; Klaassen et al., 1992; Sedinger et al., 1990).

Evaluating the potential energetic cost of carrying a transmitter is important for two reasons. First, if wearing a collar is energetically costly, then less energy is available for other functions, possibly resulting in behavioral changes (e.g., time spent feeding) or decreased reproductive output. Second, ecological energetics now benefit from accurate and reliable field techniques such as using doubly labelled water (Lifson and McClintock, 1966). The simultaneous use of radiotelemetry and doubly labelled water in field studies is promising to clarify key problems in behavioral ecology (e.g., relationship between territory size and energetic needs), but a necessary validation step is measuring the energetic cost of carrying a transmitter.

Our objective was to assess whether nonreproductive meadow voles (*Microtus pennsylvanicus*), 30–35-g mammals, increased their daily expenditure of energy when carrying a radiocollar. To achieve our goal, daily expenditure of energy for individuals was measured in large outdoor cages while animals were collared and then after collars were removed.

MATERIALS AND METHODS

Experimental approach and animals.—We measured the effect of radiocollars on daily expenditure of energy of caged voles in a single-factor experiment with two levels (collars and controls) in which each individual served as its own control. Ten voles (two males and eight females) were collared without anesthesia and their expenditure of energy was measured during a 24-h period (Day 1) after 1 week of habituation. Collars were then removed and expenditure of energy was measured again during the next 24-h period (Day 2) to compare the daily expenditure of energy of the same individuals with and without a collar. At the same time, (Days 1 and 2) energy expenditure of eight noncollared, control voles (three males and five females) was measured to test whether energy expenditure was affected by the initial handling experience, or if a variation in any environmental factors influenced energy demand. Furthermore, we measured the field metabolic rate of a third group of animals (four noncollared females) living freely in 100-m^2 enclosures (one individual per enclosure) located near our cages. This was done to verify if our estimations of metabolic rate were representative of expenditures of unrestrained individuals.

Meadow voles used in the experiment originated from a captive colony that was periodically outbred with wild voles (Berteaux et al., 1994). Voles were acclimatized to outdoor conditions 2 months before the experiment, by keeping them in individual cages that were protected from rain and direct sun. The experiment was carried out in an old field located on the campus grounds of the Université de Sherbrooke, Québec, Canada, in August 1993.

We measured daily expenditure of energy of voles in cages (60 by 60 by 40 cm) where food (fresh grass and forbs provided daily) and water (provided ad lib. in glass dishes) were freely available. Cages were placed outside to expose voles to natural photoperiod and temperature. Voles performed all ranges of behavior typical of free-living individuals (nest construction, food handling, running, etc.), except that interactions between individuals were not possible because voles were housed singly. Voles carried dummy radiocollars consisting of a plastic tie (10.5 by 2.5 cm) threaded through a 2-cm piece of rubber tube (8-mm diameter) loaded with lead weights (Berteaux et al., 1994). The entire collar packages weighed 2.5 ± 0.1 g (range, 2.3–2.6 g), which was 6.7–9.0% of body mass (7.7 ± 0.7%). Mass of the collar was characteristic of the range of radiocollars used in field studies (Lambin, 1994; Ostfeld et al., 1988; Webster and Brooks, 1981).

Measurements of energy expenditure.—Doubly labelled water was used to measure daily expenditure of energy. Individual voles were removed from their cages at the beginning of Day 1, weighed to the nearest 0.1 g, and then injected intraperitoneally with 1.6 μl/g of water containing 82.8 atom percent ^{18}O and 140 mCi ^{3}H/ml. Voles were kept for 1 h in Sherman traps for equilibration, after which a 150-μl blood sample was taken under light anesthesia (methoxyflurane, Pitman-Moore, Inc.) from the suborbital sinus using heparinized, glass capillary tubes. Voles were then returned to their cages. A second blood sample was collected 24 h after the injection from each individual for isotopic analysis, dummy transmitters were removed from collared individuals, and voles were weighed. The third blood samples were collected after 48 h. Blood samples were never collected from the same eye on 2 consecutive days. They were taken before injection of isotopes in four individuals to measure the natural abundance of ^{18}O. Blood samples were stored at 4°C for 3 months. We analyzed for tritium using liquid scintillation in a Beckman LS 6000 counter and for ^{18}O using the guanidine hydrochloride method (Dugan et al., 1985; Wong et al., 1987) and mass spectrometry analyses (VG-Isogas Sira 12 isotope-ratio mass spectrometer). All samples were analyzed in duplicate and a triplicate sample was analyzed when the coefficient of variation exceeded 2%. We calculated production of CO_2 for voles using the original single-isotope pool equation (Lifson and McClintock, 1966) and we estimated energy expenditure using the conversion value of 21.7 kJ/ml CO_2 (Nagy, 1983). For each individual, the volume of water in the body at the time of initial capture was estimated as the dilution volume of injected ^{18}O (Nagy, 1983). Total volume of body water at recapture was estimated from body mass assuming that the water fraction remained constant.

The same procedure was used to estimate the

TABLE 1.—*Body mass (without collar), daily expenditure of energy (DEE) and percentage of body water (BW) of meadow voles carrying radiocollars. Body masses were measured at the beginning of Day 1 and at the end of Day 2.*

	Day 1		Day 2	
Group and parameter	*n*	$\bar{X} \pm SD$	*n*	$\bar{X} \pm SD$
Control voles (no collar)				
Body mass (g)	8	33.2 ± 4.4	8	33.2 ± 4.5
Daily expenditure of energy (kJ/g)	8	2.8 ± 0.5	8	2.7 ± 0.8
Body water (%)	8	72.7 ± 5.4		
Collared voles (collar removed on Day 2)				
Body mass (g)	10	32.3 ± 2.9	10	32.3 ± 4.3
Daily expenditure of energy (kJ/g)	10	2.8 ± 0.5	10	2.9 ± 0.8
Body water (%)	10	70.1 ± 5.2		

daily expenditure of energy of unrestrained voles living in enclosures, except that second blood samples were collected 24 ± 2 h after injection. Third blood samples were not collected. Minimum and maximum temperatures (°C) at ground level were measured at the study site on Day 1 and Day 2.

Statistics.—Results are reported as means and standard deviations. Homogeneity of variance was tested with an F_{max}-test (Sokal and Rohlf, 1981) after which differences between means were tested for statistical significance ($P < 0.05$) with paired or unpaired *t*-tests. Mann-Whitney *U*-tests were used when homogeneity of variance was not expected. Tests generally were two-tailed, except when direction of the between-group difference was predicted (e.g., energy expenditure predicted to be higher for collared than noncollared voles). Analyses were carried out with Statview for Macintosh (Abacus Concepts, Inc., 1987).

RESULTS

Mean daily temperature at ground level was 17.6°C on Day 1 and 17.0°C on Day 2. There was no significant between-sex difference in body mass or daily expenditure of energy for either the control or the collared group, so the data from males and females were pooled in subsequent analyses. *F*-tests indicated homogeneity of variances ($P > 0.10$) between daily expenditures of energy of control and collared voles on the same day of measurement, or between days when energy expenditures of the same individual were compared. The same applied for body masses.

At the beginning of Day 1, body mass of collared voles was not significantly different from that of control ones (unpaired two-tailed $t = 0.534$, $d.f. = 16$, $P = 0.601$; Table 1). Similarly, body water content (percent of body mass) of individuals did not differ according to treatment (two-tailed Mann-Whitney *U*-test: $z = -1.11$, $P > 0.10$; Table 1).

Daily expenditure of energy of the two groups did not differ significantly during the 1st day of measurement (unpaired one-tailed $t = 0.131$, $d.f. = 16$, $P = 0.448$), and we could not detect any significant effect of time (Day 1 versus Day 2) on energy expenditures of control voles or voles carrying a radiocollar (control voles: paired two-tailed $t = 0.336$, $d.f. = 7$, $P = 0.747$; collared voles: paired one-tailed $t = 0.466$, $d.f. = 9$, $P = 0.326$; Table 1).

On Day 2, voles of the two groups were not carrying collars. Their daily expenditure of energy was not significantly different (unpaired two-tailed $t = 0.407$, $d.f. = 16$, $P = 0.690$).

The daily expenditure of energy of voles studied in the enclosures (third group) was 2.4 ± 0.4 kJ/g ($n = 4$), which was 13% less than the value obtained from our caged animals (data from Day 2 pooled for the two experimental groups). This difference was not significant (unpaired two-tailed $t = 0.880$, $d.f. = 20$, $P = 0.390$). It must be noted, however, that given the small sample for individuals studied in enclosures, the minimal difference that we were able to detect (Sokal and Rohlf, 1981) was only 0.87 KJ/g, that is a 30.9% difference between energy expenditure of caged and enclosed animals.

DISCUSSION

We detected no relationship between energy expenditure and wearing a dummy radiocollar in voles studied in outdoor cages. Body mass and volume of body water of collared and control voles were not different at the beginning of the measurement period; therefore initial differences that may have affected our between-group comparisons of energy expenditure can be excluded. Ground temperatures were similar from Day 1 to Day 2, and thus did not affect between-day comparisons of energy expenditures. We did not use true radiocollars, but simply collars with the same mass in a similar configuration to a radiocollar. To our knowledge, there is no reason to believe that the electrical components or emission would influence the energy expenditure of an animal, therefore our conclusions should apply to true radiocollars.

Our results can be explained if we consider the main source that would potentially have modified energetic needs of collared individuals. The major energetic cost of carrying a transmitter should result from the increased costs of locomotion. The cost of carrying a load in terrestrial animals is directly proportional to the mass of the load (Taylor et al., 1980). One would thus expect a 6–9% increase in energy expenditure during locomotion when voles carry a radiocollar weighing 6–9% of body mass. However, animals are not continually moving. Although we have few data about the proportion of time that voles are active within the daily activity budget (Madison, 1985), meadow voles appear to invest ≤50% of their time in activity (Madison, 1985). No data exist as to the proportion of active time spent in locomotion. A conservative estimate of caged animals is that, at most, 25% of active time is actually spent walking or running (D. Berteaux, in litt.). Accepting such a conservative assumption would mean that carrying a transmitter is expected to increase the daily expenditure of energy by no more than ca. 1%. Because intra-individual variation in daily expenditure of energy seems to be high in free-living animals (Speakman et al., 1994), any effect of load carrying would be lost in natural variation.

The energy expenditure of free-ranging voles tended to be lower than or similar to that of caged voles. This pattern suggests that caging did not reduce costs of locomotion. Therefore, we can exclude the possibility that we did not detect any effect of collars on energy expenditure simply because of an artificial reduction in locomotory costs due to caging.

Our results indicate that extra energetic costs that may accrue to radiocollared individuals should not be of concern to biologists using telemetry on small running mammals. This removes a potential argument against the use of telemetry on these species. Furthermore, it opens many new opportunities to researchers wishing to use telemetry together with the doubly-labelled-water technique. These opportunities might be of particular importance to the field of ecological energetics, because much can be learned by doing doubly-labelled-water studies on wild animals while carefully measuring or manipulating their behavior or environment (Nagy, 1989).

RÉSUMÉ

Nous avons mesuré les dépenses énergétiques quotidiennes de campagnols des champs (*Microtus pennsylvanicus*) porteurs ou non de colliers émetteurs factices. Les dépenses énergétiques quotidiennes ont été estimées par la technique de l'eau doublement marquée, alors que les campagnols étaient maintenus dans des cages extérieu-

res. Le fait de porter un collier émetteur (6.7–9.0% de la masse corporelle) n'a eu aucun effet sur les dépenses énergétiques journalières. Le métabolisme des animaux en cage n'était pas inférieur à celui d'animaux libres, ce qui suggère que la vie en cage ne diminuait pas les coûts de locomotion, et que nos conclusions demeurent valides en conditions naturelles. Nous éliminons ainsi un argument potentiel contre l'utilisation de la télémétrie chez les micromammifères. Nous validons également l'utilisation simultanée de la télémétrie et de la technique de l'eau doublement marquée sur des petits mammifères coureurs. Ceci devrait offrir de nouvelles opportunités pour étudier en milieu naturel la bioénergétique chez ces espèces.

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