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*Published in:*  
Physiological Zoology

*DOI:*  
[10.1086/639616](https://doi.org/10.1086/639616)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
1997

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Meerlo, P., Bolle, L., Visser, GH., Masman, D., & Daan, S. (1997). Basal metabolic rate in relation to body composition and daily energy expenditure in the field vole, *Microtus agrestis*. *Physiological Zoology*, *70*(3), 362-369. <https://doi.org/10.1086/639616>

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Source: *Physiological Zoology*, Vol. 70, No. 3 (May - Jun., 1997), pp. 362-369

Published by: The University of Chicago Press. Sponsored by the Division of Comparative Physiology and Biochemistry, Society for Integrative and Comparative Biology

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# Basal Metabolic Rate in Relation to Body Composition and Daily Energy Expenditure in the Field Vole, *Microtus agrestis*

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Accepted by G.K.S. 10/31/96

## ABSTRACT

Basal metabolic rate in the field vole (*Microtus agrestis*) was studied in relation to body composition and daily energy expenditure in the field. Daily energy expenditure was measured by means of doubly labelled water (D<sub>2</sub><sup>18</sup>O). In the same individuals, basal metabolic rate was subsequently derived from O<sub>2</sub> consumption in an open-circuit system in the laboratory. Body composition was obtained by dissecting the animals and determining fresh, dry, and lean dry mass of different organs. Daily energy expenditure for free-living field voles ranged from 1.8 to 4.5 times basal metabolic rate, with an average of 2.9 times basal metabolic rate. Variation in both daily energy expenditure and basal metabolic rate was best explained by body mass. Gender or reproductive activity did not have significant additive effects. Daily energy expenditure and basal metabolic rate showed significant positive relationships to body mass with similar mass exponents of 0.493 and 0.526, respectively. Overall, there was a significant correlation between daily energy expenditure and basal metabolic rate, but the mass-independent residuals (deviations from the allometrically predicted values) did not correlate. Carcass analysis revealed that a number of organs were slightly better predictors for daily energy expenditure and basal metabolic rate than was fresh body mass. Mass-independent residuals of lean dry heart mass and basal metabolic rate were positively correlated, which is in agreement with the idea that basal metabolic rate reflects the size of metabolically active organs. The study does not provide support for

an intraindividual association of basal metabolic rate with daily energy expenditure in the field.

## Introduction

The most widely assessed parameter in homeotherm energetics is basal metabolic rate (BMR), the minimum rate of energy expenditure of animals in a postabsorptive state under thermoneutral conditions in the inactive phase of the circadian cycle (Aschoff and Pohl 1970). BMR has long been considered a species-specific quantity determined primarily by body mass. The finding of a relationship between BMR and body mass with an exponent of 3/4 in between-species comparisons (Kleiber 1932; Brody 1945) initiated a long debate on biophysical models explaining this relationship (e.g., McMahon 1973; Heusner 1987). Recent analyses have demonstrated that the exponent varies with the taxonomic level of analysis, that is, species, genus, family, and so on (Hayssen and Lacy 1985; Elgar and Harvey 1987; Bennett and Harvey 1988). Furthermore, there are systematic differences between taxa that may be associated with variation in ecological niches, including feeding habits and climate (McNab 1986, 1988; Elgar and Harvey 1987). Clearly, BMR is not a simple biophysical consequence of body mass. To date, few studies have been dedicated to unravelling the real physiological nature of BMR.

It is well known that avian and mammalian tissues vary a great deal in metabolic rate (Field et al. 1939; Krebs 1950; Aschoff and Wever 1958; Hulbert and Else 1981). Some tissues, such as feathers and fur, are metabolically inactive. In the resting animal, skeleton muscles also have relatively low energy turnover compared with many of the internal organs in the thoraco-abdominal cavity and the brain. The highest metabolic rates of all tissues are usually found in the heart and kidneys (Krebs 1950; Aschoff and Wever 1958). Thus, even though these organs constitute only a small fraction of total body mass, their contribution to BMR may be disproportionately large. One might therefore anticipate that variation in BMR between and within species will be associated with variation in the relative size of the heart and kidneys. In an interspecific comparison of BMR and body composition in 22 species of birds, Daan et al. (1990) found that lean dry heart and kidney mass were indeed better predictors of BMR than was body mass. About half of the residual variance in BMR was explained by variation in heart and kidney mass. In mammals, the relationship between BMR and organ size so far has not received much atten-

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tion. In a study on laboratory mice acclimatized at different temperatures, it was found also that within a species a higher mass-independent BMR was associated with larger heart and kidneys (Konarzewski and Diamond 1994). Such an intraspecific approach to the study of the morphology and physiology underlying BMR has the advantage of excluding confounding ecological variables that occur in between-species comparisons. For the present study, we selected the field vole (*Microtus agrestis*) for an analysis of the intraspecific relation between BMR and body composition in animals from a natural population to assess whether some of the variation in BMR is indeed traceable to heart and kidney size.

Daan et al. (1990, 1991) suggested that the interspecific variation among birds in the relative size of heart and kidneys generally represents the activity of the metabolic machinery, which in itself may be adapted to support sustained peak energy metabolism in nature. This hypothesis was advanced to explain the proportionality of BMR and daily energy expenditure (DEE) first proposed by Drent and Daan (1980). Indeed, it has been found that the slope of the allometric relationship between log DEE and log body mass does not differ from the BMR to body mass relationship (Nagy 1987; Daan et al. 1990; Koteja 1991). Furthermore, a comparison of BMR and DEE during parental care in birds showed that mass-independent residuals of BMR and DEE were positively correlated (Daan et al. 1990). A similar relationship between BMR and field metabolic rate has been observed for mammals (Daan et al. 1991; Koteja 1991). In a recent analysis using phylogenetic contrasts, the mass-independent association of BMR and DEE turned out to be even stronger in mammals than in birds (Ricklefs et al. 1996). At the intraspecific level there is so far no evidence for an association between BMR and DEE (Konarzewski and Diamond 1994; Koteja 1996). Therefore, we measured DEE in free-living field voles using the doubly labelled water technique (Lifson and McClintock 1966), whereafter the same individuals were taken to the laboratory for assessing BMR and body composition.

### Material and Methods

The field site was located near Paterswolde in the northern Netherlands (53°09' N, 6°33' E). It was a meadow of about 0.25 ha, covered with a low to middle-high grassy vegetation. Besides the field vole, the study site was inhabited by other species of voles (*Microtus arvalis*, *Clethrionomys glareolus*), common shrews (*Sorex araneus*), and wood mice (*Apodemus sylvaticus*). Experiments were performed during the field vole reproductive season from June until October in 1989 and 1990. Some additional DEE measurements during the nonreproductive season were taken in February 1991.

During the period of the experiments, 48 Longworth live-traps were permanently placed at regular intervals in a grid of 4 × 12 fixed spots. Traps were filled with hay and baited with

grain and apple. When no experiments were being performed, the traps were arrested so that voles could enter and leave freely. On experimental days, traps were inspected at least every half hour. Voles caught were weighed, sexed, and on first occasion toe clipped for permanent identification. Individuals that were caught regularly were eventually selected for measurement of DEE. After DEE measurement they were taken to the laboratory for determining BMR and body composition. Animals selected for the experiments included nonreproductive subadults and both reproductive males and females. For males, reproductive status refers to individuals with fully developed testicles versus nonreproductive animals, which did not show obvious signs of testicular development. Young males with intermediate states of testicular development were not often seen in the population. For females, reproductive status refers to lactation versus no clear signs of reproductive activity. Since in voles lactation often overlaps with the next gestation, some of the females were in an early stage of pregnancy, as was assessed by later carcass analysis. Nevertheless, we think our selection of animals justifies an analysis with two reproductive categories for each sex.

### Daily Energy Expenditure

DEE was measured by means of doubly labelled water (Lifson and McClintock 1966; Nagy 1980). Animals trapped and selected for experiments were injected subcutaneously with 0.225 mL water containing H<sub>2</sub><sup>18</sup>O (90.23 atom%) and D<sub>2</sub>O (99.84 atom%) mixed in a ratio of 2.25 : 1. This dose was expected to be enough for an experiment of at least 2 d, based on a biological half-life of <sup>18</sup>O of about 0.6 d for a vole of 30 g, as calculated from a pilot study. After injection the voles were held in a box for at least 1 h to allow complete equilibration of the isotopes in the body water. Then an initial sample of isotopically enriched blood was taken by means of orbital puncture, body mass was determined, and the animal was released at the point of capture. Upon recapture about 24 or 48 h later, body mass was again determined and a second blood sample was taken. Blood samples were flame sealed in glass capillary tubes and analyzed later at the Laboratory for Isotope Physics in Groningen, the Netherlands. Water was extracted by vacuum distillation and analyzed for both isotopes by mass spectrometry. From the clearance rates of <sup>2</sup>H and <sup>18</sup>O in the initial and second sample, CO<sub>2</sub> production was calculated using equation (35) of Lifson and McClintock (1966). Because the amount of isotope injected was not always known accurately, body water volumes could not be reliably calculated from the dilution space for the injected <sup>18</sup>O molecules. Instead, body water content was set at 73.3% throughout, based on later carcass analysis. CO<sub>2</sub> production rates were converted to energy expenditure in kilojoules per day assuming an energy equivalent of 21.7 kJ L<sup>-1</sup> CO<sub>2</sub> for a plant diet (Kenagy et al. 1990).

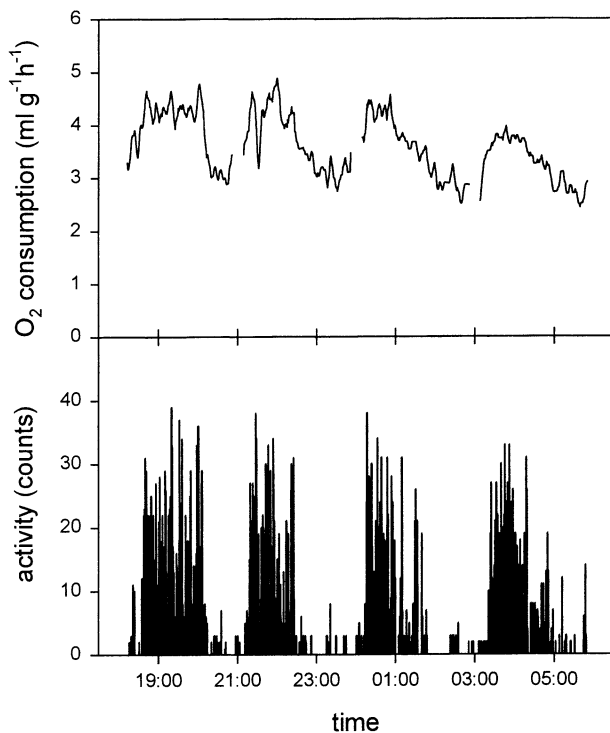


Figure 1. Recording of oxygen consumption and activity of an individual field vole, *Microtus agrestis*. Activity was recorded with a passive infrared sensor in the respiration chamber.

#### Basal Metabolic Rate

BMRs were derived from  $O_2$  consumption measured through analysis of respiratory gases in an open-circuit system. Voles caught in the field were taken to the laboratory around 4:00 P.M. and placed in a sealed respiration chamber ( $15 \times 10 \times 10$  cm). The respiration box was supplied with a thin layer of sawdust bedding. The animals had free access to water but were not fed from 2 h before the start of the measurement onwards. Measurements were performed overnight in a dark cabinet with ambient temperature controlled at  $28^\circ\text{C}$ . This temperature is known to be within the thermoneutral zone in voles (Wiegert 1961). Air was pumped through the respiration chamber, with a flow rate of  $75 \text{ L h}^{-1}$ .  $O_2$  concentrations of in- and outflow air, both dried with a molecular sieve (0.3 nm, granules approximately 2 mm, Merck), were recorded by a zirconium oxide sensor (S3A, Applied Electrochemistry). Calibration of the sensor was performed with dry air mixtures of known composition.

Field voles have an ultradian pattern in the organisation of their behaviour and physiology with a periodicity of 2–3 h, which is typical for microtine rodents (Lehmann 1976; Daan and Aschoff 1981; Gerkema and Daan 1985). Thus, during the 10–12-h period of the measurement, there was a series of four to five episodes with low levels of metabolism (Fig. 1). One may arbitrarily define BMR as the lowest level of  $O_2$  consump-

tion over a given amount of time, that is, per minute, per 10 min, per hour, and so forth. Using the extreme short calculation interval may lead to high stochastic variance, while long intervals will include periods of activity. Analyses of minimal metabolism versus calculation interval yielded monotonically increasing or reversed S-shaped curves as shown in Figure 2. We defined BMR as the minimal level of  $O_2$  consumption over an interval of 30 min, the trial interval that was virtually always at the plateau in the curve (see also Hayes et al. 1992). BMR was expressed in kilojoules per day, using an average energetic equivalent of  $20 \text{ kJ L}^{-1} O_2$  (Schmidt-Nielsen 1990).

#### Body Composition

After respirometry the animals were killed by ether overdose and stored in a freezer for later analysis of body composition. Carcass analysis was done by dissecting the body into the following components: brain, heart, lungs, liver, kidneys, spleen, digestive tract (empty), gonads, leg muscles, skin, and a remaining component, which included the skeleton and remaining muscles. Each component was weighed and then dried to constant mass in an oven at  $60^\circ\text{C}$  for at least 3 d. After reweighing to obtain dry mass, each component was packed in filter paper, and fat was extracted by washing six to eight times with heated petroleum benzine (Soxhlet technique). After fat extraction, all components were dried again to obtain lean dry mass.

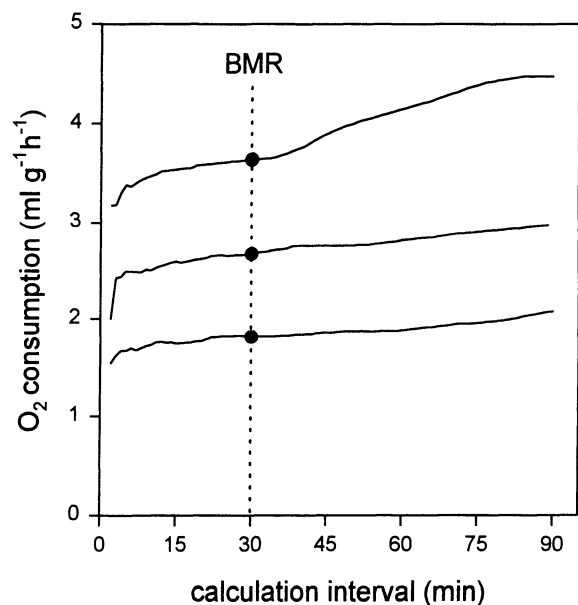


Figure 2. The minimal average  $O_2$  consumption in relation to the length of the interval used for calculation. Curves of three individual animals are shown, covering the range of  $O_2$  consumption levels present in the data set. The middle curve represents the vole whose pattern of  $O_2$  consumption and activity is shown in Figure 1. In the present study, BMR was defined as the lowest level of  $O_2$  consumption over a 30-min interval.

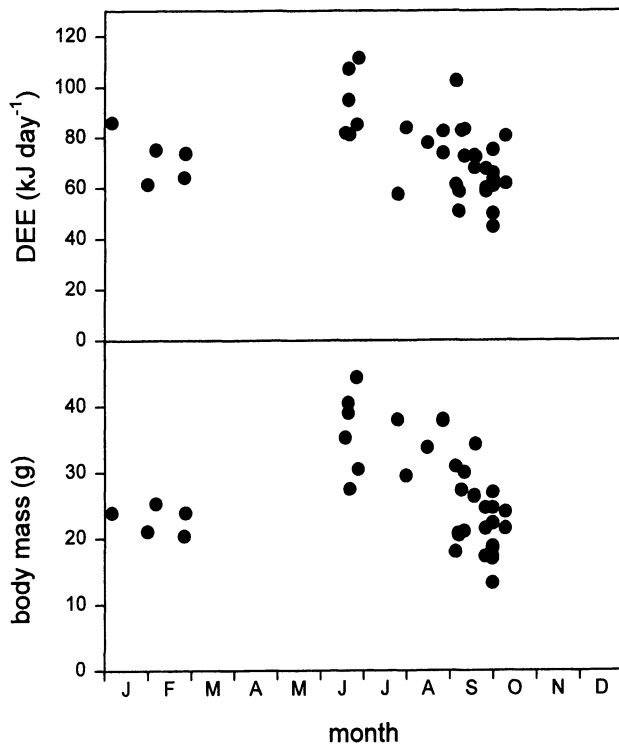


Figure 3. DEE and body mass in the field vole, *Microtus agrestis*, in relation to time of year.

#### Data Analysis

Relationships between energy expenditure, body mass, and component mass were examined by least squares regression analysis using log-transformed data (Zar 1984).

### Results

#### Daily Energy Expenditure in Free-Living Field Voles

During the reproductive season of two consecutive years, from June until October, DEE in the field was measured in 34 animals of different age and gender: 10 nonreproductive animals, 6 reproductive males, and 18 reproductive females. Five additional measurements were performed during the nonreproductive winter season following the second year. DEE and body mass throughout the year are shown in Figure 3. For the whole set of 39 voles, the average DEE was  $72.7 \text{ kJ d}^{-1}$  (SD = 15.1), with an average body weight of 26.5 g (SD = 7.6). Stepwise multiple regression was performed on log DEE ( $\text{kJ d}^{-1}$ ) using log body mass (g), gender (male = 0, female = 1), reproductive status (nonreproductive = 0, reproductive = 1), season (winter = 0, summer = 1), and all interactions as independent variables. Only body mass contributed significantly to the explained variance ( $r^2 = 0.470$ ) in DEE. The association between

DEE and body mass for the total group of animals (Fig. 4) is described by the equation:  $\log \text{DEE} (\text{kJ d}^{-1}) = 1.159 + 0.493 \log \text{mass} (\text{g})$  ( $n = 39$ ,  $r^2 = 0.470$ ,  $P < 0.001$ , SE of the exponent = 0.086). From this sample of 39 animals, 21 were taken to the laboratory directly after DEE measurement for determination of BMR and body composition: five males (three reproductive) and 16 females (12 reproductive). When only this subset of animals is considered, the relationship between DEE and body mass does not differ substantially from that using all animals:  $\log \text{DEE} (\text{kJ d}^{-1}) = 1.186 + 0.454 \log \text{mass} (\text{g})$  ( $n = 21$ ,  $r^2 = 0.437$ ,  $P < 0.01$ , SE of the exponent = 0.118).

#### Basal Metabolic Rate

During the months from June until October, a total of 32 voles of different age and gender were taken into the lab for determination of BMR and body composition: 11 males (four reproductive) and 21 females (13 reproductive). As described in the previous paragraph, in 21 of these animals field DEE had been measured during the preceding days. For the whole set of 32 animals, the average BMR was  $23.0 \text{ kJ d}^{-1}$  (SD = 5.6) and average body weight was 21.7 g (SD = 6.9). Stepwise

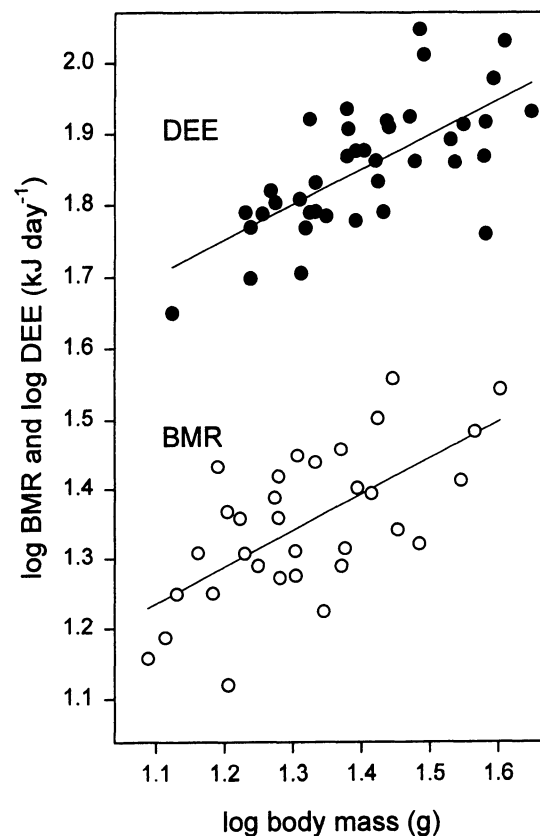


Figure 4. Allometric relationship of DEE and BMR with body mass in the field vole, *Microtus agrestis*.

multiple regression was performed on log BMR using log body mass, gender, reproductive status, and all interactions as independent variables. Only body mass contributed significantly to the explained variance ( $r^2 = 0.421$ ) in BMR. The association between BMR and body mass for the whole data set (Fig. 4) is described by the equation:  $\log \text{BMR (kJ d}^{-1}\text{)} = 0.657 + 0.526 \log \text{mass (g)}$  ( $n = 32$ ,  $r^2 = 0.421$ ,  $P < 0.001$ , SE of the exponent = 0.113). When only animals for which DEE was also determined are taken into account, the equation becomes:  $\log \text{BMR (kJ d}^{-1}\text{)} = 0.823 + 0.404 \log \text{mass (g)}$  ( $n = 21$ ,  $r^2 = 0.272$ ,  $P < 0.05$ , SE of the exponent = 0.152).

The ratio between DEE and BMR ranged from 1.8 to 4.5 and was on average 2.9 (SD = 0.6). This ratio was independent of body mass (linear regression,  $P > 0.10$ ). Overall, there was a significant correlation between log DEE and log BMR (linear regression,  $n = 21$ ,  $r^2 = 0.216$ ,  $P < 0.05$ ). To evaluate whether BMR and DEE were associated independent of the variation related to body weight, we tested for a relationship between mass-independent residuals. For the subsample of 21 voles for which both DEE and BMR were measured, we removed the influence of body mass by calculating the residual log BMR (log BMR measured – log BMR predicted from regression) and residual log DEE (log DEE measured – log DEE predicted from regression). The residual BMR and DEE were not significantly correlated ( $n = 21$ ,  $r^2 = 0.004$ ,  $P > 0.10$ ).

Although the regression analysis indicated that variation in both DEE and BMR was best explained by body mass and that gender or reproductive status did not have an additive effect, we also performed the above described residual analysis for different cohorts of animals. When the analysis was restricted to only males ( $n = 5$ ), to only females ( $n = 16$ ), to only reproductive females ( $n = 12$ ), or to reproductive animals of both sexes ( $n = 15$ : three males, 12 females), there was also no significant relationship found between DEE and BMR residuals ( $P > 0.10$  in all cases).

### Body Composition

Table 1 presents the different body components as fractions of body mass as well as the regressions of component mass on total body mass. This is done for both fresh and lean dry component mass. Since gonad tissue structurally differs between males and females, regressions in this case are given for the two sexes separately. As expected, most body components showed a significant positive correlation with body mass. The two exceptions are brain mass and total body fat. Brain mass appeared rather stable throughout the whole range of body weights represented in the sample. Consequently, brain mass seemed to be independent of age.

Table 2 presents the relationships of DEE and BMR with lean dry component mass, as well as with water and fat. Some of the components turned out to be better predictors of DEE and BMR than total fresh body mass, explaining more of the

variation in energy turnover. For DEE the best predictors were lungs, kidneys, and, for males, gonads. For BMR the better predictors were the heart, kidneys, liver, and, again for males, gonads.

For the subsamples of voles for which both DEE and body composition were determined ( $n = 21$ ), and the sample for which BMR and body composition were determined ( $n = 32$ ), we calculated the residual log component mass (log component mass measured – log component mass predicted from regression). No significant correlation was found between mass-independent DEE residuals and residuals of heart, kidney, or other organs. BMR residuals were significantly correlated with residual lean dry heart mass ( $n = 32$ ,  $r^2 = 0.140$ ,  $P < 0.05$ ). The correlation between BMR residuals and residual lean dry kidney mass was not significant ( $n = 32$ ,  $r^2 = 0.041$ ,  $P > 0.10$ ). Residual lean dry kidney mass did, however, show a significant positive relation with residual lean dry heart mass (Spearman  $r = 0.384$ ,  $n = 32$ ,  $P < 0.05$ ), indicating a trend in the expected direction. None of the other residual body components was correlated with residual BMR.

### Discussion

Variation in BMR in the field vole was best explained by body mass. Gender or reproductive activity did not have significant additive effects. However, these factors by themselves may of course have a large impact on body mass. BMR was related to body mass with an exponent of 0.526. This value is a little lower than the slopes found in most interspecific allometric relations of BMR in mammals (Hayssen and Lacy 1985; Elgar and Harvey 1987; Daan et al. 1991) or the exponent of 2/3 predicted for homomorphic change (Heusner 1984, 1987). One could indeed expect a smaller intraspecific slope since it seems that within the species a higher body mass is associated with a larger proportion of metabolically inactive tissue (Weinsier et al. 1992). In the voles, the amount of body water and the remaining component (containing mainly inactive tissues like skeleton and muscles) had mass exponents larger than 1. Several organs that are known to have a high metabolic rate, such as the heart, had mass exponents smaller than 1. Brain mass, probably also contributing a great deal to BMR (Aschoff and Wever 1958), was almost constant over the whole body mass range. In contrast to this, between-species comparisons have revealed a clear positive association between brain mass and body weight (Stahl 1965). Moreover, in interspecific analyses, metabolically active tissues like the heart and kidneys even have mass exponents close to 1 (Stahl 1965).

The body composition analysis revealed that a number of organs were slightly better predictors for BMR than is total fresh body mass: heart, kidneys, liver, and, in males, also gonads. The residuals of lean dry heart mass (deviations from the allometrically predicted values) were positively correlated with residuals of BMR. For the other body components, the

Table 1: Body composition in the field vole, *Microtus agrestis*

Component	Fresh Component				Lean Dry Component			
	% Total Mass	<i>a</i>	<i>b</i>	<i>r</i> <sup>2</sup>	% Total Mass	<i>a</i>	<i>b</i>	<i>r</i> <sup>2</sup>
Gonads:								
Males .....	1.81 (±1.88)	-6.41	4.22	.85	.34 (±.35)	-7.21	4.27	.85
Females .....	1.34 (±2.10)	-8.43	5.61	.57	.18 (±.24)	-8.48	5.09	.59
Brain .....	2.68 (±.90)	-.25	.05	.01 <sup>#</sup>	.41 (±.13)	-1.14	.01	.00 <sup>#</sup>
Heart .....	.93 (±.21)	-1.49	.56	.50	.22 (±.04)	-2.22	.60	.65
Lungs .....	1.50 (±.28)	-1.70	.88	.72	.30 (±.05)	-2.46	.93	.81
Kidneys .....	1.43 (±.16)	-1.82	.95	.90	.34 (±.04)	-2.45	.95	.88
Spleen .....	.34 (±.21)	-2.24	.76	.17	.08 (±.05)	-2.91	.78	.17
Liver .....	5.19 (±.77)	-1.10	.83	.79	1.30 (±.20)	-1.74	.86	.77
Gut .....	8.48 (±2.46)	-.43	.47	.24	1.74 (±.43)	-1.19	.53	.40
Leg muscles .....	8.71 (±1.29)	-1.37	1.21	.87	2.06 (±.34)	-2.06	1.25	.86
Skin .....	12.80 (±2.20)	-.72	.84	.70	5.38 (±.91)	-1.21	.93	.74
Remainings .....	43.68 (±4.43)	-.63	1.18	.93	12.46 (±1.21)	-1.16	1.19	.96
Water .....	...	...	...	...	73.34 (±2.76)	-.25	1.06	.98
Fat .....	...	...	...	...	2.18 (±1.63)	-.95	.37	.04 <sup>#</sup>

Note. Mass of fresh and lean dry carcass components are given as a percentage of fresh total body mass (±SD). Average body mass was 21.7 g (±6.9). Regressions of component mass on total body mass are described by the equation:  $\log \text{component mass(g)} = a + b \log \text{body mass(g)}$ .  $r^2$  = fraction of variance in log component mass explained by log body mass. In case of a nonsignificant relationship, the  $r^2$  is marked with #. Total data set on body composition:  $n = 32$ , 11 males and 21 females. For gonads, regressions are given separately for males and females. For all other components, the regressions include the total set of 32 animals.

Table 2: Relation between energy turnover and body composition in the field vole, *Microtus agrestis*

Component	DEE				BMR			
	<i>a</i>	<i>b</i>	<i>r</i> <sup>2</sup>	<i>P</i>	<i>a</i>	<i>b</i>	<i>r</i> <sup>2</sup>	<i>P</i>
Gonads:								
Males .....	2.00	.12	.74	<.01	1.55	.13	.57	<.01
Females .....	1.85	.03	.05	>.10	1.40	.03	.04	>.10
Brain .....	2.37	.49	.10	>.10	1.77	.37	.03	>.10
Heart .....	2.58	.56	.28	<.05	2.34	.72	.48	<.001
Lungs .....	2.42	.50	.53	<.001	1.96	.49	.40	<.001
Kidneys .....	2.38	.49	.52	<.001	2.00	.54	.45	<.001
Spleen .....	1.94	.07	.04	>.10	1.68	.17	.17	<.05
Liver .....	2.05	.40	.29	<.05	1.70	.58	.48	<.001
Gut .....	2.03	.44	.28	<.05	1.48	.28	.08	>.10
Leg muscles .....	1.95	.35	.46	<.001	1.49	.36	.35	<.001
Skin .....	1.81	.42	.40	<.01	1.35	.42	.31	<.01
Remainings .....	1.67	.38	.47	<.001	1.18	.41	.38	<.001
Water .....	1.22	.50	.50	<.001	.80	.47	.39	<.001
Fat .....	1.83	.04	.01	>.10	1.38	.06	.02	>.10
Total lean dry mass .....	1.49	.46	.49	<.001	1.04	.46	.38	<.001
Total fresh body mass .....	1.19	.45	.44	<.01	.66	.53	.42	<.001

Note. Regressions of log DEE and log BMR on log lean dry component mass and log fresh total body mass are described by the equation:  $\log \text{DEE or BMR (kJ d}^{-1}) = a + b \log \text{mass(g)}$ .  $r^2$  = fraction of variance in DEE or BMR explained by component mass or body mass. For DEE regressions:  $n = 21$  (five males and 16 females); for BMR regressions:  $n = 32$  (11 males and 21 females). For gonads, separate regressions are given for males and females.



residuals did not correlate with BMR residuals. The data are thus in agreement with the expectation that variation in BMR between individuals of the same species to some extent reflects variation in the size of metabolically active organs like the heart, as was first reported in an interspecific comparison in birds (Daan et al. 1990). Recently, also in a study in laboratory mice acclimatized at different temperatures, a correlation between mass-independent residuals of resting metabolic rate and heart and kidney size was found (Konarzewski and Diamond 1994). The relation between BMR and the size of metabolically active organs such as the heart thus seems to be a general phenomenon, occurring in mammals as well as in birds, both between and within species. Our study shows that the within-species relation between BMR and heart size also holds true for animals directly sampled from a natural population.

As was the case with BMR, variation in DEE in the field vole was best explained by body mass. Gender, reproductive activity, and season (winter or summer) did not have significant additional effects. Again, these factors by themselves may of course have a large impact on body mass. DEE was related to body mass with an exponent of 0.493. As with BMR, this slope is also somewhat lower than is found in most interspecific allometric relations in mammals (Nagy 1987; Daan et al. 1991; Koteja 1991). In the present study, lean mass of kidneys and lungs were slightly better predictors for DEE than was total fresh body mass. For males, gonad mass was also strongly correlated with DEE. However, for none of the body components was a correlation found between residual organ mass and residual DEE. Thus, the data obtained within one species do not support the idea that the size of the metabolic machinery is associated with the level of energy turnover in the field (Daan et al. 1990, 1991; Koteja 1991).

DEE in free-living field voles ranged from 1.8 to 4.5 times BMR, with an average of 2.9 (SD = 0.6). The DEE/BMR ratio did not depend on body mass. Overall, there was a significant correlation between DEE and BMR, as could be expected, since DEE and BMR were related to body mass with similar exponents. However, the mass-independent residuals (deviations from the allometrically predicted values) did not correlate, meaning that the interindividual variation in DEE is not reflected in the level of BMR, as was found for interspecific comparisons in both birds (Daan et al. 1990) and mammals (Daan et al. 1991; Koteja 1991; Ricklefs et al. 1996). Also, in other intraspecific studies concerning mass-independent variation in BMR and peak sustained metabolic rate, no correlation was found (Konarzewski and Diamond 1994; Koteja 1996). Thus, the hypothesis that BMR is a fixed ratio of DEE, and therefore a reliable index of energy expenditure of free-living animals (Daan et al. 1990; Koteja 1991), so far has no support at the intraspecific level. However, we should be aware that the hypothesis of a constant DEE/BMR ratio was advanced not for everyday existence but for maximal sustained natural energy metabolism such as that which occurs during parental

care (Daan et al. 1990). In cases where DEE is submaximal and liable to large fluctuations, one may not find a relation with BMR and body composition. Therefore, one could speculate that in the present study the association has broken down because individuals with a submaximal energy expenditure, for example, those in nonreproductive states, were included. However, when the analysis was performed for only reproductive animals, we also did not find a significant association between residuals of BMR and DEE. This analysis was necessarily restricted to a reduced size range and smaller number of data points, which renders definitive conclusions questionable. A further reason why an association at the intraspecific level is less likely to be established is the stochastic nature of within-species data. Each data point in the intraspecific analysis is based on a single measurement, while in interspecific analysis the database typically consists of averages over considerable numbers of measurements.

In conclusion, the present data confirmed the prediction that a large relative heart size goes hand in hand with high BMR, within a species and under natural conditions. The study did not provide support for an intraindividual association of BMR with DEE in the field.

#### Acknowledgments

We wish to thank Ina Everts, Magda Kalk, and Dico de Klein for practical assistance and Arjen Strijkstra and Menno Gerkenema for critically reading the manuscript.

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