Ann. Zool. Fennici 30:233–238
Helsinki 13 September 1993

ISSN 0003-455X

Metabolic rates of the bank voles (*Clethrionomys glareolus*) in Europe along a latitudinal gradient from Lapland to Bulgaria

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Received 26 June 1992, accepted 21 May 1993

Metabolic rates at the thermoneutral zone and at 0°C were measured in bank voles from four localities: Pallasjärvi (Finland, lat. 68°N), Loppi (Finland, 60°45′N), Niepołomice (Poland, 50°N) and Vitosha Mts. (Bulgaria, 43°N, elevation 1500 m). The seasonal times of measurement were chosen to secure that animals were in summer or winter pelage, respectively. Seasonal trends were found in body mass, metabolic rates at thermoneutrality and at 0°C, but no clear relation to latitude was revealed. We conclude that the lack of distinct popoulation differences in the metabolic response to cold exposure may be due to similarity in the microclimatic conditions of the habitats of the voles.

1. Introduction

The bank vole (*Clethrionomys glareolus* Schreber, 1780) is a species widely distributed in Europe, reaching beyond the Arctic Circle in the North, and to the Apennine and Balkan Peninsulas in the South (Fig. 1; Raczyński 1983). Such a broad distribution might have been achieved either by physiological adaptations in geographically separated populations to local environments, or by selection of habitats that assure similar microclimatic conditions over the whole range of species distribution. Indeed, in the southernmost part of its range, the species is found only in the mountains, evidently avoiding hot summer conditions. There is also much evidence that even during boreal winters the microclimate under the snow allows voles to reproduce (Kaikusalo & Tast 1984). Winter breeding in the bank vole has also been documented (Bujalska 1983).

On the other hand, it has also been shown for many species of rodents that they may develop both geographic and seasonal adjustments in physiology, to cope with the varying climatic conditions (Gòrecki et al. 1990, Heldmaier et al. 1990, Merrit & Zegers 1991). Seasonal changes in thermoregulatory heat production have also been found in the bank vole (Gòrecki 1968, Grodziński 1985, Klaus et al. 1988).

The aim of this study was to check whether a similar variation in metabolic characteristics occurs among the geographically distant populations of the bank vole.

2. Study sites, material and methods

Simple metabolic indices: oxygen consumption of postabsorptive, resting voles at thermoneutral temperatures (basal metabolic rate, BMR), and at 0°C, were measured in two seasons at four localities, using uniform procedures.

The populations studied came from sites located on almost the same meridian (20–24°E) but extending over a latitudinal distance of about 26 degrees (3000 km), from northern Finland to southern Bulgaria (Fig. 1). Basic environmental characteristics of all study sites are given in Table 1. In all these areas the bank vole populations occupy coniferous forests: a mixed pine-spruce forest with a rich layer of dwarf shrubs and moss at Pallasjärvi (Northern Finland); a spruce-dominated mixed forest in Loppi (Southern Finland); a mesic mixed pine forest with a rich understorey in Niepołomice (Southern Poland, near Krakòw); a montane spruce forest with admixture of pine in the Vitosha Mts., close to Sofia in Bulgaria.

In northern Finland, abundant and stable snow cover lasts from October to May. In southern Finland, and even more so in Poland, the snow conditions are much more variable and occasionally snow-melts may occur during winter. In the Vitosha Mts., similar to the situation in northern Finland, the snow cover lasts from mid-October till the end of May (Table 1).

The animals were trapped and transferred to the university laboratories in Helsinki (Pallasjärvi

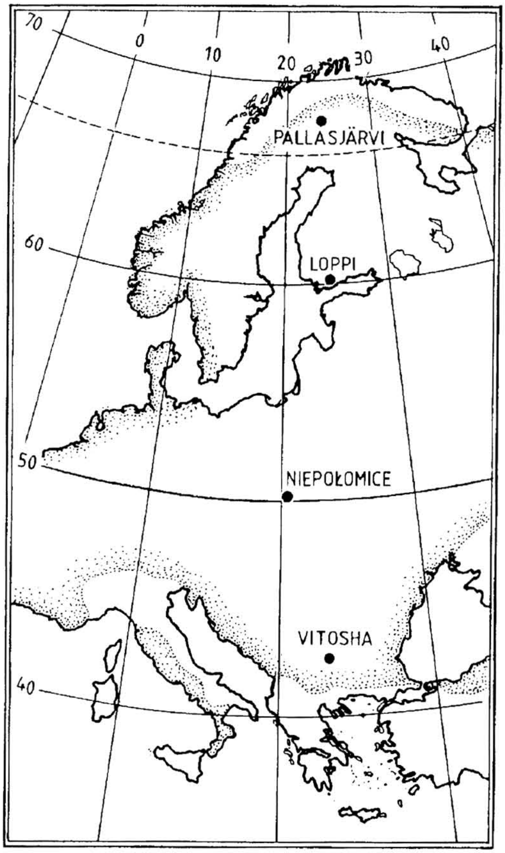

Fig. 1. Limits of distribution of the bank vole, *Clethrionomys glareolus*, in Europe (dotted) and locations of study sites.

Table 1. Description of research sites.

Locality	Position		Altitude (m asl)	Coldest and warmest mean monthly temp.		Snow cover	Sample size summer	Sample size autumn
Pallasjärvi	68°03′N	24°9′E	270	−14°C	+13°C	Oct.–May	19	16–17
Loppi	60°45′N	24°30′E	110	−8°C	+16°C	Dec.–Apr.	13	18–20
Niepołomice	50°05′N	20°20′E	190	−4.8°C	+17.9°C	End Dec.–Feb.	8–22	21–24
Vitosha Mts.	43°35′N	23°16′E	1700	−8.3°C	+9°C	Oct.–May	11	11–17

and Loppi voles: experiments in 1981–1982), Krakòw (Niepołomice voles; 1981) and Sofia (Vitosha Mts. voles; 1985 and 1987), where they were kept for about three days before the study. The voles trapped in Finland (Pallasjärvi and Loppi) in June were mature individuals from a breeding population. Those trapped in autumn were subadult. The cyclic Pallasjärvi population peaked in 1981–1983 (Laine & Hettonen 1987), whereas the population at Loppi was in an undetermined state, as it is not a cyclic one and had not been monitored. In other localities (Niepołomice, Vitosha Mts.) the summer samples already contained subadults and adults in unknown proportions.

Metabolic rates were measured in a closed-system Kalabukhov-Skvortzov's respirometer (Gòrecki 1975). Before measurements the animals were deprived of food for 3 hours to achieve a postabsorptive state. Then, after being weighed to the nearest 0.1 g, voles were placed in metal cages (4 × 4 × 7 cm) that restricted their mobility. The cages were then placed in plastic chambers of 0.5 l capacity and submerged in a temperature-controlled water bath. Each trial lasting 20 min. was preceded by an acclimation period of about 20 min. at the corresponding temperature. All measurements were performed during the daytime. Summer experiments were executed in June (Helsinki, Sofia) or August (Krakòw). The schedule of autumn series was adjusted to the time of a complete pelage change into the winter coat. Thus, the autumn measurements were done at the end of September/beginning of October with the voles from Pallasjärvi, in late October/early November with these from Loppi and Krakòw, and in November in Sofia.

Measurements were made at temperatures representing the thermoneutral zone (+25°C in Sofia or 30°C in Krakòw and Helsinki), and in 0°C (all localities). The measurements of body temperatures taken at the end of each trial proved to be flawed with systematic errors; therefore, they are neither reported here nor used in any calculations. The results are expressed as ml O_2/h/animal, and per unit body weight (ml O_2/g/h).

At all localities and seasons groups of 8 to 22 individuals were used (Table 1), with quite a similar proportion of each sex. The effects of season and locality upon the group means were estimated using two-way ANOVA (non-orthogonal design: method of fitted constants and weighted means). If sex was taken into account as the third factor (body mass analysis), 3-way ANOVA (non-orthogonal design, method of unweighed means) was applied. Scheffe's method was used for multiple contrasts.

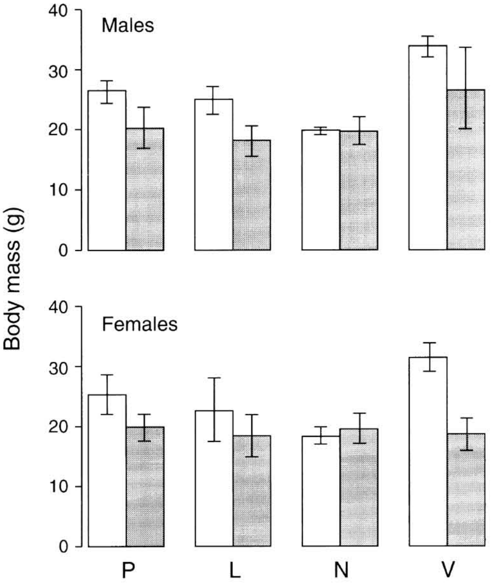

Fig. 2. Body mass (g, averages and *SD*) of bank voles from various localities and seasons. White bars: summer; shaded bars: autumn. P – Pallasjärvi, L – Loppi, N – Niepołomice, V – Vitosha Mts.

3. Results

3.1. Body mass

The effects of sex, season and locality upon the body mass were all significant ($P < 0.01$, 3-way ANOVA). In all localities female voles tended to be smaller than males (but all pairwise Scheffe's contrast were not significant); autumn animals were usually smaller than summer ones (Fig. 2). Only in Niepołomice was the seasonal difference not significant. Summer animals in the Vitosha Mts. were distinctly larger than any other bank voles under study, whereas autumnal voles from Loppi, and all voles from Niepołomice were the smallest (Fig. 2).

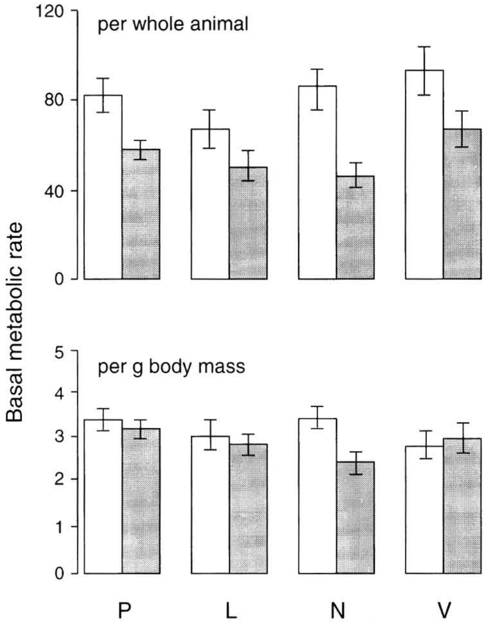

Fig. 3. Basal metabolic rates (cm^3O_2/h) of bank voles from various localities and seasons (other explanations as in Fig. 2).

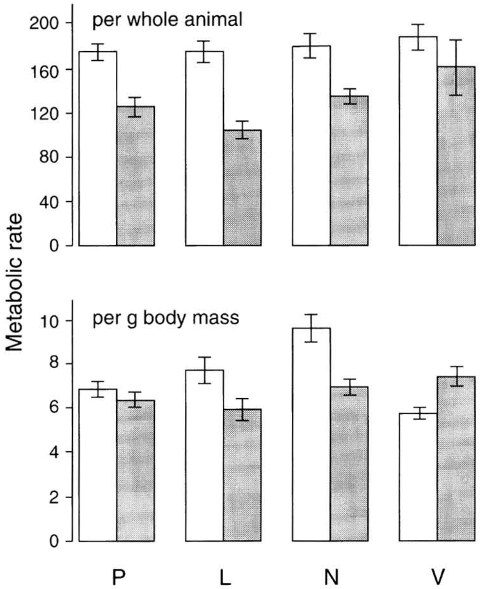

Fig 4. Metabolic rates (cm^3O_2/h) of bank voles from various localities and seasons at an ambient temperature of 0°C.

3.2. Basal metabolic rate (BMR)

Since no effect of sex upon the BMR was revealed (3-way ANOVA), in all further analyses the sexes were treated jointly and only two factors, season and locality, were taken into consideration.

The summer values of BMR were consistently higher than in autumn (Fig. 3). This effect is statistically significant when BMR is expressed per whole body as well as per 1 g of the body mass (2-way ANOVA). Seasonal differences in BMR (per gram) were significant only in Niepołomice and and Vitosha (Scheffe's pairwise comparisons; $P < 0.05$).

The effect of locality upon the BMR was obscured, owing to a significant interaction ($P < 0.05$). The BMR values in autumn tend to differ more between localities than they do in summer (Fig. 3). The lowest BMR occurred in Niepołomice voles in autumn (44.6 cm^3 O_2/h/animal, or 2.3 cm^3 O_2/g/h), the highest (on per-gram basis) in Niepołomice and in Pallasjärvi in summer (3.41 and 3.31 cm^3 O_2/g/h, respectively; Fig. 3). Whole animal BMR's were greatest in the Vitosha Mts. and in Niepołomice in summer (91.9 and 83.9 cm^3 O_2/h/per animal, respectively; Fig. 3).

3.3. Metabolic rates at O°C

In all localities the bank voles developed distinctly higher metabolic rates when thermoregulating at O°C in summer, than they did in autumn ($P < 0.01$; Fig. 4). This pattern is less apparent when the metabolic rate is expressed per gram of the body mass (Fig. 4). The lowest metabolic rates at 0°C were attained by the autumn-acclimated voles from Loppi (104.9 cm^3 O_2/h/animal), the highest by the summer bank voles from the Vitosha Mts. (163.2 cm^3 O_2/h/animal; Fig. 4). During summer the metabolic rates of voles from all populations were almost equal (Fig. 4).

The whole-body metabolic rates at 0°C were 2.35 ($SD = 0.34$) times larger than the BMR values at the same season and locality.

4. Discussion

The bank voles from the Vitosha Mts. were the largest of all the voles studied (Fig. 2). This character, among others, has prompted some authors to distinguish a separate subspecies: *C. g.*

pirinus (Christov & Markov 1972), which is not, however, recognized by others (Raczyński 1983). In autumn the female bank voles from all localities were almost of the same size; among males only the voles from the Vitosha Mts. were larger then the others, but the large variation in this group (Fig. 2) may suggest that the transition from the summer to winter body mass had not yet been completed in this area.

Hence, it seems that 19–20 g is a characteristic autumnal body weight for bank voles over their whole range of occurrence, while in summer the voles attain larger body sizes, with some local variation. The summer body mass increment is largest in the Vitosha Mts., and smallest in Niepołomice. This results in a much greater geographical variation in body mass during summer than during autumn (Fig. 2).

On the other hand, the reproductive status and the exact age of the animals have not been recorded for all samples. Some variation in body weight(s), as well as in metabolic rate(s), may be due to the different proportions of adult and subadults in particular experimental groups.

In small mammals the body-mass change is the most pronounced effect of seasonal acclimatization (Dehnel 1949, Hyvärinen & Heikura 1971, Merrit 1984, Merrit & Zegers 1991). This is true also for *Clethrionomys glareolus* (Sawicka-Kapusta 1974, Grodziński 1985). It has been shown that their smaller winter body size may help Djungarian hamsters to diminish their energy expenditure for thermoregulation, in spite of the increased area/volume ratio of the body (Heldmaier & Steinlechner 1981). Indeed, the smaller bank voles in autumn use substantially less energy to thermoregulate at 0°C: they use 14% less in the Vitosha Mts. to as much as 40.5% less in Loppi (Fig. 4).

The autumnal metabolic rates at 0°C are lower than in summer also when expressed per gram of body mass (ANOVA, $P < 0.01$), although the difference is much smaller (Scheffe's contrasts are statistically significant only in Niepołomice; in the Vitosha Mts. the per-gram metabolic rate at 0°C was higher during autumn than in summer; Fig. 4). This suggests that besides the smaller body size, other factors (most probably improved insulation) contribute to the energy savings.

If the challenge of climatic conditions is to be reflected in the degree of seasonal acclimatization, then the most difficult conditions for bank voles should be expected in southern Finland. The main reason is the relatively harsh winter temperature regime with a very variable snow cover, and a poor food supply (Table 1). On the other hand, the subarctic population enjoys relatively stable and mild conditions under the snow. This is also true for the montane population of bank voles located some 3000 km further south in Bulgaria. The bank voles in southern Poland are much more exposed to the local climate than are the northern Finnish and Bulgarian populations, but the temperature conditions are milder in Poland.

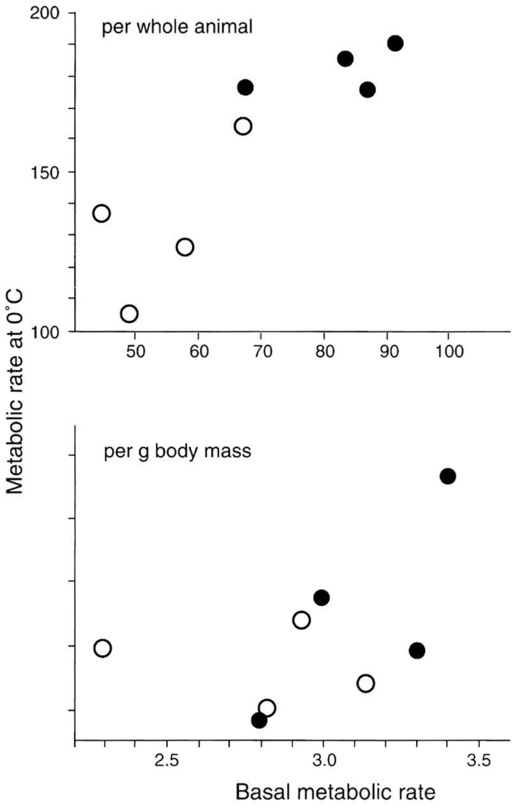

Fig 5. Correlation between basal metabolic rates and metabolic rates at 0°C in bank vole populations from various localities in two seasons. Open circles: summer values, closed circles: autumn values.

The summer values of BMR expressed per whole body were consistently higher than the autumn values. When expressed per g body weight this difference remains significant only for the Niepołomice voles (Fig. 3). This suggests a genuine difference between BMRs in summer and in autumn, because Niepołomice is the only locality in which body weights in both seasons were almost identical. In all other localities body weights of the summer animals were higher than of those trapped in autumn. Larger animals have lower metabolic rates per unit body weight, which offsets the effect of a higher BMR in the summer.

Whole animal metabolic rates at basal conditions, and at 0°C, are strongly correlated ($r = 0.88$, $df = 6$, $P < 0.05$; Fig. 5), but this relationship is much weaker if metabolic rates are recalculated per g of the body mass ($r = 0.47$, $df = 6$, $P > 0.25$; Fig. 5). The association between the BMR and other metabolic indices have been intensively discussed (Koteja 1987, 1991). The patterns revealed in this study suggest that BMR may indeed be functionally linked with energy budgets in natural conditions. On the other hand, the common procedure of making comparisons of metabolic rates expressed per g of body-mass may be invalid if the species under study demonstrates a body mass variation related to season and/or geographical provenance.

Acknowledgements. This study was possible as a result of the exchange program between the University of Helsinki and the Jagiellonian University in Krakòw. The concept of this study was initiated by the late Professor W. Grodziński. The authors are indebted to Dr. Heikki Henttonen for critically reading the manuscript.

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