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Metabolic Rate and Energy Budget in the Bank Vole*

[With 4 Figs & 7 Tables]

The average daily metabolism rate (*ADMR*), basal metabolism rate (*BMR*), and resting metabolism rate (*RMR*) have been studied during different seasons in the bank vole, *Clethrionomys glareolus* (Schreber, 1780) ($N = 140$) from southern Poland. *ADMR* has been determined for diurnal runs in big chambers, while *BMR* and *RMR* measurements lasted for 1—2 hours and were taken in small chambers. *ADMR* measured at 20°C is highest during summer — 0.494 kcal/g/day, and lowest during winter — 0.420 kcal/g/day. The intensity of heat production for thermoregulation within the range of actual environmental temperatures is somewhat lower in winter (5.27%/°C) than in summer (6.04%/°C). *BMR* in the thermoneutral zone (30°C) amounts to 2.33 cm³ of O₂/g/hour. During the maximum activity the metabolism increases by 90% in voles. Voles kept in groups, consisting of two to four animals, lowered their daily metabolism rate on an average by 13.3%. During all seasons the activity rhythm had a two-peaks patterns, mainly nocturnal one. Voles are active for the longest time during summer, while for the shortest one — during autumn. *ADMR* was accepted as a base for the daily energy budget (*DEB*) in voles. It allowed for heat production for thermoregulation in nest and outside it, amendments for group effect and breeding costs. So calculated *DEB* expressed in kcal/g/day amounts to 0.486 in winter and 0.556 in summer. The *DEB* calculated for a vole with mean body weight of 21 g amounts to 10.2 kcal during a winter day and to 10.6 kcal (19 g) during a summer day.

I. INTRODUCTION

The bank vole, *Clethrionomys glareolus* (Schreber, 1780) is a dominant rodent in majority of forests within the European moderate zone. It inhabits almost whole Europe and the western part of Asia. The vole plays an important role in the functioning of forest ecosystems, and often becomes a serious pest in forest management. This is very likely the reason why the bank voles became a frequent and favourite object of ecological studies, both field population studies and laboratory ones on breeding biology, food, metabolism, etc.

* This study was carried out under the Small Mammal Project of the International Biological Programme in Poland.

Resting metabolism rate (*RMR*) of voles has been studied on several occasions and from various standpoints. There were found differences in metabolism connected with geographical variation (Smirnov, 1957; Bashenina, 1965; Grodziński & Górecki, 1967), seasonal variation (Sun-žu jun, 1958; Smirin, 1961; Bashenina, 1966; Visinescu, 1965; 1967; Górecki 1966), age and body weight variation (Grodziński, 1961). Also the influence of increased activity of voles upon the resting metabolism rate (*RMR*) was studied (Jánský, 1958). However, the average daily metabolism rate (*ADMR*) in voles has never been determined and which provides the most convenient base for the calculation of bioenergetic balances and seems to be the most »ecological« measure of metabolism.

The purpose of this work was the determination of diurnal energy requirements of bank voles and the construction of their bioenergetic model just from the average daily metabolism rate (*ADMR*), measured by oxygen consumption. Since the enormous majority of assimilated energy is spent by rodents on cost of maintenance (Davis & Golley, 1963) and only its small portion on the tissue production therefore the development of possibly precise model of their bioenergetics is indispensable for the calculation of energy flow through the population of the animals.

II. MATERIAL AND METHODS

The bank voles for experiments were trapped in beech woods (*Fegetum carpaticum*) in the Ojców National Park near Kraków (50° 13'N, 19° 40'E). Before each experiment animals have been acclimated to laboratory conditions during the period of 2–3 days — with illumination rhythm similar to natural one (Grodziński, 1965¹); Smirin, 1961; Górecki, 1966). During autumn and spring 12 hours of daylight were maintained, in winter — 8 hours, and in summer — 16 hours. During all experiments animals were fed with a mixture of oats and wheat, and carrot. Water and food were given always in surplus.

Metabolism rate was measured in voles by oxygen consumption and in the whole work there were used three measures of metabolism. These measures differed fundamentally in the duration of measurements and in size of chambers, in which animals were confined.

1. The average daily metabolism rate (*ADMR*) presents an average value obtained from 24 hours measurements in large chambers, at the temperature similar to that, in which the animal lives. It was determined in 9 l metabolic chambers connected with modified Morrison's respirometer (Morrison, 1951) at the temperature of 20°C. These chambers, with the size of 37×19×16 cm, were built of aluminium, provided with Metaplex (methyl methacrylate) cover which enabled the observation of animals during experiment. In the chamber there was placed a cage made of metal net (33.5×16×12 cm), in which animal was confined and a container with granulated potassium hydroxide, absorber of carbon dioxide. Cages were supplied with a nest, running wheel, feeder, and drinking bottle. Before and after each measurement animals were weighed and

¹ Grodziński W., »Program of bioenergetics studies on the productivity of small rodents«. 1965. M. S.

their rectal temperature was measured with telethermistor thermometer. Altogether during four seasons *ADMR* was determined in 74 voles, and in each species oxygen consumption was measured for 16 up to 21 animals (Table 1).

2. Basal metabolism rate (*BMR*) represents the minimum value of consumed oxygen in the thermoneutral zone, during periods of complete quietness (Blaxter, 1966; Grodziński & Górecki, 1967). Before measurement the animal was starved during several hours to eliminate specific-dynamic action of food (*SDA*) — (Kleiber, 1961). The thermoneutral zone in voles is situated between temperatures of 28 and 30°C (Bashenina, 1958; 1966; Pearson, 1962; Górecki, 1966; Visinescu, 1967) and therefore the *BMR* was measured at temperatures of 28, 30, and 32°C, measurements were taken at this temperature, in small chambers with the volume of *circa* 145 cm³ which were connected also with Morrison's respirometer. Chambers for the determination of basal metabolism were built of stainless sheet with size of *ca* 5×3×10 cm. In these chambers there were placed tiny cages made of network (3×3×7.5 cm), around which granulated KOH was placed. The measurement lasted for about 2 hours and for

Table 1.

Bank vole material used in subsequent seasons for *ADMR* measurements.

Season & Month	Number of voles	Sex		Body weight (in g)	C.v. (in %)
		♂	♀		
Spring — May	16	8	8	23.9±3.5	14.8
Summer — July	17	9	8	23.7±3.9	16.6
Autumn — November	20	9	11	19.3±2.4	12.4
Winter — February	21	9	12	19.8±3.5	17.6
Total & Means	74	35	39	21.7±3.3	15.4

calculations, periods with the lowest oxygen consumption were selected (McNab & Morrison, 1963). Basal metabolism rate was studied in 16 bank voles during summer.

3. Resting metabolism rate (*RMR*) exceeds the value of *BMR* by *SDA* and, usually, by thermoregulation costs at temperatures lower than thermoneutral zone. This metabolism has been measured in a modified Kalabukhov-Skvortzov respirometer (Kalabukhov, 1951; 1962; Skvortzov, 1957) in one hour runs, in small cages (4×4×9 cm), without nest, considerably restricting the mobility of voles. The resting metabolism rate and thermoregulation in voles have been measured here at intervals of 5°C within the range of environmental temperatures from 0 up to +35°C. Altogether 231 measurements were taken in 45 voles during summer and winter (Table 4).

All metabolism measurements involved 140 bank voles (Table 1, 4).

There was also studied so-called »group effect« in voles through the determination of *ADMR* for groups of two and groups of four animals kept together in metabolic chamber and its later comparison with the *ADMR* of the same voles examined singly. There were taken here 29 diurnal measurements of the average daily metabolism rate.

Parallely to *ADMR* measurements in these same voles there were recorded the rhythm and sum of diurnal activity in metabolic chambers. Two-way contacts

for the registration of the duration of animal staying in nest and on »run« were installed in nesting houses (Górecki & Hanusz, 1968). The running of voles in the installed wheel with the diameter of ca 12 cm was recorded in the same metabolic cages (Kalabukhov, 1951).

Oxygen consumption, duration of staying in nest and outside it, and running in wheel have been recorded on 12 path Jaquet's polygraph (Electro-Polygraph Jaquet No. 662), with the speed of tape travel at 0.5 mm/sec. (18 cm/hour). The number of turns for wheel has been additionally recorded by counters.

Besides two other procedural experiments were carried out: the influence of duration of animal stay in metabolic chambers upon *ADMR* value and the influence of cage size upon diurnal activity of voles were examined. In the first experiment there voles were kept in metabolic chambers during three subsequent days and nights and during all this time oxygen consumption was recorded in the second experiment rhythm and sums of diurnal activity were recorded in 16 voles in large cages of »Białowieża« type (with size of 40×25×14 cm), and later compared with the activity of the same animals recorded in metabolic chambers. Significance of differences were examined with Student's test *t*.

III. RESULTS

1. Average Daily Metabolism Rate (*ADMR*)

ADMR is highest in voles during summer, somewhat lower during spring and appeared to be lowest during autumn and winter (Table 2).

Table 2.

Average daily metabolism rate (*ADMR*), maximum and minimum metabolism rate in voles in diurnal cycle. All values relating to the temperature of +20°C.

Season	N	Body temp. (°C)	<i>ADMR</i> in ccm O ₂ /g/h		<i>BMR</i> in ccm O ₂ /g/h			
			Avg. ± S.D.	C.v. (in %)	Max. ± S.D.	C.v. (in %)	Min. ± S.D.	C.v. (in %)
Spring	16	37.0	4.07±0.62	15.2	6.14±0.80	29.3	3.33±0.57	17.1
Summer	17	37.2	4.29±0.64	14.9	6.64±0.58	8.7	3.36±0.75	45.0
Autumn	20	37.1	3.79±0.36	9.5	5.29±0.69	13.0	2.93±0.45	15.3
Winter	21	37.1	3.65±0.53	14.5	6.03±0.84	13.9	3.80±0.47	12.3
Mean for year	—	37.1	3.95±0.54	13.5	6.02±0.98	16.2	3.09±0.56	19.3

For the above conversions there was accepted the respiratory quotient (*RQ*) = 0.8, in which the caloric value of 1 l of oxygen corresponds with 4.8 kcal (Kleiber, 1961).

The values obtained for summer differed statistically significant (*P* < 0.02) from values for winter and autumn, in spite of fact that body weight in voles was in summer significantly higher (*P* < 0.001) than body weight in winter and autumn (Fig. 1).

During a complete rest (sleep) and during short spells of maximum activity (usually running of vole in wheel) one can well compare metabolism in daily measurements of *ADMR*. Oxygen consumption during maximum activity amounts on an average for the whole year to $6.02 \text{ cm}^3/\text{g}/\text{hour}$ (Table 2), while during the complete rest (usually

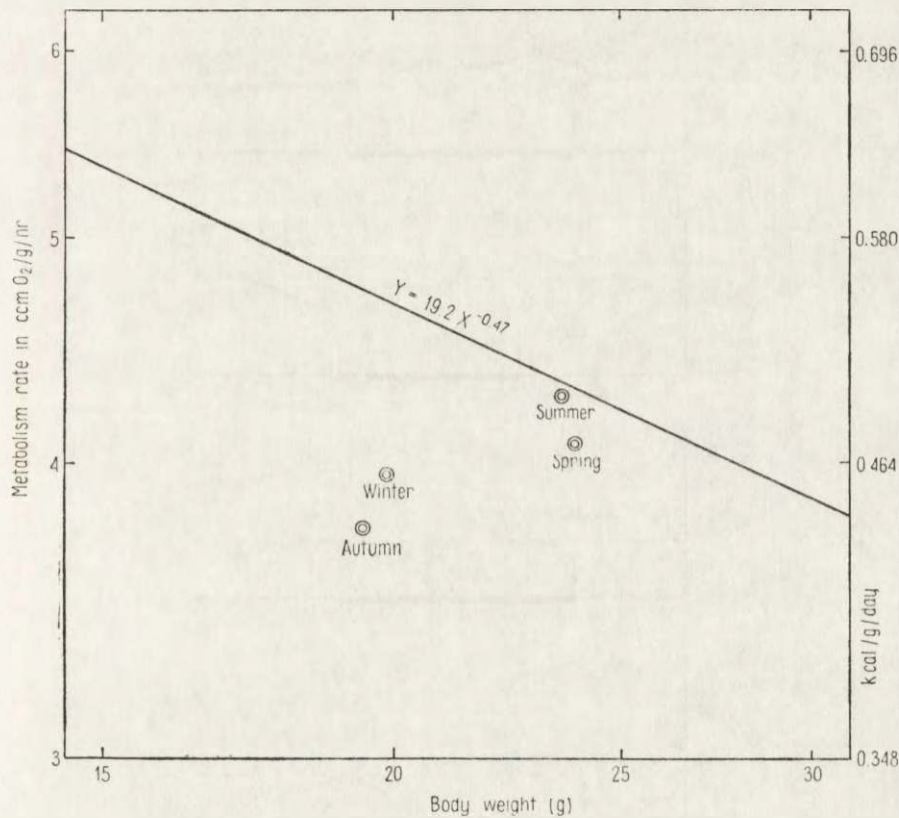


Fig. 1. Average daily metabolism rate (*ADMR*) in bank voles in various seasons in relation to their body weight (double logarithmic scale). For comparison the regression line representing summer values of *ADMR* for several rodent species. After Grodziński & Górecki (1967) slightly modified.

sleep) the consumption is lower by *circa* 90% (Table 2). The ratio between maximum and minimum oxygen consumption is rather similar during all seasons and is always included within limits of 1.59—1.97 (Table 2).

Body temperatures in voles measured before and after each *ADMR* measurement during all seasons were almost identical and amounted on an average to 37.1°C on annual basis (Table 2).

Diurnal activity rhythm expressed by oxygen consumption (at two hour intervals) was compared for studied seasons (Fig. 2). The highest metabolism rate occurred, in general, in studied animals at twilight and at dawn, and differences in oxygen consumption were always lower than 20%. Two hour intervals use for calculations obviously

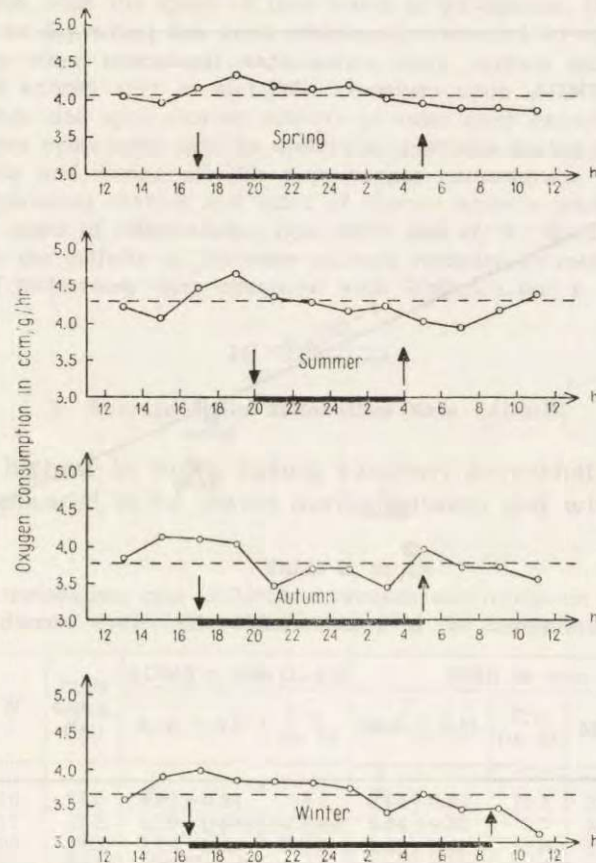


Fig. 2. Daily rhythm of metabolism rate in bank voles in various seasons. The intermittent line stands for *ADMR* level. Arrows denote duration of night. All curves represent mean values for 16–21 individuals.

levels the curve of oxygen consumption because voles in the course of day and night cycle have many short spells of intensive activity (Gródzinski, 1962).

The average daily metabolism rate does not depend upon the duration of animal stay in metabolic chamber. Oxygen consumption during the first day and night cycle was almost identical with oxygen consumption in the subsequent second and third cycle. During the first

day animals consumed 0.389 ± 0.07 kcal/g/24 hours and in the second and third cycle together — on an average 0.380 ± 0.06 kcal/g/hour. These differences are not significant statistically ($P > 0.5$).

The extent of *ADMR* does not depend upon sex and is connected exclusively with the body size. And so, *e.g.* during and autumn, when body weights in males and females were almost identical (in winter 19.7 and 19.9 g and in autumn 19.2 and 18.8 g) the average daily metabolism rate in males and females was also almost identical. In winter it differed only by 1.5%, oxygen consumption in males amounted on an average to $3.81 \text{ cm}^3/\text{g}/\text{hour}$, while in females — to $3.76 \text{ cm}^3/\text{g}/\text{hour}$. In autumn such difference was even smaller and amounted to ca 1%; here males consumed on an average 3.78 cm^3 of $\text{O}_2/\text{g}/\text{hour}$, while females — 3.82 cm^3 of $\text{O}_2/\text{g}/\text{hour}$. Corresponding differences in spring and summer are also statistically insignificant and result exclusively from differences in body weight between males and females.

Table 3.

Relationship between metabolism rate and body weight.

Body wt. (in g)	Summer		Spring	
	N	ccm/g/hr	N	ccm/g/hr
17.0—20.0	—	—	5	4.88
20.1—23.0	4	4.71	7	4.10
23.1—28.0	8	4.20	4	3.63
28.1—32.0	5	3.76	—	—

ADMR reveals on the other hand a clear correlation with animal size. In spite of fact that the material was very uniform in respect to body weight (coefficient of variation was in all seasons lower than 18% — Table 1), nevertheless in two seasons with the highest variation it was possible to classify animals into three classes of body weight and to follow the variation in *ADMR* in them (Table 3). In the two remaining seasons voles were classified into two classes of body weight. Lighter (younger) animals consumed distinctly more oxygen per body weight unit, when compared with heavier (older) animals.

2. Daily Activity of Voles

The sum of daily activity in voles, measured by the time of animal staying outside the nest, amounts on an average for the whole year to 3 hours and 47 minutes. The longest activity show voles during summer, since not less than 4 hours and 23 minutes (Table 4). When activity

duration in summer is accepted as 100%, then in winter voles are active about 89% of this time, during spring — 85%, while in autumn only about 73% of summer activity (Table 4). During all seasons males have somewhat higher sums of activity (from 8 to 12 minutes) than females but these differences are not statistically significant.

During winter the activity of voles was examined as control in large cages of »Białowieża« type and it was compared with sums and rhythm of activity determined for these same voles in metabolic chambers. Activity rhythm was very similar to that determined in chambers, while the sum of daily activity was almost identical. For the two compared groups of 16 and 21 voles mean sums of activity differed only by 2 minutes, with no statistical difference.

Table 4.
Daily activity of voles at various seasons.

Season	N	Activity out—of—the—nest			Running on the wheel (min.)*
		minutes \pm S.D	C.v. (in %)	Hours and min.	
Spring	16	223.0 \pm 12.8	5.74	3 43	158.2
Summer	17	263.4 \pm 24.8	9.41	4 23	196.8
Autumn	20	190.2 \pm 12.9	6.78	3 10	95.0
Winter	21	233.1 \pm 17.5	7.50	3 53	94.1
Means for year	—	227.4 \pm 17.0	7.36	3 47	151.0

*) Four or five voles have used the activity wheel in each season.

During all four seasons activity rhythm in voles was distinguished by split standard (A s c h o f f, 1966) — mainly nocturnal (bigeminus). Generally both peaks of activity occur during night hours, one after darkness, another one before dawn (Fig. 3). The whole activity rhythm outside the nest overlaps to a considerable degree with the rhythm obtained from oxygen consumption by voles (compare Fig. 2).

During summer, and to a lesser extent during autumn, in relation to the shortest night, one of the peaks, occurring between 12 p. m. and 2 a. m., is by far more conspicuous than other one which occurs about 8 p. m. (Fig. 3).

The time of maximum activity — animals running in wheel was also highest in summer — 196.8 min./day (Table 4, Fig. 2). In autumn and winter the time of running in wheel was twofold lesser (on an average 94.5 minutes/day). These results concern, however, only 20 to 30% of the studied voles in each series, since only they run in wheel at all. At

the maximum during a day there were recorded for one of the studied voles in summer about 9.500 turns of the wheel with a diameter equal to 12 cm, what is an equivalent of the way of about 3.6 km long.

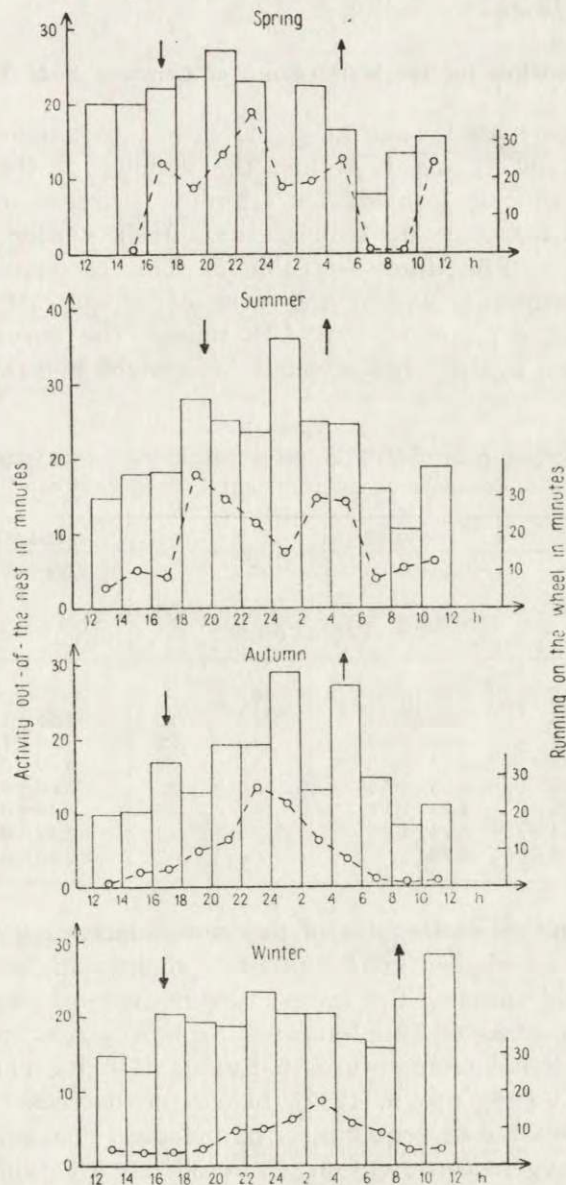


Fig. 3. Daily rhythm of activity in voles during four seasons. Columns — duration of animal activity outside nest in minutes (mean for 16—21 voles). Intermittent line — animal running in wheel in minutes (mean for 4—5 voles, which used wheel). Scale of activity in wheel is by twice smaller, than that for the total activity. Arrows denote the duration of night.

Rhythm of vole running in wheel is, similar as the activity rhythm outside nest two-peaks nocturnal in spring and mixed one in summer. On the other hand in autumn and winter it is distinctly one-peaked, also nocturnal (Fig. 3).

3. Heat Production for the Maintenance of Constant Body Temperature

During winter season voles have the lowest metabolism rate at the temperature of 30°C and it is just the vicinity of this point where thermoneutral zone is located. The absolute increase in oxygen consumption from this zone up to 0°C amounts in winter to 6.17 cm³/g/hour (increase = 2.62 times — Table 5). This corresponding increase in oxygen consumption within the zone of 30 to 5°C is lower and amounts to 4.87 cm³/g/hour, *i. e.* 1.78 times. The curve for chemical thermoregulation in voles has a course of straight line (Fig. 4, Table 5).

Table 5.

Resting metabolism rate (RMR) in voles expressed by oxygen consumption under various environmental temperatures.

Ambient temperature (°C)	Winter			Summer		
	N	Oxygen consumption		N	Oxygen consumption	
		ccm/g/h ± S.D.	C.v. (in %)		ccm/g/h ± S.D.	C.v. (in %)
0	8	9.96 ± 0.81	8.1	—	—	—
5	13	8.66 ± 0.31	3.6	22	8.55 ± 1.20	14.0
10	13	7.08 ± 0.73	10.3	22	7.16 ± 1.03	14.5
15	13	6.08 ± 0.72	11.9	22	6.49 ± 0.88	13.5
20	14	4.83 ± 0.75	15.6	22	5.00 ± 0.56	11.3
25	15	4.20 ± 0.76	18.1	22	4.16 ± 0.57	13.7
30	14	3.79 ± 0.72	19.0	22	3.52 ± 0.62	17.5
35	2	4.53 ± —	—	7	3.43 ± 0.61	17.6

In summer the general course of thermoregulation curve is similar to winter curve, but oxygen consumption is slightly higher here (Fig. 4, Table 5). During summer the lowest consumption of oxygen occurs at the temperature of 35°C. This temperature, however, is adjacent already to the zone of lethal temperatures for voles (Bashenina, 1966; Górecki, 1966; Visinescu, 1967), hence the decrease in metabolism may present here the consequence of pathological changes. The absolute increase in oxygen consumption from 30 to 5°C amounts to 5.02 cm³/g/hour, *i. e.* 2.42 times (Table 5).

Heat production calculated in cal/g/hour/°C differ somewhat in winter and in summer. Within the whole studied zone it amounted during winter to 0.987 cal/g/hour/°C — (0 to 30°C), in summer it was lower —

0.965 cal/g/hour/°C — (5 — 30°C). When, however, heat production will be compared within the range of environmental temperatures occurring under natural conditions (*e. g.* in beech forest near Cracow), then in winter within the range of 0—20°C the production amounts to 1.31 cal/g/hour/°C what is equivalent to 5.29%/°C, while in summer — with range from 15 to 20°C it is distinctly higher and amounts to 1.45 cal/g/hour/°C or 6.04%/°C. This difference is partially the result of

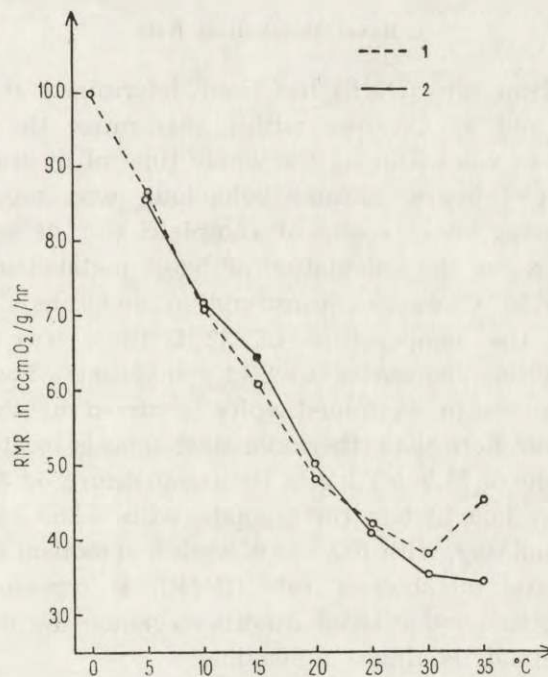


Fig. 4. Curves of chemical thermoregulation in voles during winter (1) and summer (2).

seasonal changes in isolation properties is partially the result of seasonal changes in isolation properties of body.

Isolation index was calculated according to the formula by Hart & Héroux (1955).

$$Ii = \frac{\text{Body temperature} - \text{Environmental temperature}}{\text{Oxygen consumption}}$$

Body temperature in voles within the range of environmental temperatures from 0 to 35°C did not reveal any serious directional changes and all measurements were included within limits of 36.3 up to 38.0°C.

Hence as a base for calculation the mean for 30 voles — temperature of 37.4° C has been accepted. Voles from winter season have at all examined temperatures by far better isolation properties than voles from the summer season. Within the whole range of temperatures isolative properties in voles from winter are higher by some 7%, while within the range of temperatures 5—20° it is higher by not less than 12% in voles from winter season.

4. Basal Metabolism Rate

Basal metabolism rate (*BMR*) has been determined at three temperatures: 28, 30, and 32° C, since within this range the thermoneutral zone is enclosed in voles. During the whole time of measurement, which lasted for about 2 hours, animal behaviour was recorded. Oxygen consumption during short spells of complete rest of animal was exclusively selected for the calculation of basal metabolism rate. At the temperature of 28° C oxygen consumption amounted to 2.60 ± 0.34 cm³/g/hour. At the temperature of 32° C there was a very similar oxygen consumption amounting to 2.42 ± 0.26 cm³/g/hour. The lowest oxygen consumption in examined voles occurred at the temperature of 30° C since just here their thermoneutral zone is located. Voles with mean body weight of 24.6 ± 1.1 g at the temperature of 30° C consumed 2.33 ± 0.25 cm³/g/hour what corresponds with 0.269 ± 0.36 kcal/g/day or 6.62 kcal/animal/day, with *RQ* = 0.8. Such metabolism is not obviously entirely the basal metabolism rate (*BMR*), it represents rather the value of metabolism under basal conditions, since the measurement of *BMR* in wild animals is almost impossible.

5. Thermal Economy of »Group Effect«

Average daily metabolism rate (*ADMR*) in the group of two voles kept together, when converted into gram of body weight amounts to 3.20 ± 0.15 cm³O₂/g/hour, what corresponds with 0.369 ± 0.028 kcal/g/day. Four voles kept together consume 3.29 ± 0.38 cm³O₂/g/hour what is equivalent to 0.379 ± 0.030 kcal/g/day. Thus two voles decrease their metabolism by 13.9%, while four voles decrease it only by 12.7%. Reasons for the lesser lowering of metabolism by a larger group of animals might be sought after in the utilization of nest. Two voles always slept together in nesting house, while out of four animals usually only two or three were sleeping in nest, while remaining ones, in spite of the previous accommodation of animals to each other, were on the run during all the day.

IV. DISCUSSION OF RESULTS

1. Metabolism Rate in Bank Voles

Many authors on numerous occasions determined *RMR* for bank voles. Results of these measurements obtained at the temperature of 20°C deviate from each other rather considerably (Table 6). All are contained within rather broad limits from 3.27 to 6.82 ccm/g/hour. Results of *RMR* obtained in the present paper are also contained within these limits.

Table 6.

Basal metabolism rate (*BMR*) and resting metabolism rate (*RMR*) in voles determined by oxygen consumption according to various authors. Data arranged according to the increasing body weight.

Body weight (in g)	ccm/g/hr		Autor & type of respirometer
	<i>BMR</i> or <i>RMR</i> in 30°C	<i>RMR</i> in 20°C	
17.5	2.21	3.72	Pearson, (1962) — 1
17.5	3.20	3.30	Jánský, (1958) — 1
19.5	3.52	4.98	Górecki, (1966) — 2
20.0	2.70	3.27	Visinescu, (1965; 1967) — 2
20.0 ?	2.84	3.90	Bashenina, (1966) — 2
20.9	—	5.37	Grodziński, (1961) — 2
21.0	2.86	—	Rigaudiere & Delost, (1964) — 3
22.0	3.45	6.82	Sun-Zu-jun, (1958) — 2
24.0	3.10	4.85	Smirin, (1961) — 2
24.6	2.33	—	This study — 4

1 — Haldan; 2 — Kalabukhov & Skvortzov; 3 — Bargetons; 4 — Morrison.

Differences in *RMR* are probably connected with geographical variation in metabolism rate (Bashenina, 1965; Grodziński & Górecki, 1967), seasonal one (Sun-Zu-jun, 1958; Smirin, 1961; Bashenina, 1966; Visinescu, 1965, 1967; Górecki, 1966), age and body weight one (Grodziński, 1961). This variation results also from various accuracy of measurements in various types of respirometers (Table 6). Northern vole populations at +20°C are distinguished in general by a higher *RMR*, than forms from the south. Seasonal differences in metabolic rate are very concordant with different authors. Winter metabolism is almost always lower, than the summer one. Smaller voles have the higher oxygen consumption per unit of their body weight (Table 6).

From *RMR* values obtained in short runs one can calculate the daily oxygen consumption, which for values from Table 6 will be contained between 0.358 kcal/g/day and 0.786 kcal/g/day. So calculated the daily energy requirement is, however, burdened with rather serious error,

since *RMR* is not very »ecological« measure of metabolism. During a short measurement in a cramped cage without nest, rodents are probably so stressed that in spite of limited activity their metabolism rate is higher, than in the 24-hour runs of *ADMR*, in which periods of increased activity and rest are summed (Grodziński & Górecki, 1967).

Indicated differences between *RMR* and *ADMR* in vole, measured at 20° C reach the value of 32% in winter and 16% in summer, *RMR* being always higher. Similar difference for *Apodemus flavicollis* amounts to some 19% (Gębczyński, 1966), while for *Microtus arvalis* — to 18% (Grodziński, 1967). In these both cases *RMR* is also higher, than *ADMR*, what may be explained mainly by the lack of nest in chambers for *RMR* measurements. These values are quite reliable, since in all mentioned rodent species, both measurements of metabolic rate were taken on the same animals.

2. Energetic Costs of Activity

In order to construct the daily energy budget (*DEB*) it is necessary to answer two questions: (1) how the normal activity of rodent increases its metabolism, (2) for how long animal is active throughout diurnal cycle or what is its rhythm (pattern) of activity.

When voles are forced to intensive running on wheel (Jánský, 1958), such »working« metabolism exceeds its *BMR* by 4 times during longer spells of effort, and during short, maximum efforts even by 7 times. Under natural conditions voles never perform such drastic efforts.

With 24-hours long *ADMR* measurements one can compare the metabolism rate during spells of sleep (*RMR*) and short spells of maximum activity. This ratio reaches 1.5 in *Clethrionomys rutilus* and 1.6 in *Microtus oeconomus* (Grodziński, 1966) and similarly (1.6) in *Pitymys subterraneus* (Gębczyński, 1964). Results obtained in the present work are very similar, the ratio amounting to 1.9 in *Clethrionomys glareolus* (Table 2). And so, under the impact of increased activity the metabolism rate in mice and common voles is increased only by 50—100% in relation to *RMR*.

There are much more numerous laboratory data about the daily activity of small rodents, than field observations. The diurnal sum of activity is in winter usually smaller than in summer, and additionally in winter animals are active mainly during warmer hours of a day (Osterman, 1956). Females of mice are throughout a year usually less active than males (Saint Girons, 1960; 1966), what was confirmed also in the present work.

Bank voles represent the group of rodents with a two-peaks activity pattern, mainly, but not exclusively, nocturnal (Buchalczyk, 1964), (Fig. 2, 3). Their activity lasts for 2—4 hours in winter and up to 5 hours in summer (Smirnov, 1957; Saint Girons, 1960; 1961; Grodziński, 1962; Pearson, 1962). They are thus active for about 20—25% of daily cycle (Table 4).

3. Daily Energy Budget (*DEB*) Calculated From the Average Daily Metabolism Rate (*ADMR*)

Daily energy requirements of rodents might be at best determined on the base of *ADMR* or *BMR*, or *RMR*. First of them gives more empirical, simple model of daily bioenergetics, in which corrections are restricted to thermoregulation out-of-the-nest, to the influence of »group effect« and breeding costs. Models based on *BMR* and *RMR* are by far more speculative.

Pearson (1948) was first who used the value of daily metabolism rate, afterwards Grodziński (1966) defined *ADMR* and suggested budgets based on this value, what has been developed in further papers (Gębczyński, 1966; Grodziński & Górecki, 1967).

Other ecologists constructed bioenergetic models based on »pure« *RMR* values (Pearson, 1960) and some took here allowances for activity and thermoregulation costs (Grodziński, 1961; Wiegert, 1961). Finally McNab (1963) started from *BMR* and *RMR* created the most mathematical model of the daily energy budget (*DEB*).

3.1. Thermoregulation

Heat production for thermoregulation presents the main item in rodent bioenergetics. Intensity of chemical thermoregulation, measured by oxygen consumption, was determined by Bashenina (1966 a) for voles on 5.24%/°C in winter and 7.92%/°C in summer (for the range of 5—30°C). These results are higher from those obtained in the present work for the identical range of temperatures (Table 5, Fig. 4) by about 28% in winter and not less than 95% in summer; they are also slightly higher than results obtained by Sun-Žujun (1958). Visinescu (1967) found the lower intensity of chemical thermoregulation in voles during winter (3.1%/°C), while in remaining seasons it was higher (on an average 4.2%/°C). It could hardly be decided if so considerable differences in thermoregulation are connected with geographical variation (Moscow — Cracov — Ploesti) or whether they result from different procedure of measurements.

The lower intensity of chemical thermoregulation in winter rodents

owing to the better physical thermoregulation, as well as mechanisms of metabolism adaptation (Hart, 1964; Jánský, 1965). In bank and common voles the insulating power of winter fur is increased by 5 up to 13% in relation to the summer one (Bashenina, 1962; Gębczyński & Olszewski, 1963; Górecki, 1966). Changes in insulating power depend mainly upon the increase in fur thickness, as well as upon the number of hair, first of all downy one (Volčaneckaja, 1954; Bashenina, 1962).

3.2. Influence of »Group Effect« and Breeding Period

»Group effect« and the period of pregnancy and lactation modify very remarkably the daily level of metabolism rate in voles. The first of them decreases slightly the energetic requirement in all animals, while the other increases it considerably in breeding females. Ponugaeva (1960) found that rodents kept in groups of 3—5 animals, lower their metabolism rate by 8 to 17%. In the present work the decrease of metabolic rate by the group of voles (two up to four animals) studied together amounted to 13%. This allowance is remarkable in *DEB*, since most of their diurnal cycle voles spend in groups in nests.

The bank vole is the only one rodent in wild, for which the bioenergetics of pregnancy and lactation has been studied (Kaczmarecki, 1966). To bear and raise one litter the bank vole female has to assimilate additionally 364 kcal, out of which for lactation (18—20 days) there falls not less than 289 kcal. Energetic requirement of pregnant bank vole is higher on an average by 24%, while that of the lactating one — by not less than 92%. One can accept most generally that the energetic requirement of females during breeding season is raised by more than a half (on an average by 58%).

3.3. Bioclimate of Vole Environment

In order to combine data about the thermoregulation in voles with their diurnal activity, one should determine thermal relations of their habitats, *i. e.* nest and the inhabited area. Considerable portion of a day voles spend in nests (Table 4), which function as well isolated thermostats and permit a considerable lowering of metabolic rate. Pearson (1960) determined this lowering in metabolic rate in *Reintrodontomys* on some 17%, Grodziński (*in litt.*) obtained for *Microtus arvalis* a similar result — decrease in metabolic rate by not less than 24%.

In the nest of bank vole there was recorded during a longer period of time a very uniform temperature of 17—19° C, with a negligible day

and night amplitude ($\pm 2.2^{\circ}\text{C}$) (Daniel, 1964). Nest temperature is lower than that in thermoneutral zones in voles (30°C), but it is very close to their thermopreferendum ($18\text{--}23^{\circ}\text{C}$ — Kalabukhov, 1957).

In summer, during vegetation season, temperature fluctuations in the close-to-ground air layer are very small owing to forest floor vegetation. In winter voles move usually below snow, where prevail considerably higher temperatures, than on surface. Due to this voles have environmental temperature close to 0°C or by only few centigrade degrees lower (Coulianos & Johnels, 1962). In beech forest in vicinity of Cracow these temperatures amount in winter (January, February) close to ground to *circa* 0°C , while in summer (June until August) to some 15°C (Klein, 1967; Klein, *in litt.*).

3.4. Daily Energy Budget (DEB)

Seasonal differences in the intensity of heat production, body insulation power, and also in environmental climate are quite remarkable. In winter and in summer these parameters differ most radically. This is why the construction of at least two models of daily bioenergetics (DEB) in voles: summer and winter budgets — is necessary.

ADMR of bank vole determined by oxygen consumption at the temperature of 20°C reaches $4.29\text{ cm}^3/\text{g}/\text{hour}$ in summer and $3.65\text{ cm}^3/\text{g}/\text{hour}$ in winter, what corresponds with 0.494 and $0.420\text{ kcal}/\text{g}/\text{day}$ (Table 2, 7). During summer vole stays outside the nest for 4.5 hours, while in winter — for 4 hours (Table 4, 7). The level of metabolism in voles at nest temperature of $17\text{--}19^{\circ}\text{C}$ (Daniel, *l. c.*) is higher than ADMR measured at 20°C by $10\text{--}12\%$ (Table 5). »Group effect« in nest, lowering the metabolic rate in voles by 13% on average, entirely eliminates, however, this correction. Thus it is fully justified simplification to accept ADMR values for the time of animal stay in the nest (Table 7). Environmental temperature of voles in beech forest in vicinity of Cracow amounts during winter to *circa* 0°C and to 15°C in summer (Klein, 1967). Intensity of heat production from 20°C to these temperatures amounts during summer months to $6.04\%/^{\circ}\text{C}$, while in winter — to $5.29\%/^{\circ}\text{C}$. Thus the increase in oxygen consumption outside the nest is almost doubled (by 92%) in winter, while in summer only by 30% (Table 7). During hours of running activity the energy consumption reaches thus on summer day — $1.204\text{ kcal}/\text{g}$ and on winter day — $1.350\text{ kcal}/\text{g}$.

Correction for breeding concerns exclusively the summer DEB. Sex ratio in bank vole population amounts to $1:1$ while the per cent of breeding females reaches on average $20\text{--}25\%$ (Kubik, 1965). When

Table 7.
Daily energy budget (*DEB*) in bank vole during winter and summer day.

	W i n t e r (kcal/g/day)	S u m m e r (kcal/g/day)
<i>ADMR</i> (20°C) in the nest, including group effect (13%)	20 hr × 3.65 ccm O ₂ /g/hr = 0.351	19.5 hr × 4.29 ccm O ₂ /g/hr = 0.401
Metabolic rate during periods of out-of-the-nest activity (0°C or 15°C)	4 hr × 7.03 ccm O ₂ /g/hr = 0.135	4.5 hr × 5.57 ccm O ₂ /g/hr = 0.121
Cost of reproduction	—	6.5% <i>ADMR</i> = 0.034
Corrected <i>ADMR</i> values × average body weight <i>DEB</i> in kcal/voles/day	0.486 × 21.0 g 10.21	0.556 × 19.0 g 10.56

the allowance for the period of pregnancy and lactation (on an average 58% increase in metabolism rate K a c z m a r s k i, *l. c.*) will be distributed among all individuals in population, it will amount to about 6.5% (Table 7).

ADMR together with discussed corrections is distinctly higher in summer, than in winter (0.556 and 0.486 kcal/g/day). The mean body weight in adult voles amounted in beech forest in the vicinity of Cracow to about 21 g in winter and 19 g in summer. *DEB* calculated for such animals amounts in summer to 10.56 and in winter to 10.21 kcal/vole/day. The fact that the winter *DEB* is less expensive, than the summer one, is probably possible owing to the acclimatization of metabolism to lower temperatures, to the better insulating power of body, and to the reduction of activity outside the nest in winter, and also owing to the thermal economics of a nest. The winter budget in vole is also not burdened with cost of breeding.

4. Daily Energy Budget (*DEB*) Calculated From the Basal Metabolism Rate (*BMR*)

BMR is the most physiological and comparable measure of metabolism (K a y s e r & H e u s n e r, 1964). There were numerous attempts of studying it in voles in various types of respirometers (Table 6). For voles with body weight from 17.5 up to 24.6 g the *BMR* measured by oxygen consumption by various authors has been included within limits of 2.21 to 3.52 cm³/g/hour (Table 6). The value obtained in the present work (2.33 cm³ of O₂/g/hour) is close to the lowest known determinations for the bank vole (Table 6). The *BMR* per the unit of body weight may be calculated from the equation: $M = 3.42 W^{-0.25}$ ($\log M = \log 3.42 - 0.25 \log W$) — K l e i b e r, 1961, where *M* — so-called »predicted« metabolism rate in cm³ of O₂/g/hour, *W* — body weight in grams.

Such calculated metabolism amounts for these same voles from 1.47 to 1.67 cm³ of O₂/g/hour and is by far lower than obtained in experimental way. The difference is lowest with measurements with the aid of Morrison's respirometer (by some 58%), while with measurements with other types of respirometers it is very high and fluctuates from 83 to 122%.

M c N a b (1963) suggests the calculation of *DEB* just from *BMR*. The basis provides here oxygen consumption within thermoneutral zone, to which M c N a b (*l. c.*) adds first of all corrections for activity and for heat production at temperatures below thermoneutral zone.

DEBs for vole in a summer day were calculated according to M c N a b's model. *BMR* empirically determined as 2.33 cm³ of O₂/g/hour was accepted as a basis. This value has been measured, how-

ever, on a series of rather big voles ($\bar{x} = 24.6$ g), while the mean body weight in voles during summer amounted to about 19.0 g. The *BMR* value »reduced« for vole with 19 g (according to regression function — Grodziński & Górecki, 1967) reaches about 3.0 cm³ of O₂/g/hour. During the vole's stay in the nest one should add some 30% increase in *BMR* within the range of temperatures 30—20° C, what for 19.5 hours amounts to about 0.365 kcal/g. During animal's stay outside the nest (in summer about 4.5 hour) at the temperature of 15° C the metabolism rate will be increased in relation to *BMR* by some 55%, what gives 0.110 kcal/g. Altogether during a diurnal cycle vole will disperse 0.475 kcal/g. In summer vole is active for about 1/5 of a day and during its activity the metabolism rate is increased by 60—95% (Table 2). When converted into the whole diurnal cycle the activity will amount to *circa* 15% of energetic expenses. The *DEB* of whole animal will be thus closed definitely in $19 \text{ g} \times 0.546 \text{ kcal/g/day} = 10.37 \text{ kcal/animal/day}$.

DEB calculated from *ADMR* for an animal with the same weight of 19 g amounts to 10.56 kcal/day and thus is almost identical (Table 6). One should, however, keep in mind that McNab's (*l. c.*) budget does not allow for breeding costs. When increased by these costs (6.5%) it would be only slightly higher than the budget based on *ADMR* (with *BMR* = 11.05, while with *ADMR* — 10.56 kcal/animal/day).

The difference between both budgets is thus negligible (4.4%) and the calculation of budget from *BMR* is more complicated, since one has not to correct the *DEB* calculated from *ADMR* by activity, which is already included in *ADMR* measurement.

When such calculated budgets of the bank vole would be compared with budgets for other species of common voles and mice (Grodziński & Górecki, *l. c.*) they are rather similar. Values of all these *DEBs* are closed within limits from 10 up to 15 kcal/animal/day. Rodent species with various body weights may have a similar bioenergetics owing to the negative correlation between metabolic rate and body weight.

5. Verification of *DEB* Model For the Bank Vole

The daily energy budget for voles calculated from respiration may be verified with feeding tests. Results obtained for the bank vole with simple methods of food rations (Górecki & Gębczyńska, 1962) amount to 0.690 kcal/g/day and are higher by about 51% when compared with the annual mean calculated from *ADMR*. Results obtained in a similar way by Grodziński (1962) amount to 0.596 kcal/g/day, thus exceeding data obtained from *ADMR* by some 30%.

In nutritional experiments carried out in metabolic cages, when animal during the experiment does not change its body weight, all the assimilated energy is equal to maintenance costs (Blaxter, 1966; Drożdż, 1967; 1968). This is why the assimilated energy may be compared with respiration measured as *ADMR*. Daily costs of maintenance in vole at the temperature of 20°C calculated from assimilated energy reach 0.558 kcal/g/day with compound diet (Drożdż, 1968). *ADMR* determined in the present paper at the same season amounts to 0.494 kcal/g/day, and thus the value calculated from the food balance is higher by about 11.5%. The difference may be, however, attributed to the lack of nest in metabolic cage and to a lesser extent also to the influence of activity (Pearson, 1960; Grodziński, 1967; Grodziński & Górecki, 1967).

Until now there is none good method for the determination of metabolism in small rodents under natural conditions. For larger animals such method may provide telemetric measurements, in which respiration rhythm, heart rhythm and body temperature of animal is recorded (Folk, 1966), on the base of which the metabolism of these animals might be rather accurately calculated. Further development in telemetry and miniturization of electronic elements will perhaps enable the future use of this method for small rodents (Rawson & Hartline, 1964).

Another method, which undergoes an intensive development, provides the determination of metabolism of animals in field with the aid of the measurement of radioisotope excretion (e.g. Zn^{65} — Golley, Wiegert & Walter, 1965; Golley, 1967). This method requires, however, further studies, which would permit to correlate metabolism with the bioelimination of radioisotopes.

Acknowledgment: I wish to express my thanks to Dr. W. Grodziński for valuable advice during this investigation and critical reading of the manuscript.

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Received, April 3, 1968.

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METABOLIZM I BUDŻET ENERGETYCZNY NORNICY RUDEJ

Streszczenie

W celu określenia dziennego zapotrzebowania energetycznego nornic rudyh, *Clethrionomys glareolus* (Schreber, 1780) i skonstruowania modelu ich bioenergetyki zbadano respirację tych zwierząt w różnych sezonach (Tabela 1, 4). Łącznie u 140 nornic przestudiowano średni metabolizm dobowy (ADMR), meta-

bolizm podstawowy (*BMR*), oraz metabolizm spoczynkowy (*RMR*). *ADMR* określano w przebiegach dobowych w dużych komorach wyposażonych w gniazdo i pokarm, podczas gdy pomiary *BMR* i *RMR* trwały 1–2 godzin i odbywały się w małych klatkach. Równoległe z metabolizmem dobowym u tych samych nornic rejestrowano rytm i sumy aktywności dobowej.

1. *ADMR* mierzony w 20°C jest najwyższy w okresie lata — 0,494 kcal/g/dobę, a najniższy w zimie — 0,420 kcal/g/dobę. Wartości dla wiosny i jesieni są pośrednie (0,469 i 0,437 kcal/g/dobę). Wartości uzyskane dla lata różniły się statystycznie od wartości dla zimy i jesieni (Tabela 1, 2, Ryc. 1).

2. Przy maksymalnej aktywności metabolizm nornic wzrasta o 90% (minimalny poziom metabolizmu w ciągu doby — 3,09 cm³ O₂/g/godz. maksymalny 6,02 cm³ O₂/g/godz. Tabela 2, Ryc. 2).

3. Wartość *ADMR* nie jest związana z płcią, wykazuje natomiast wyraźną korelację z wielkością ciała zwierząt. Zawsze zwierzęta lżejsze (młodsze) posiadały wyższy metabolizm na jednostkę ciężaru ciała, niż zwierzęta cięższe (starsze) (Tab. 3).

4. Suma aktywności dobowej osiąga u nornic średnio dla całego roku 3 godz. 47 minut. Najdłużej nornice są aktywne w okresie lata (4 godziny i 23 minuty), a najkrócej w jesieni (3 godziny i 10 min.). Zimą i wiosną są aktywne średnio 3 godz. i 48 minut. We wszystkich sezonach rytm aktywności odznaczał się wzorcem dwudzielnym, głównie nocnym (Tabela 4, Ryc. 2, 3).

5. Intensywność produkcji ciepła na termoregulację w zakresie aktualnych temperatur środowiska jest nieco niższa w zimie — 5,29%/°C, niż w lecie — 6,04%/°C. W obu sezonach strefa termoneutralna nornic leży wokół temperatury 30°C, a krzywe termoregulacji od 0°C do tej strefy mają przebiegi prostolinijne (Tabela 5, Ryc. 4).

6. Metabolizm podstawowy (*BMR*) w strefie termoneutralnej u zwierząt o średnim ciężarze ciała 24,6 g wynosił 2,33 cm³ O₂/g/godz., co odpowiada 0,269 kcal/g/dobę (Tabela 6).

7. *ADMR* grupy dwóch nornic trzymanyh razem wynosi 3,20 cm³ O₂/g/godzinę, a grupy czterech nornic 3,29 cm³ O₂/g/godz. Dzięki efektowi grupowemu nornice mogą obniżyć swój metabolizm o około 13% (12,7–13,9%).

8. Za podstawę dobowego budżetu energetycznego (*DEB*) przyjęto *ADMR*. W budżecie tym uwzględniono produkcję ciepła na termoregulację w gnieździe i poza nim, a także poprawki na „efekt grupowy” i koszty rozrodu. Tak wyliczony *DEB* wyrażony w kcal/g/dobę osiąga 0,486 w zimie i 0,556 w lecie. *DEB* obliczony dla nornicy o średnim ciężarze ciała (21,0 g) wynosi 10,2 kcal w dniu zimowym i 10,6 kcal (19,0 g) w dniu letnim (Tabela 6).

9. Podobny letni budżet wyliczony dla nornic o tym samym ciężarze ciała z *BMR* zamyka się w 11,0 kcal/zwierzę/dobę, jest więc minimalnie wyższy (o 4,4%) od budżetu opartego na *ADMR*. Wartości *DEB* mających za podstawę pomiary zużycia tlenu, są zgodne z zapotrzebowaniem energetycznym określonym z asymilacji pokarmu.