A C T A   T H E R I O L O G I C A

VOL. XIV, 14: 181—190.   BIAŁOWIEŻA   30.VIII.1969

Andrzej GÓRECKI

Metabolic Rate and Energy Budget of the Striped Field Mouse*

[With 7 Tables & 2 Figs.]

In the striped field mouse, *Apodemus agrarius* (Pallas, 1771), deriving from the neighbourhood of Warszawa (N = 98) the average daily metabolic rate (*ADMR*) and resting metabolic rate (*RMR*) were studied in winter and summer. *ADMR* was determined in daily runs in 9 liters metabolic chambers while *RMR* was measured in 1—2 hr experiments in small cages. *ADMR* determined in the temperature of 20°C is equal to 0.552 kcal/g/day in summer and 0.573 kcal/g/day in winter in mice with average body weight of 20.5 g. The intensity of heat production for thermoregulation in the range of temperatures of natural habitat amounted to 7.75%/°C in winter and 3.71%/°C in summer. During maximum activity the metabolism of mice increases by approximately 130% (minimum 3.31 ccm O_2/g/hr on the average, maximum 7.65 ccm O_2/g/hr). Mice kept in groups of 2 or 3 animals decrease their metabolism by 28% on the average. In both seasons the daily activity rhytm of mice showed a two peaks pattern, with the main peak occurring at night. The mean period of the out-of-the--nest activity in summer and winter amounted to 4 hr 36 min. *ADMR* was assumed as a basis for the construction of daily energy budget (*DEB*) of the field mouse. To calculate *DEB* the heat production for thermoregulation in the nest and outside as well as corrections for the effect of huddling and the cost of reproduction were taken into consideration. *ADMR* calculated from the regression equation: $M = 15.2\ W^{-0.40}$ was used for the construction of *DEB* for mice of body weights 8 to 28 g. The values of *DEB* varied from 0.513 to 0.845 kcal/g/day in winter and from 0.553 to 0.776 kcal/g/day in summer.

I. INTRODUCTION

The knowledge of daily energy requirement of small rodents is essential for the calculation of energy flow through the population of these animals. The daily costs of maintenance of rodents are easily and accurately determined by taking into consideration their average metabolic rate (*ADMR*), resting metabolic rate (*RMR*) and basal metabolic rate (*BMR*). The model of the bioenergetics based on *ADMR* is simple and empirical, and the corrections applied are reduced to the

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

out-of-the-nest activity, the effect of huddling and costs of reproduction (Grodziński & Górecki, 1967).

The striped field mouse belongs to 2 species of rodents dominating in the field ecosystems of Central Europe. Due to this fact it was selected for detailed studies under the Small Mammals Project included in the International Biological Programme in Poland.

II. MATERIAL AND METHODS

The striped field mice, *Apodemus agrarius* (Pallas, 1771), used in the experiments were captured in Łazienkowski Park in Warszawa [1]). Before every measurement the animals were acclimatized to laboratory conditions for 2—3 days with the light rhytm resembling the natural one (Smirin, 1961; Grodziński, 1965 [2]); Górecki, 1966). Metabolism of mice was determined by the oxygen consumption with two independent procedures differing in the duration of measurements as well as in the size of metabolic chambers.

The average daily metabolic rate was measured in the Morrison closed system respirometer in 9 l. chambers in 20°C (Morrison, 1951; Morrison & Grodziński, 1968). On the whole *ADMR* was determined in 44 mice in winter and summer (Table 1).

Table 1.

Animals used for measurements of *ADMR*.

Season and Month	Number of mice	Sex ♂♂ ♀♀	Body weight in g $\pm$ *S. D.*	*C. V.* in %
Summer — August	23	14 + 9	20.55 $\pm$ 2.91	14.2
Winter — February	21	12 + 9	20.55 $\pm$ 3.12	15.4
Total and Means	44	26 + 18	20.41 $\pm$ 3.01	14.8

The resting metabolic rate was measured in a modified respirometer of the Kalabukhov — Skvortzov system in small cages (Kalabukhov, 1962). *RMR* and thermoregulation in the field mouse were estimated in the range of temperature from 0 to 30°C in 10° intervals. Total number of determinations was 156 employing 40 mice in both seasons (Table 6, see page 186).

Moreover, the »huddling effect« was studied by measuring *ADMR* of a group consisting of 2 or 3 animals kept together in the metabolic chamber and comparing the result with the *ADMR* value obtained for the same mice studied separately. For this purpose 21 daily runs of the *ADMR* were carried out. Additionally the »nest effect« was determined in 8 field mice by measuring *ADMR* in chambers lacking the nest house.

Parallel to *ADMR* measurements the daily rhytm and the sum of daily activity of the same animals in metabolic chambers were recorded. The nest houses equipped with two way switches in order to register the time of staying of the animal in the nest or outside were used (Górecki, 1968; Górecki & Ha-

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[1]) The author is greatly indebted to Mrs. K. Adamczewska-Andrzejewska, M. Sc. and Dr. R. Andrzejewski for providing the mice used in the experiments.

[2]) Grodziński W., »Program of bioenergetics studies on the productivity of small rodents«, MS.

n u s z, 1968). Additional the locomotoric activity of animals was also registered and expressed as the time of running of the animal on the activity wheel installed inside the cage (G ó r e c k i, 1968).

Oxygen consumption, time of staying in the nest and outside as well as time of running on the activity wheel were registered on the Jaquet polygraph tape (at the tape speed 180 mm/hr), while the number of wheel turns was recorded by using the counter. The t-test was applied for the evaluation of statistical significance of the observed differences.

III. RESULTS

1. Average Daily Metabolic Rate

ADMR of the field mice determined in 20°C is almost identical in summer and winter (0.573 and 0.552 kcal/g/day). The difference amounts to 4% only and is not significant. When computing the oxygen consumption into calories (Table 2) the respiratory quotient (*RQ*) equal to

Table 2.

Average daily metabolism rate (*ADMR*), maximum and minimum metabolism rate of the field mouse in summer and winter. All the values are relating to 20°C.

Season	N	Body temp. °C	*ADMR* in ccm O_2/g/h		*DMR* in ccm O_2/g/h			
			Avg ± *S.D.*	*C.V.* in %	Max. ± *S. D.*	*C. V.* in %	Min. ± *S. D.*	*C. V.* in %
Summer	23	36.9	4.79 ± 0.73	15.2	7.54 ± 0.85	11.3	3.25 ± 0.44	13.5
Winter	21	35.8	4.97 ± 0.65	13.1	7.75 ± 0.81	10.4	3.37 ± 0.47	13.9
Mean for year	—	36.4	4.88 ± 0.69	14.1	7.65 ± 0.83	10.8	3.31 ± 0.46	13.7

Table 3.

Relationship of *ADMR* and motoric activity of field mice.

	Body weight, g	*ADMR* (kcal/g/day)	*DMR* $\frac{\text{Max}}{\text{Min}}$
Mice running on the wheel	23.2	0.562	2.96
Mice non-running on the wheel	23.2	0.486	2.43
Difference in per cents	0	16	20
Significance *)	—	+	+

*) + significant, — non-significant difference.

0.82 was assumed, corresponding to the caloric value of 4.8 kcal per 1 l. of oxygen.

The ratio of maximum and minimum oxygen consumption is very similar in both seasons and equal to 2.31 on the average (Table 2).

Daily activity pattern of field mice was expressed as oxygen consumption in 2 hr intervals (Fig. 1). The highest metabolism of the studied animals appeared during the night in both seasons (Fig. 1). Body temperature (rectal) measured before and after every determination of *ADMR* was higher in summer by approximately 1°C (Table 2).

ADMR determined in body seasons for a group of mice showing high activity on the running wheel installed in the metabolic chamber was compared with corresponding figures obtained for mice with did not used the wheel (Table 3). The mean time of activity of mice running on the wheel markedly exceeded the mean activity of all the animals during a year (Table 5).

Table 4.
Relationship of *ADMR* and body weight of mice in summer.

Body weight, g	Number of mice	*ADMR* (kcal/g/day)
13.1 — 18.0	8	0.704
18.1 — 24.0	9	0.527
24.0	6	0.481
Average	—	0.552

Table 5.
Seasonal changes of the daily activity of field mice.

Season	Number of animals	Activity out-of-the-nest			
		Minutes ± *S. D.*	*C. V.* in %	Hours	and minutes
Summer	14	268.0 ± 24.3	9.1	4	28
Winter	15	284 0 ± 31.3	11.0	4	44
Means for year	—	276.0 ± 27.8	10.0	4	36

ADMR of field mice does not exhibit a statistically significant variability related to sex. On the other hand the apparent correlation with the body size of animals is visible (Table 4). The relation between average daily metabolic rate (*M*) and body weight (*W*) may by expressed by general equation: $M = 15.2\ W^{-0.40}$ (see page 187, Table 7).

2. Daily Activity of Field Mice

The total daily activity of mice was measured by the time of staying of the animal out-of-the-nest. These totals for winter and summer differ very little without reaching the level of statistical significance (Table 5). In both seasons the activity rhytm was characterized by a two-peaks bimodal pattern, mainly at night. One of the activity peaks appeared at nightfall, the other one — in the middle of night in summer, or just before daybreak in winter. The whole pattern of the out-of-the--nest activity corresponded fairly well to the rhytm obtained from oxygen consumption (Figs. 1 & 2). Only 9 animals used to run on the

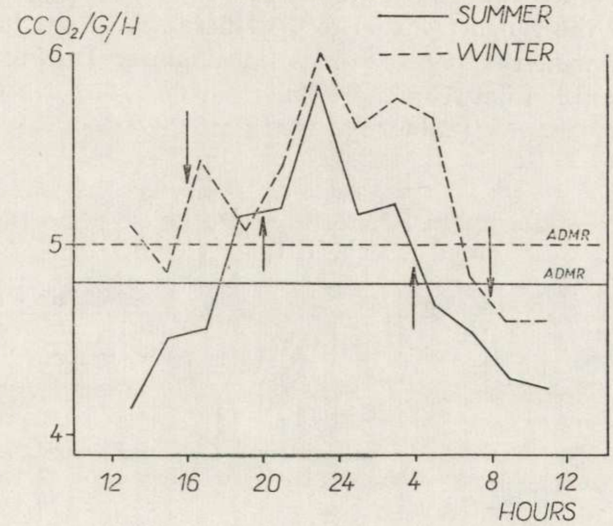

Fig. 1. Daily rhytm of metabolism rate in field mice in winter and summer. Solid line — summer, dashed line — winter, horizontal intermediate lines — *ADMR* levels. Arrows denote the duration of night.

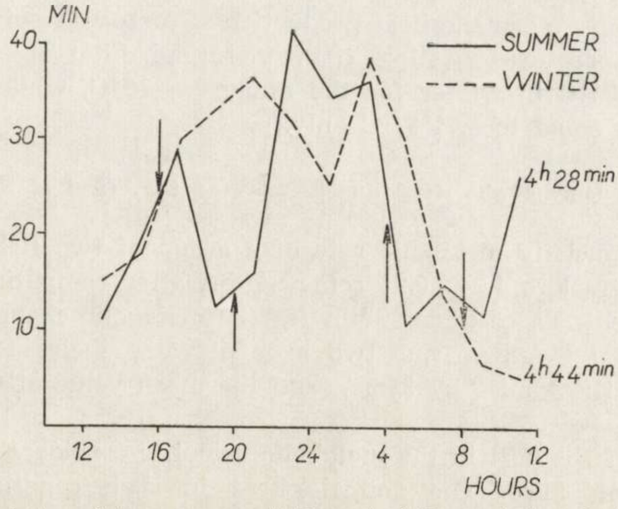

Fig. 2. Daily rhytm of the mouse activity out-of-the-nest, in minutes, during two seasons. Arrows denote the duration of night.

wheel during both seasons, the average time spent on the wheel amounting to 63% of their out-of-the-nest activity.

3. Thermoregulation

Oxygen consumption by the field mice was lowest at 30°C in both seasons. The thermoneutral zone for these animals is probably located around this temperature (Smirnov, 1960; 1968). Oxygen consumption determined in the range from 30 to 0°C increases in absolute terms by 2.18 times in winter and 2.10 times in summer. During the winter oxygen consumption between the temperature of 10 and 0°C is slightly higher than in summer (Table 6).

Table 6.
Resting metabolism rate (*RMR*) in mice expressed by oxygen consumption under different ambient temperatures.

Ambient temp. in °C	Summer				Winter			
	N	Body wt. g	ccm O_2/g/h ± *S.D.*	*C.V.* in %	N	Body wt. g	ccm O_2/g/h ± *S.D.*	*C.V.* in %
0	20	20.8	9.76 ± 0.73	7.5	16	19.3	10.10 ± 0.82	8.1
10	20	20.6	6.98 ± 0.71	10.2	20	19.3	7.33 ± 0.65	8.8
20	20	20.6	5.81 ± 0.65	11.2	20	20.8	5.17 ± 0.73	14.1
30	20	21.2	3.15 ± 0.54	17.1	20	20.6	3.18 ± 0.70	22.0

The heat production in per cents per 1°C within whole studied range of temperature is almost constant and amounts to 7.25 in winter and 6.99 in summer. When the heat production is compared only within the range of temperatures existing in the natural habitat of field mice, it reaches 7.75%/°C in winter for the range 0 — 20°C, while in summer (10—20°C) is equal to 3.71%/°C only.

4. Thermal Economy of the »Huddling Effect« and the Effect of Nest on *ADMR*

The average daily metabolic rate of a group of two field mice kept together is equal to 4.24 ± 0.21 ccm O_2/g/hr, after computing per gram of body weight. Three mice staying in the metabolic chamber consume 3.55 ± 0.12 ccm O_2/g/hr. Thus two mice decrease their metabolism by 16.9% while three mice by 29.2%, and the mean value of these figures is 23.1%.

The lack of the nest in the metabolic chamber considerably increased *ADMR* of field mice. The animals kept in such conditions in 20°C consumed on the average 1.302 kcal/g/day. The same animals studied in chambers equipped with a nest consumed 0.464 kcal/g/day only. The increase of oxygen consumption by animals without the nest amounted to 180%. The differences between both experimental groups were highly significant ($P < 0.001$) while the body weight of animals was similar (0.6 g difference). The ratio of maximum to minimum oxygen consumption was lower in animals deprived of the nest and equal to 2.1 while in mice provided with the nest the corresponding figure was 2.9.

IV. DISCUSSION

Empirical determination of all the data concerning the energy budget is not possible, hence daily energy budget (*DEB*) is constructed on the basis of average daily metabolic rate with the application of essential corrections (Grodziński & Górecki, 1967). The number of corrections and method of calculations may vary thus some details of the applied procedure are described below.

Table 7.
Computation of daily energy budget (*DEB*) in field mice with different body weight, during winter and summer day.

Body wt in g	*ADMR* ccm O_2/g/h	*DEB* in kcal/g/day						
		Summer				Winter		
		In the nest	Out of the nest	Breed	Total	In the nest	Out of the nest	Total
8.0	6.65	0.622	0.154	—	0.776	0.622	0.223	0.845
10.0	6.08	0.569	0.141	—	0.710	0.569	0.203	0.772
12.0	5.66	0.530	0.131	—	0.661	0.530	0.189	0.719
14.0	5.32	0.498	0.123	—	0.621	0.498	0.178	0.676
16.0	5.04	0.472	0.117	0.102	0.691	0.472	0.169	0.641
18.0	4.82	0.451	0.112	0.097	0.660	0.451	0.161	0.612
20.0	4.62	0.432	0 107	0.093	0.632	0.432	0.155	0.587
22.0	4.44	0.416	0.103	0.089	0.608	0.416	0.149	0.565
24.0	4.29	0.402	0.099	0.087	0.588	0.402	0.144	0.546
26.0	4.16	0.389	0.096	0.084	0.569	0.389	0.139	0.528
28.0	4.04	0.378	0.094	0.081	0.553	0.378	0.135	0.513

Table 7 shows *ADMR* of the field mice of body weight ranging from 8.0 to 28.0 g calculated from the regression equation ($M = 15.2\ W^{-0.40}$) and *DEB* construction for these animals. Since empirically determined *ADMR* did not differ significantly in summer and winter, all the values were cumulated to obtain the mean *ADMR*.

In both seasons the mice stayed for 4.5 hr out-of-the-nest (Smirnov, 1960; Table 3). The level of metabolism of mice in the nest temperature around 18°C (D a n i e l, 1964) exceeds by approximately 12% *ADMR* determined in 20°C (Table 4) but the group effect decreases the metabolism in the nest by 28% and actually surpasses the eventual correction.

The natural habitat of the field mouse consists of the field scrub or edges of the forest. The mean temperature of such habitat in Southern Poland was assumed to be around 0°C in winter and 18°C in summer (K l e i n, unpublished data). The intensity of heat production amounts in summer to 3.71 and in winter to 7.75%/°C. Consequently during the period of out-of-the-nest activity the dissipation of energy varies between 0.154—0.094 kcal/g in a summer day and 0.223—0.135 kcal/g in winter (Table 7).

The sex ratio in the mice population is close to 1:1 and approximately half of all the females is in the course of reproduction (P e l i k á n, 1965). Period of pregnancy and lactation increasing the female metabolism in voles by 70% (K a c z m a r s k i, 1966; T r o j a n & W o j c i e c h o w s k a, 1967; M i g u l a, 1969). If the correction is computed for all the individuals in mice population, the increase of *ADMR* amounts to 17.5%. This correction was added only for animals of the body weight above 16.0 g (Table 7).

The mean body weight of the field mouse in summer approaches 20 g (H a i t l i n g e r, 1962; P e l i k á n, 1965). *DEB* calculated for such animal is equal to 12.64 kcal in a summer day.

When the data from Table 7 are used for calculation of the energy flow through whole population *DEB* values should be divided into several classes related to the body weight of mice. The construction of the table enables adaptation of the budgets to various conditions of climate and reproduction of the studied population.

DEB of the field mouse may be checked by the nutrition methods. Daily costs of maintenance of the mouse in 20°C calculated from the assimilated food amount on the average to 0.528 kcal/g/day in animals fed with oat (D r o ż d ż, 1968; 1968a). *ADMR* determined in the present study for animals of the same body weight and the same season is higher by 4% only. Similarly the daily energy requirement of the field mouse calculated by G r o d z i ń s k i (1961) from the resting metabolism rate (*RMR*) is equal to 0.599 kcal/g/day in winter and differs from the figure determined in the present experiments by not more than 6%. The higher accuracy of determination of *DEB* of the field mouse may be possible after better understanding various conditions influencing the budget: microclimate of the nest and the natural habitat of mice, activity pattern of these animals as well as costs of reproduction under the natural conditions.

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Andrzej GÓRECKI

METABOLIZM I BUDŻET ENERGETYCZNY MYSZY POLNEJ

Streszczenie

U myszy polnych — *Apodemus agrarius* (Pallas, 1771) z okolic Warszawy (N = 98) w zimie i w lecie studiowano średni metabolizm dobowy (*ADMR*), oraz metabolizm spoczynkowy (*RMR*). *ADMR* określano w przebiegach dobowych w dużych 9 litrowych komorach połączonych z automatycznym respirometrem systemu Morrison'a, a pomiary *RMR* przeprowadzano w 1—2 godzinnych przebiegach w małych klatkach w respirometrze systemu Kalabukhova — Skvortzova (Tabele 1, 3).

ADMR mierzony w temperaturze 20°C wynosi w lecie 0,552 kcal/g/dobę i w zimie 0,573 kcal/g/dobę u zwierząt o ciężarze ciała 20,5 g (Tabela 2). Intensywność produkcji ciepła na termoregulację w zakresie temperatur środowiska wynosi w zimie 7,75%/°C i w lecie 3,71%/°C (Tabela 4). Przy maksymalnej aktywności metabolizm myszy polnych wzrasta o około 130% (minimalny średnio 3,31 cm³ O_2/g/ /godzinę, maksymalny 7,65 cm³ O_2/g/godzinę — Tabela 2). Myszy trzymane w grupach dwu i trzech zwierząt razem obniżają swój metabolizm średnio o 28%.

Zarówno w zimie, jak i w lecie dobowy rytm aktywności myszy polnych posiadał wzorzec dwudzielny, głównie nocny (Ryc. 1, 2). Średnio w obu sezonach myszy polne były aktywne (poza gniazdem) 4 godziny 36 minut (Tabela 3).

ADMR przyjęto jako podstawę do konstruowania dobowego budżetu energetycznego (*DEB*) myszy polnych. Uwzględniono w nim produkcję ciepła na termoregulację poza gniazdem, poprawki na efekt grupowy i koszty rozrodu. *DEB* obliczony dla myszy polnych o cieżarach ciała 8,0—28,0 g w oparciu o *ADMR* wyliczony dla tych zwierząt z równania regresji: $M = 15{,}2\ W^{-0.40}$ był zawarty w granicach 0,513—0,845 kcal/g/dobę w zimie i 0,553—0,776 kcal/g/dobę w lecie (Tabela 5). W przeliczeniu na mysz polną o ciężarze ciała 20,0 g wynosi to 12,6 kcal/dzień w lecie i 11,7 kcal/dzień w zimie.

Received, December 14, 1968.

Department of Animal Genetics and Organic Evolution,
Jagiellonian University,
Kraków 2, Krupnicza 50, Poland.