

Marek GĘBCZYŃSKI, Andrzej GÓRECKI
& Andrzej DROŻDŻ

**Metabolism, Food Assimilation and Bioenergetics
of Three Species of Dormice (*Gliridae*)**

[With 7 Tables & 7 Figs.]

Oxygen consumption was determined in the fat dormouse, forest dormouse and common dormouse in late spring and early summer, and in autumn. Since 24-hr measurements were obtained the activity of these animals could be also evaluated. Moreover, food consumption of the fat dormouse was determined in spring. Considerable seasonal differences metabolic rate were observed. Cost of maintenance as estimated from food consumption is slightly higher than that calculated from oxygen consumption. The daily energy budget (*DEB*) was computed for all 3 species. *DEB* of hibernating rodents in the period of their active life appears identical with that of non-hibernating animals. In an attempt to estimate annual cost of maintenance it was calculated that in the half-year hibernation period, these species consume less than 10% of their total annual energy budget.

CONTENTS

1. Introduction	272
2. Material and methods	272
3. Results	273
3.1. Fat dormouse	273
3.2. Forest dormouse	277
3.3. Common dormouse	278
3.4. Food consumption in the fat dormouse	279
4. Discussion	282
4.1. Daily energy budget	283
4.1.1. Fat dormouse	284
4.1.2. Forest dormouse	286
4.1.3. Common dormouse	286
4.2. Food consumption and respiration	287
4.3. Comparison of <i>DEB</i> in hibernating and non-hibernating rodents	287
4.4. Annual energy budget	288
References	292
Streszczenie	294

1. INTRODUCTION

Dormice (*Gliridae*) differ from the majority of rodents not only in their ability to hibernate but also in their arboreal life style. For this reason trapping them is difficult and they have been insufficiently investigated although their numbers may be high in various areas (Likhachev, 1954; Rosický & Kratochvíl, 1955; Pielowski & Wasilewski, 1960; Golodushko & Padutov, 1961; Angermann, 1963). Physiological studies carried out hitherto principally concerned their hibernation (cf. Kayser, 1961) and energy requirements during this period. Only fragmentary data are available on metabolism of active dormice (Kayser, 1939). For this reason an attempt was made to determine oxygen consumption and food requirement of these animals in late spring (May) and early summer (June), and for comparison also in autumn (November — October). This allowed calculation of the daily energy budget for comparison with that of non-hibernating rodents. Moreover, the annual energy requirement of dormice has been calculated.

2. MATERIALS AND METHODS

The investigations were carried out on 26 fat dormice, *Glis glis* (Linnaeus, 1776), 5 forest dormice, *Dryomys nitedula* (Pallas, 1779), and 12 common dormice, *Muscardinus avellanarius* (Linnaeus, 1758). Fat and forest dormice were captured in eastern Poland (Białowieża National Park, 52°42'N, 23°51'E) and southern Poland (surroundings of Krakow, 50°47'N, 19°44'E), while common dormice came from central Poland (Kampinoska Forest, 52°20'N, 20°44'E). Most experiments were accomplished within a few days after capture of the animals, but in some cases dormice stayed in the laboratory several weeks before the measurements. They were fed hempseed, hazel-nuts, jam, carrots and apples. Natural daily light rhythm was maintained and the temperature of room ranged from 16 to 20°C.

Oxygen consumption was used as the indication of heat production rate, and this was measured in a closed-circuit respiratory metabolism apparatus. For daily runs (ADMR) a 10.8 l chamber and a Morrison respirometer (Morrison & Grodzkiński, 1968) were used, while for short-term measurements (RMR) a Kalabukhov-Skvortzov apparatus with 1 l chamber was employed (Gębczyński, 1963; Górecki, 1968).

Food consumption, digestibility and assimilation in *G. glis* were determined by the balance method (Drożdż, 1968a). The animals were supplied for 14 days either with hazel-nuts alone, which constitute their preferred food (Holišova, 1968), or additionally the diet was supplemented with carrot. Both in the initial period and in the main experiment, food was supplied *ad libitum*. The main experiment extended to 5 or 6 days. During this time the animals were isolated in metabolism cages (Drożdż et al., 1971). Feces and urine were quantitatively collected daily, and combusted in calorimetric bomb after desiccation (Drożdż, 1968b). All feeding experiments were carried out at 20°C under 12D:12L using in the first series of the experiment 8, and in the second series 7 fat dormice.

3. RESULTS

3.1. Fat Dormouse

Chemical thermoregulation. Both in spring and autumn the resting metabolic rate (RMR) was determined at different ambient temperatures in the range from 0 to 25°C (Fig. 1). In spring at 10°C the level of oxygen consumption was exactly two times higher than at 20°C. A change of temperature by 1°C in this range caused an increase of oxygen consumption by 0.11 ccm/g hr. A similar change of metabolism occurred in the range of 0 to 10°C.

In autumn oxygen consumption was found to be higher than in spring (Fig. 1), and the differences between seasons at ambient tempe-

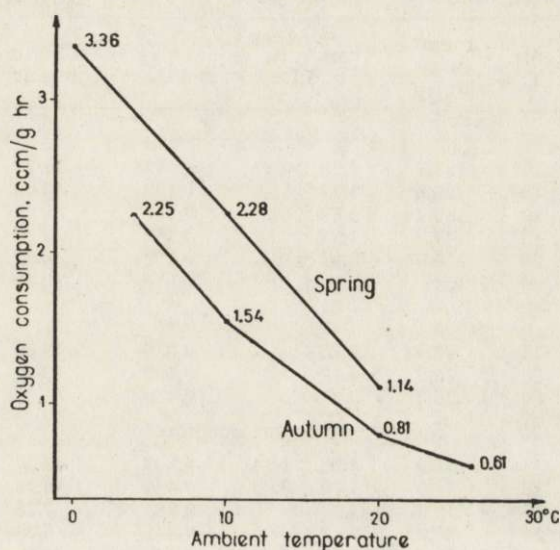


Fig. 1. Resting metabolism rate at different temperatures in *Glis glis* in spring and autumn.

rate below 20°C are highly significant ($P < 0.01$). Nevertheless, the rate of change of metabolism related to changes of ambient temperature is also high in autumn and amounts to 0.09 ccm/g hr per 1°C at 4 to 20°C. At higher temperatures this rate decreases considerably, barely reaching 0.03 ccm/g hr per 1°C.

Average daily metabolic rate (ADMR). ADMR determinations were carried out at 15 and 20°C, in both spring and autumn, and additionally at 30°C in autumn (Table 1). Spring ADMR of fat dormice at 15°C is higher by 37% compared with ADMR determined at 20°C. The dif-

ference in the average daily oxygen consumption resulting from the temperature gradient is similar to that determined in short-term measurements of oxygen consumption (*RMR*) for the same temperatures and amounts to 0.12 ccm/g hr per 1°C.

In autumn *ADMR* at 15°C is higher by 47% from *ADMR* at 20°C, and the latter value lower by 35% from that at 30° (Table 1). In this season a change of *ADMR* caused by differences in ambient temperatures is exactly the same as in *RMR* measurements. *ADMR* in autumn is lower than in spring both at 15 and 20°C, the difference being statistically significant ($P < 0.01$).

Table 1
Mean daily oxygen consumption by dormice in spring and autumn.

Month	Temp. °C	Mean body wt., g	ccm/g hr ± S.D.	kcal/g per day ¹	kcal/animal per day	kcal/kg ^{0.75} per day	n
Fat dormouse							
May—June	15	157.7	2.22 ± 0.37	0.262	41.32	164.6	11
	15 ²	133.8	1.12	0.132	17.66	79.9	1
	20	160.4	1.62 ± 0.17	0.191	30.63	121.1	4
Sept.—Oct.	15	147.3	1.34 ± 0.23	0.158	23.27	97.8	6
	20	154.9	0.91 ± 0.19	0.107	16.57	66.8	8
	30	151.7	0.59 ± 0.14	0.070	10.62	43.9	4
Forest dormouse							
May—June	15	23.7	5.25	0.620	14.69	240.8	2
	20	26.5	4.12	0.487	12.90	198.5	2
Oct.	20	25.3	3.88	0.458	11.59	183.9	1
Common dormouse							
May—June	15	20.2	5.09 ± 1.14	0.601	12.14	220.0	4
	20	21.0	4.10 ± 0.88	0.484	10.16	184.7	4
Sept.—Oct.	15	19.0	3.24	0.383	7.28	145.6	3
	20	21.2	2.63	0.311	6.29	119.8	3
	30	18.7	1.68	0.198	3.70	74.0	2

¹ It was assumed that *RQ* equals 0.9 and hence the caloric coefficient of oxygen amounts to 4.924 kcal/l. ² One individual examined for 75 hr non-stop (see Fig. 3). During each day it was torpid 15 hours and for 9 hours it was active.

Circadian rhythm. Considerable changes in the rate of oxygen consumption are observed during 24 hr period, and a definite rhythm is visible. This rhythm is largely independent of measurement temperatures and the pattern of activity shows one definite peak (Fig. 2). Increased activity begins before nightfall but the maximum oxygen consumption corresponds to the first hours of darkness. Subsequently a prompt decrease of activity is observed with a minimum occurring before sunrise. The period of low activity correspond in all cases to morning hours (Fig. 2). Although the period of increased activity includes

evening hours, and activity is reduced before daybreak, nocturnal activity still prevails. The amount of oxygen consumed during the night was always 33 to 45% higher in the daytime.

Individual fat dormice in laboratory show considerable deviations in daily rhythm from the pattern described above. During the day the fall into a state of torpor, and awake from it for only a few hours. The rhythm of oxygen consumption in such an individual was determined experimentally and compared with the rhythm of another animal which

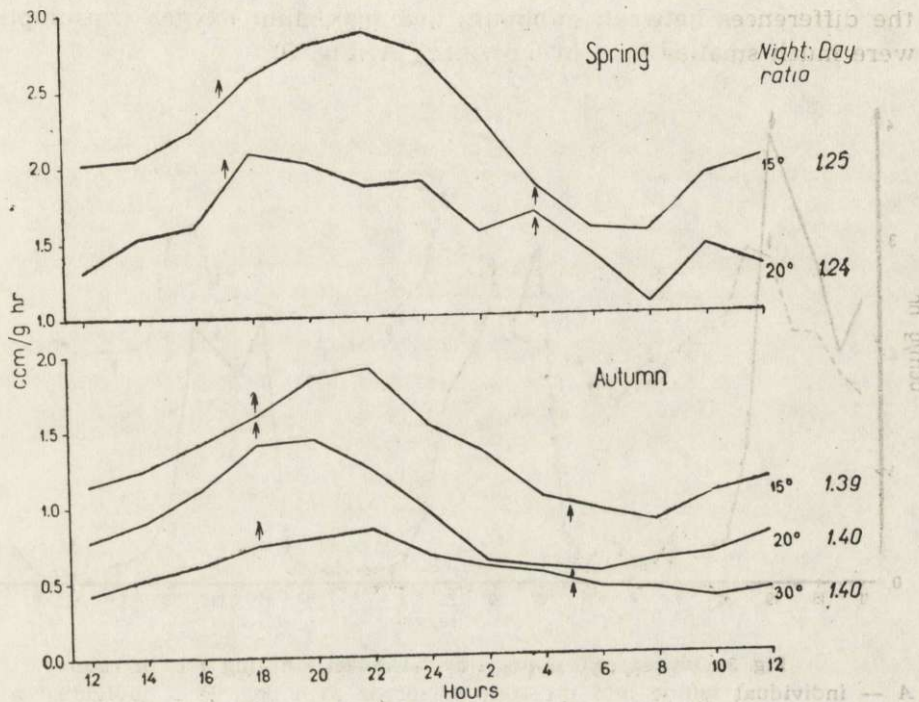


Fig. 2. Circadian rhythm of oxygen consumption in fat dormouse (*G. glis*) in spring and autumn. Arrows indicate the beginning and end of night.

did not fall into torpor, although experiencing considerably reduced activity. In order not to disturb the natural rhythm of activity of the fat dormice, measurements were continued non-stop for 3 days (Fig. 3).

The two oxygen consumption curves show a definite peak during 24-hour period. However, the dormouse falling into torpor (individual A) awoke during the day and immediately consumed more oxygen, hence the period of increased activity begins (Fig. 3). This occurred at exactly 3 p.m. throughout experiment. The period of increased oxygen con-

sumption lasted 9 hours. During this time average oxygen consumption was 2.26 ccm/g hr, whereas in the remaining 15 hours, it dropped to 0.25 ccm/g hr, 9 times lower. The maximum oxygen consumption fell in this individual during dusk and early night hours, and this was followed by a decrease equally sharp as the initial rise (Fig. 3.)

The period of maximum oxygen consumption in individual *B*, which did not become torpid, correspond to night-time consumption beginning at dusk. Hence the period of increased activity in the individual *B* commenced later than in *A*. Also, maximum consumption was delayed and the differences between minimum and maximum oxygen consumptions were much smaller than in individual *A* (Fig. 3).

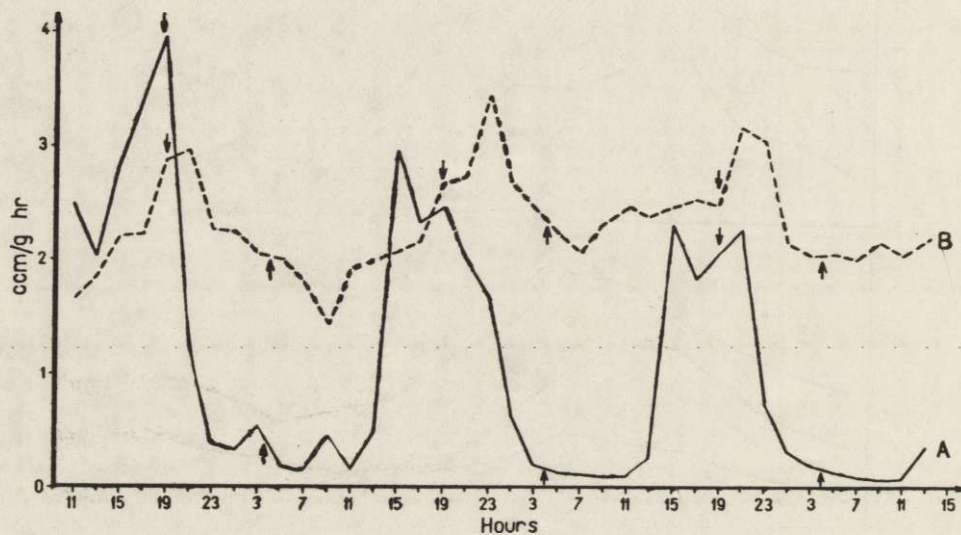


Fig. 3. Oxygen consumption by fat dormice during a 75 hr run. *A* — individual falling into the state of torpor each day, *B* — individual active all the time.

Due to the uninterrupted three-day measurements it was also possible to establish that the conditions of this experiment did not affect the daily rhythm and the total activity of the animals examined. In all consecutive days the oxygen consumption rhythm was well retained, although the total amount of oxygen consumed by fat dormouse *A* during its period of activity was higher the first day than in the two remaining days. This is probably related to arousing the animal while weighing it before the start of measurements. Dormouse *B*, however, showed no considerable changes of oxygen consumption in consecutive days.

3.2. Forest Dormouse

Since only a few forest dormouse were captured the experiments were limited to 5 individuals. In spring *ADMR* was measured at 15 and 20°C, in autumn — only at 20°C. *RMR* could be determined at different ambient temperatures also only in the spring.

Chemical thermoregulation. The change of metabolic rate associated with differences of ambient temperature in the forest dormouse is even more distinct than in the fat dormouse since between 2 and 20°C mean oxygen consumption changes by 0.14 ccm/g hr per 1°C (Fig. 4). Above 20°C this value decreases to 0.07. Hence in both dormice

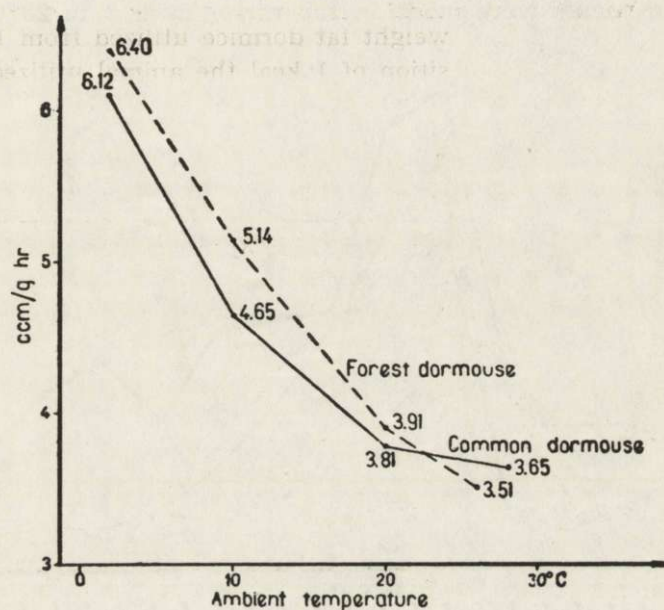


Fig. 4. Resting metabolism rate at different temperatures in *Dryomys nitedula* and *Muscardinus avellanarius* in spring.

species a strong increase in oxygen consumption was observed below 20°C. This reaction is considerably smaller in more favourable thermal conditions.

ADMR of forest dormouse is slightly higher in spring than in autumn (Table 1). At 20°C, employed in both seasons, this difference amounts to 6.2%. In spring *ADMR* determined at 15°C is higher by 27.4% than at 20°C.

Daily rhythm of oxygen consumption by the forest dormouse shows a clear maximum (Fig. 5), similar to that in the fat dormouse. In spring the period of increased activity begins later during the day than in autumn, but it also terminates later. In both seasons the increased activity occurs before dusk, and the reduction — before sunrise. Hence the forest dormouse may be regarded as a species crepuscular and nocturnal (Fig. 5).

3.3. Common Dormouse

Chemical thermoregulation. This character was determined in the spring, because only then were sufficient animals available. The measurements were made in the range from 2 to 28°C. Metabolic

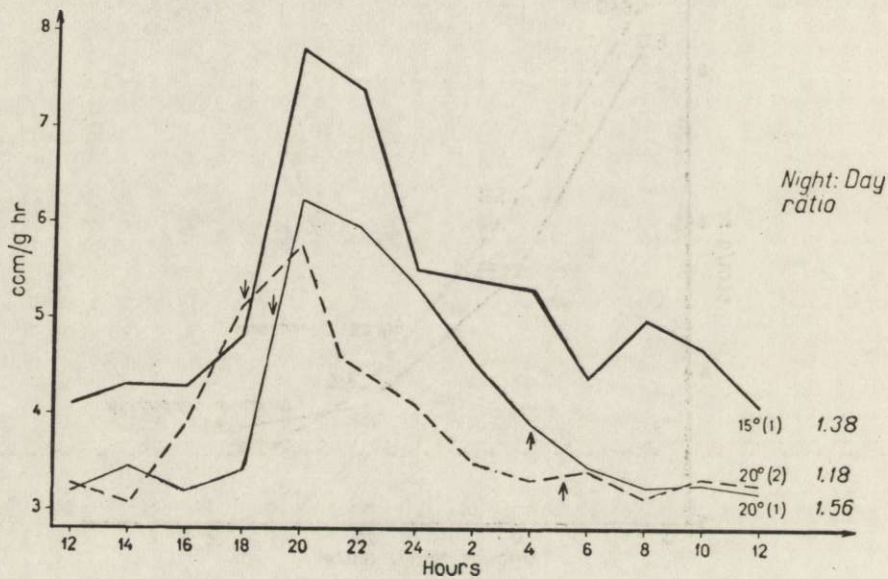


Fig. 5. Circadian rhythm of oxygen consumption by forest dormouse (*D. nitedula*) in spring (1) and autumn (2).

change in this temperature interval is not uniform (Fig. 4). The most marked change was found between 2 and 10°C (0.18 ccm/g hr per 1°C). From 10 to 20°C this value was reduced to 0.07, and above 20°C was almost completely cancelled. Hence chemical thermoregulation in the common dormouse is similar to that in forest dormouse, but more pronounced at lower temperatures.

The ADMR value is higher in spring than in autumn, similarly to that of other dormice species. This difference is, however, particularly strong

because in spring *ADMR* at 15 and 20°C is higher than in autumn by approximately 56% (Table 1). It was also possible to conclude that in autumn *ADMR* at 15°C is 23% higher than at 20°C, while the difference between 20 and 30° is 26% only.

Circadian rhythm. The activity pattern of this species can be described as the night pattern with one strongly pronounced maximum (Fig. 6). In spring the period of increased activity was more clearly

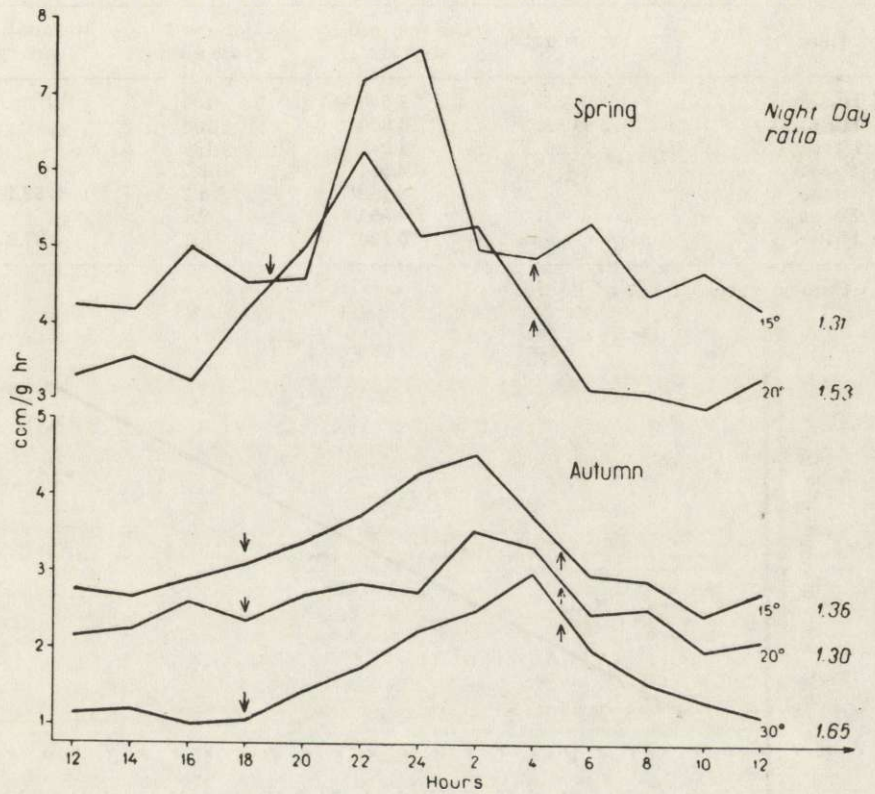


Fig. 6. Circadian rhythm of oxygen consumption by common dormouse (*M. avellanarius*) in spring and autumn.

visible than in autumn when the maximum fell for the second part of night instead of midnight. The common dormouse increases its activity only after nightfall and terminates it before dawn.

3.4. Food Consumption in Fat Dormouse

Feeding experiments were carried out on fat dormice in the spring (April) to verify respirometric determination. The cost of maintenance

were calculated from the metabolizable energy (*ME*) consumed, *i.e.*, assimilation. The digestibility of hazel-nuts was $91.3 \pm 0.4\%$, and in a mixture of hazel-nuts and carrots it amounted to $90.9 \pm 0.5\%$ of gross energy (consumption) and was characterized by minimum variability

Table 2
Coefficient of digestibility and food utilization by fat dormice.

Item	Dry mass %	Caloric value/g dry weight	Per cent of gross energy	Metabolizable energy
I Hazelnuts	94.65	8.030	100	
II Hazelnuts	94.65	8.030	100	
Carrot	14.25	3.987	100	
I Feces	—	4.591	8.7	
Urine	—	0.153 ¹	3.2	88.1
II Feces	—	4.555	9.1	
Urine	—	0.128 ¹	3.1	87.8

¹ Caloric value of 1 g of liquid.

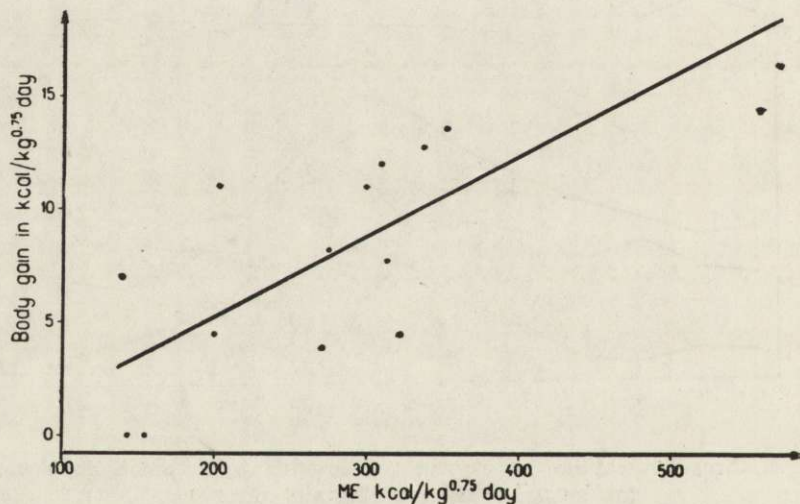


Fig. 7. Relation between intake of metabolizable energy (*ME*) and body gain expressed in kcal/kg^{0.75} day. $y = -1.627 + 0.035x$.

(*C.V.* = 0.4%). Metabolizable energy of the food supplied amounted to $88.1 \pm 0.7\%$ of the gross energy for hazel-nuts and $87.8 \pm 0.8\%$ for mixed hazel-nuts and carrots (Table 2).

Fat dormice consumed the two foods in amounts considerably exceeding their daily energy requirements. The amount of *ME* consumed daily

Table 3
Energy balance in fat dormice fed with hazel-nuts (series I — 5-day period), and hazel-nuts and carrot (series II — 6-day period).

No. of animal	Avg. body wt., g	ME kcal/day	ME kcal/kg ^{0.75} per day	Gain in g/day	Gain in kcal/day	Gain/day in kcal/kg ^{0.75}	kcal ME/1 g of gain ³	kcal ME/1 kcal depo ³	Efficiency of gain $\frac{\sum P}{\sum ME} \times 100\%$	Calculated production	
										kcal	$\frac{ME-P^1}{ADMR}$ kcal/kg ^{0.75}
Series I											
1	129.9	43.1	199.7	2.4	22.1	111	17.9	1.9	51.2	21.0	97.0
2	126.0	90.0	428.0	6.4	58.9	138	14.0	1.5	65.4	31.1	147.3
3	126.5	120.6	571.0	10.2	93.8	164	11.8	1.3	77.7	26.8	127.0
4	116.0	59.2	297.7	3.6	33.1	111	16.4	1.8	55.8	26.1	131.1
5	125.0	73.7	351.0	5.2	47.8	133	14.1	1.5	64.8	25.9	123.3
6	132.5	68.4	312.0	2.6	23.9	78	26.3	2.9	34.9	44.4	202.2
7	148.0	36.7	152.0	0	0	0	—	—	—	36.7	153.2
8	189.0	38.4	133.0	1.0	9.2	69	38.4	4.2	23.9	29.2	101.4
\bar{x}	136.5	66.3	305.5	3.9	36.1	101	19.8	2.2	53.4	30.1	135.3
Series II											
1 ²	165.2	70.1	270.0	1.2	11.0	40	57.6	6.3	16.0	59.1	228.0
2	160.0	68.7	271.0	2.5	23.0	84	27.5	3.8	33.4	45.7	181.0
3	201.0	42.5	141.8	0	0	0	—	—	—	40.5	135.2
4	134.0	74.2	332.8	4.7	43.2	129	15.9	1.7	57.8	31.0	139.0
5	155.0	49.2	198.2	0.9	8.3	47	59.0	6.4	15.5	40.9	164.7
6	142.5	73.0	309.5	4.0	36.8	119	17.5	1.9	62.0	36.2	156.0
7 ²	139.5	73.0	318.9	1.5	13.8	43	48.7	5.3	18.9	59.2	258.6
\bar{x}	156.8	64.4	263.2	2.1	19.4	66	37.7	4.2	32.3	44.7	180.3

¹ It was assumed that 1 g of P has the value of 9.2 kcal. ² Very active animals. ³ Calculated only for the animals showing body weight gain.

ranged from 36.7 to 120.6 kcal (Table 3), i.e. from 133 to 571 kcal/kg^{0.75} day. Such large differences in energy intake resulted in different daily body gain, which varied from 0 to 10 g. Assuming that fat dormice deposited the excess of energy as adipose tissue [this being possible due to a high caloric value of their food (Table 2), and assuming the caloric value of 1 g body gain as equal to 9.2 kcal], it was possible to calculate that their daily energy retention varied from 0 to 94 kcal/animal (Table 3). The highest value corresponds to 16.4 kcal/kg^{0.75} of deposited energy per day. A relationship between assimilation per kg^{0.75} (X) and energy retention expressed in kcal deposited per kg^{0.75} (Y) is expressed by the regression equation: $Y_{ME} \text{ kcal/kg}^{0.75} \text{ day} = -1.627 + 0.035 X$ (Fig. 7).

Such high energy retention indicates that for the gain of 1 g of body weight fat dormice utilized from 12 to 59 kcal of ME, i.e. for the deposition of 1 kcal the animal utilized 1.2 to 6.4 kcal ME (Table 3). Hence the efficiency of the process of growth is in this case very high. The relationship of total production (P) expressed in calories to the total ME taken up in the period of experiment and expressed in per cent amounts to a maximum of 77.7% in the extreme case (43.7% mean for both types of food) (Table 3). Such high efficiency has never been observed in other animals. Of course the results obtained are related to the great attractiveness of the supplied food, to rather short experimental period and unusual abilities of fat dormice to prompt deposition of reserve substances. Despite such large excess of ME consumed the costs of maintenance calculated from the difference between ME consumed and production (P) varied in a rather narrow range. For the animals staying at the temperature of 20°C these costs amount to 30.1 kcal/day or 135.3 kcal/kg^{0.75} day for the first type of food and 44.7 kcal/day, or 180.3 kcal/kg^{0.75} day for the second type of food (Table 3). The higher costs of maintenance estimated for the second type of food result from higher activity of animals in these experiments when fat dormice stayed in considerably larger cages.

4. DISCUSSION

The estimation of efficiency of physiological mechanisms in the animals hibernating during the period of their life activity varies to a great extent. Kayser (1939) concluded that in summer the short-term reaction to cold is extremely high in hibernators. Also according to Kalabukhov (1960) the metabolic rate and chemical thermoregulation level in hibernators is in this period no lower than in non-hibernating mammals. This enables hibernators to endure relatively sharp ambient temperature drops during period of activity. Due to this

fact such physiological processes as reproduction, growth and moulting occur normally, as well as accumulation of energy reserves for the period of hibernation. Nevertheless, the hibernators have their own characteristics even during aestival activity state (Kayser, 1965; South & House, 1967). Hibernators, for example, show greater body temperature fluctuations in comparison with other mammals, their mean body temperature being slightly lower (Eisentraut, 1956). It was also found that in summer some individuals became torpid (cf. Fig. 3). This phenomenon was observed in natural conditions as well, as reported for *Muscardinus avellanarius* (Likhachev, 1965). The number of *M. avellanarius* individuals found in torpor depends on season, and in the spring 41% of animals were observed in this state, in summer 12%, and in autumn 34%. The phenomenon shows also a clear circadian rhythm and between hours 7 and 9 a.m. 57% individuals were found asleep, while between 1 and 3 p.m. only 12% (Likhachev, 1965).

4.1. Daily Energy Budget

The energy budget can be calculated on the basis of any measure describing the energy requirement of a given species. The most useful, however, is the average daily metabolic rate (*ADMR*) which requires the lowest number of corrections (Grodziński & Górecki, 1967).

Table 4
Air temperature (°C) 2 m above the ground level in *Tilio-Carpinetum*
in Białowieża National Park at 1 hr intervals (1958—1961).

Month	Hours.												
	18	19	20	21	22	23	24	1	2	3	4	5	6
May	13.8	12.5	10.8	9.5	8.5	8.0	7.5	6.9	6.7	6.3	6.1	6.4	7.6
June	16.4	15.6	14.4	13.4	12.2	11.6	11.0	10.6	10.2	9.9	9.9	10.3	11.3
Sept.	11.0	10.0	9.1	8.5	8.1	7.7	7.4	7.3	7.0	6.9	6.8	6.7	6.8
Oct.	7.2	6.5	6.1	5.8	5.5	5.2	5.0	4.8	4.6	4.5	4.4	4.4	4.3

Also, in the case of *Gliridae* species discussed here, the budget is based on *ADMR* measurements. It should be added that at present our knowledge concerning the basal or resting metabolism of these animals is still limited (Kayser, 1939, 1965; Kayser & Hildwein, 1966).

There is no doubt, however, that in summer aroused hibernators have a very considerable chemical thermoregulation ability (Kayser, 1965), and this was confirmed in the present study. For conversion of oxygen consumption into kilocalories the respiratory quotient (*RQ*) was assumed

to be 0.9, hence slightly higher than in non-hibernating rodents. Kayser (1961) reported that in hibernating hibernators RQ is equal to 0.7 and during arousal increases from 0.8 to 1.0. At RQ equals 0.9 the caloric equivalent of oxygen reaches 4.924 kcal/l.

One of the essential corrections to *ADMR* concerns increased chemical thermoregulation during activity out of nest. All species of the investigated *Gliridae* to date are active at night but in some cases they leave the nest at dusk. The period of activity out of the nest lasts for 7 to 9 hours (Ostermann, 1956; Saint Girons, 1960, 1965; Saint Girons & Lenkiewicz, 1965; Walhovd, 1971). For this reason the ambient temperature during the period of out-of-the-nest activity of *Gliridae* was taken into consideration. The values of temperature determined at the level of 2 m above ground in a *Tilio-Carpinetum* stand of the Białowieża Forest are reported in Table 4. On this basis mean temperatures in the period of activity of studied rodent species were calculated.

No data are available on the exact temperature inside dormice nests. For other small non-hibernating mammals inhabiting the temperate zone the temperature of 20°C was generally accepted (Gębczyński, 1966; Grodziński & Górecki, 1967; Górecki, 1968, 1969). However, in summer the nests of the *Gliridae* are found in trees it may be assumed that they are subjected to greater changes of temperature. Hence data on *ADMR* determined both at 20 and 15°C were used for the calculations in Table 7 (see p. 290).

4.1.1. Fat dormice

In summer and spring fat dormice are active an average of 8 hours a day (Ostermann, 1956, data reported here). In autumn the activity extends for similar interval of time (Kayser & Hildwein, 1966). In these hours (from 8 p.m. to 4 a.m.) the mean air temperature 2 m above ground in May is 7.8°C and in June 11.5°C, hence the mean value in 9.6°C. After rounding off this value the correction for out-of-the-nest thermoregulation as calculated for 10°C by extrapolating the *ADMR* value determined at 15°C (Table 1). Such calculation is justified by the found value of chemical thermoregulation (Fig. 1), which is rectilinear in the range from 0 to 20°C. The calculated correction amounts to $8 \times 1.20 \text{ ccm/g hr} = 9.60 \text{ ccm/g 8 hr per day}$. The reaction of the fat dormouse to cold is strong and thus the correction reaches a relatively high value. Altogether the fat dormouse consumes 38.29 kcal/day (Table 5).

Other essential corrections include an increased energy requirement in pregnant and lactating females. For a whole population of non-hiber-

nating rodents this correction amounts to 6.5% in the bank vole (Kaczmarowski, 1966), and about 10% in common vole (Trojan & Wojciechowska, 1967; Migula, 1969). On the other hand, however, a decreased rate of metabolism due to social thermoregulation in animals huddling in the nest should be taken into consideration. Since this value may reach approximately 14% of the daily energy requirements in rodents (Gębczyński, 1969) it was assumed that these two corrections cancel each other. In such a case the daily energy requirement is equal to *ADMR* plus correction for out-of-the-nest activity (Table 5).

The daily energy budget of fat dormice was also calculated on basis of *ADMR* determined at 15°C (Table 5). This budget was found to be 21.2% higher than the *DEB* calculated above. Moreover, the daily energy expenses were calculated for an individual which became torpid (cf. Fig.

Table 5
Daily energy budget (*DEB*) in three species of *Gliridae* in spring (May—June) and autumn (September—October).

Season	°C	<i>ADMR</i> ccm/g hr	Cost of activity ccm/g hr ¹	<i>DEB</i> kcal/g day	kcal/animal day
Fat dormouse					
Spring	20	1.62	1.22	0.239	38.29
	15	2.22	0.60	0.289	45.10
	15 ²	1.12	0.60	0.144	22.76
Autumn	20	0.91	1.14	0.152	23.61
	15	1.34	0.71	0.186	27.44
Forest dormouse					
Spring	20	4.12	2.26	0.576	15.26
	15	5.25	1.13	0.664	15.76
Autumn	20	3.88	1.51	0.518	13.10
Common dormouse					
Spring	20	4.10	1.98	0.562	11.81
	15	5.09	0.99	0.640	12.92
Autumn	20	2.63	1.52	0.371	7.86
	15	3.24	0.91	0.419	7.96

¹ In all cases it was assumed that the period of activity outside the nest lasted 8 hours. ² Fat dormouse torpid 15 hours a day.

3). Its *DEB* is approximately one half that of an active individual. In this particular case the period of increased oxygen consumption amounted to 9 hours (Fig. 3). It is likely that in the initial period body temperature rose and this was followed by the phase of activity. Hence the correction for increased heat losses due to remaining outside the nest was calculated not for 9 but for 8 hours. In this period oxygen consumption is exactly the same as during activity of fat dormice not falling

into torpor, thus the correction is also identical. In the remaining period of the day oxygen consumption was decreased to 0.27 cc/g hr on the average. After adding the first hour of increased oxygen consumption, when the return to normal body temperature occurred, the *DEB* amounted to 22.76 kcal/animal day. Hence the energy consumption in the hypothermic fat dormouse is 50% lower than in an individual showing smaller amplitude of oxygen consumption during the day. This means a considerable saving of energy and for this reason in unfavourable thermal conditions some individuals fell into the state of torpor also in the summer.

Using *ADMR* determined at 20°C to calculate *DEB* for the fat dormouse in early autumn (September), *DEB* amounts to 23.61 kcal/animal day (Table 5). For *ADMR* measured at 15°C *DEB* increases by 16.2%, hence the difference is of the same order of magnitude as in the analogous case in spring. It should be emphasized that the energy requirement in autumn is much smaller than in spring.

4.1.2. Forest dormouse

The forest dormouse, like the fat dormice, is a nocturnal animal, the period of its out-of-the-nest activity ranging from 7 to 9 hours (Angermann, 1963; Smirnov, 1964; Saint Girons & Lenkiewicz, 1965). The activity of forest dormice shows certain seasonal variations and is highest in the period of reproduction. They have then been observed to be active even during the day (Saint Girons & Lenkiewicz, 1965). In May and June the time spent outside the nest is 8 hours (Saint Girons & Lenkiewicz, 1965; data presented here), from 8 p.m. to 4 a.m. During that period the mean air temperature in a *Tilio-Carpinetum* forest 2 m above ground level averages 10°C. The calculated correction for thermoregulation during 8 hours of activity out of the nest constitutes an additional 18.08 ccm/g, and hence for *ADMR* equal to 4.12 ccm/g hr, 15.26 kcal/animal day (Table 5).

In autumn *DEB* as similarly calculated for the fat dormouse, amounts to 13.10 kcal/animal day (Table 5), and is thus only slightly lower from the values reported for spring.

4.1.3. Common dormouse

Although the daily activity of this species was investigated by Ostermann (1956) and Likhachev (1965) the length of the period of activity out of the nest remains unknown. Only Waldhovd (1971) reports that the activity of common dormice begins at sunset and ends some 70 min before sunrise, thus lasting approximately 8 hours on aver-

age. The activity of common dormice depends on season and weather. Likhachev (1965) observed that during unfavourable weather, common dormice, especially those nursing young, do not leave the nest for several consecutive days. Moreover, young individuals are more active than adult, especially in autumn.

Our results (Fig. 6) permit the conclusion that the pattern of daily activity of common dormice is similar to that in the two other species of *Gliridae*. For this reason it was assumed that common dormice leave the nest for 8 night-time hours, i.e., from 8 p.m. to 4 p.m.; corrected DEB's are presented in Table 5.

4.2. Food Consumption and Respiration

Since cost of maintenance were estimated by two methods, oxygen consumption and food consumption, it was possible to compare the results. The costs of maintenance of fat dormice determined by respirometry was 30.6 kcal/animal day, or 121.0 kcal/kg^{0.75} day. This value is similar to that obtained for food I: 30.1 kcal/animal day, or 135.3 kcal/kg^{0.75} day, but at the same time is lower than for food II (Table 3). The mean values of the costs of maintenance for the two types of food are equal to 158 kcal/kg^{0.75} day. Hence the respirometric determinations are in agreement with the results of the feeding experiments which were carried out in cages of similar size to respirometric chambers. On the other hand, an increased activity of animals in large cages causes the costs of maintenance to rise by a value considerably deviating from respirometric determinations.

The costs of maintenance determined by food consumption in fat dormouse are, however, very similar to those estimated by this way in other non-hibernating rodents. For example these costs amount to: 167 kcal/kg^{0.75} day in gray squirrels (Ludwick, Fontenot & Mosby, 1969) and 152 kcal/kg^{0.75} day for the water vole (Drożdż *et al.*, 1971). For small rodents these costs are enclosed within 150 to 220 kcal/kg^{0.75} day (Drożdż, 1968a).

4.3. Comparison of DEB of Hibernating and Non-hibernating Rodents

Since both forest and common dormice are approximately the same size as bank voles (*Clethrionomys glareolus*) or striped field mice (*Aodemus agrarius* Pallas, 1771) it was possible directly to compare the DEB of these species. On the other hand, the fat dormouse was compared with the northern flying squirrel (*Glaucomys sabrinus yukonensis* Osgood, 1900).

In late spring and early summer the daily energy requirement in the forest dormouse amounts to 0.578 kcal/g day, in the common dormouse

to 0.562, while during the summer in bank voles, it reaches 0.556 (Górecki, 1968), and in striped field mice of similar body weight it is between 0.569 and 0.608 kcal/g day (Górecki, 1969). Similarly, northern flying squirrel *DEB* (0.289 kcal/g day — Grodziński, 1971) and fat dormouse *DEB* (0.289 kcal/g day) are comparable. These data confirm the theory that during activity the energy requirement of the *Gliridae* is similar to that of other rodents. They are also in agreement with Kalabukhov's (1960) opinion of the metabolic similarity in hibernating and non-hibernating rodents. Nevertheless, a considerable difference exists in physiological mechanisms due to the fact that hibernating rodents are able to »switch off« themselves from active life for a certain period of time. This inactivity may last 12 hours or more and may be repeated regularly every day (Likhachev, 1965; this paper, Fig. 3), or may be prolonged to several days (Likhachev, 1965; Walhovd, 1971; authors' observations on common and fat dormice kept in laboratory). Hence in any considerations of energy flow through a population of these animals the fact should be taken into consideration that among hibernating rodents some individuals may be periodically inactive.

The physiological differences of hibernating rodents is also confirmed by considerable seasonal fluctuations of metabolic rate, as distinct from winter sleep. In the three dormouse species investigated autumn oxygen consumption is lower than in the spring-summer period, in some cases by as much as 80%. In non-hibernating rodents, seasonal differences are never so high (Kalabukhov, 1969).

4.4. Annual Energy Budget

Although the daily energy requirement in the period of active life of the *Gliridae* is similar to that of non-hibernating rodents, the Glirid annual budget is markedly different. The difference arises from the fact that dormice spend a considerable part of the year hibernating, during which the rate of metabolism is several times lower than in the active period (Table 6). Although the data on metabolic rate in forest dormice during winter hibernation are lacking an attempt was made to calculate the annual budget for all three species. The data for forest dormouse were assumed equal to those of common dormouse since these two species show physiological similarities as indicated by metabolic rates in spring-summer and in autumn (cf. Table 1).

The length of the hibernation period is not constant. Moreover, it was observed that in the periphery of an area inhabited by a given species, the animals may be active all year, e.g., *D. nitedula* in Israel (Nevó &

Amir, 1961). In central Europe, the *Gliridae* always fall asleep for 5 to 7 months in winter (Kowalski, 1964). The length of hibernation depends also on sex and age of animals, adult females enter hibernation first, than adult males, and lastly, young of the year (Vietinghoff-Riesch, 1960; Angermann, 1963).

For simplification, of the following calculation, it was assumed that winter hibernation lasts from the beginning of October until the end of March, that is, exactly 181 days. A similar extended period of hibernation is also characteristic for other hibernating rodents, e.g., ground squirrel (*Citellus citellus* Linnaeus, 1776) sleeps for 186 days a year (Kayser, 1953).

For calculating the annual budget it was also assumed that the period of full activity lasts 4 months, from May to August (123 days), while

Table 6
Oxygen consumption and energy requirement in three species of *Gliridae* during hibernation.

	<i>Glis glis</i>	<i>Muscardinus avellanarius</i>	<i>Dryomys nitedula</i>
No. of measurements	89 ¹	7 ²	—
Avg. body weight, g	121.0 ¹	22.5 ¹	29.3 ²
Environmental temp., °C	9.7 ¹	10.1 ¹	—
O ₂ ccm/kg hr	27.52 ¹	40.0 ¹	40.0 ³
O ₂ ccm/g hr	0.027	0.040	0.040
kcal/g day ⁴	0.003	0.004	0.004
kcal/animal day ⁴	0.368	0.099	0.117

¹ Data after Kayser (1961). ² Body weight of *D. nitedula* in this period was established after data of Mammals Research Institute at Białowieża. ³ Assumed data. ⁴ It was assumed that during hibernation RQ equals 0.7 and caloric coefficient of oxygen is 4.6 kcal/l.

April and September (30 days each) are the transitory periods. For the latter period data on *DEB* obtained for summer at 20°C were used. This is justified by the fact that the mean temperature in April and September is lower than during the summer months.

Two variants of the annual budget of fat dormouse are presented. In the first one it was assumed that the animals are fully active from May until August, while on the other — that they periodically fall into a state of torpor. In the second variant, calculations were based on the measurements on an individual which was inactive for 15 hours daily (cf. Fig. 3, Table 1). For the common and forest dormouse the energy requirement was calculated only for individuals fully active in summer.

The annual energy budget data of the three species are shown in Table 7. They indicate a striking disproportion of energy consumption during active life and during hibernation. In all three species the con-

sumption of energy during true hibernation accounts for less than 1% of the annual budget, although hibernation extend for over 5½ months. Even when this value is added to the periods of activity, during which oxygen consumption is much higher, energy consumption during winter hibernation does not exceed 10% of the annual budget. The remaining 90% of energy is metabolized during 6 months of active life. It should be also emphasized that the relative distribution of this consumption in

Table 7

Energy consumption in different seasons of the years by fat, common and forest dormice. For *Glis glis* in the 1st variant it was assumed that the animals are active in the period from April to September, and in the 2nd variant — that they occasionally became torpid (cf. Table 5).

Months Days	April 30	May—August 123	Sept. 30	Oct.—March 181	Year, total 364
<i>Glis glis</i>					
1st variant					
DEB, kcal	27.44	38.29	27.44	0.368	
kcal/animal	823.2	4709.7	823.2	61.8 ¹ + 511.1 ²	6929.0
Per cent	11.9	68.0	11.9	0.9 + 7.3	100.0
2nd variant					
DEB, kcal	27.44	23.09 ³	27.44	0.368	
kcal/animal	823.2	2840.1	823.2	61.8 ¹ + 511.1 ²	5059.4
Per cent	16.3	56.1	16.3	1.2 + 10.1	100.0
<i>Muscardinus avellanarius</i>					
DEB, kcal	7.28	10.16	7.28	0.099	
kcal/animal	218.4	1249.7	218.4	16.6 ¹ + 137.3 ²	1840.4
Per cent	11.9	67.9	11.9	0.9 + 7.4	100.0
<i>Dryomys nitedula</i>					
DEB, kcal	11.59 ⁴	12.90	11.59	0.117	
kcal/animal	347.7	1586.7	347.7	16.6 ¹ + 162.5 ²	2464.2
Per cent	14.1	16.4	14.1	0.8 + 6.6	100.0

¹ The value of oxygen consumption in the period of true hibernation which lasts 168 days, similarly to that in the ground squirrel (K a y s e r, 1953). ² Amount of energy consumed during 13 days of awakening, when it was assumed that the rate of metabolism is 8.27 times higher (see K a y s e r, 1953). ⁴ DEB was calculated from ADMR determined in autumn at 20°C.

particular seasons is similar in all species (Table 7). Even assuming that fat dormice periodically fall into torpor the proportion of energy consumption during hibernation only slightly exceeds 10% of the annual budget.

A similarly low energy requirement during winter hibernation is characteristic of other hibernating rodents. K a y s e r (1953) reported that the ground squirrel consumed barely 70 kcal during 171 days of hibernation. This corresponds almost exactly to the value found for the slightly smaller fat dormouse. However, the ground squirrel does not sleep continually, and 579 kcal consumed when the squirrel was awake

for 14 days should be added to the above-mentioned energy requirement. For this reason the energy requirement during hibernation in the *Gliridae* was calculated on the basis of determinations reported by Kayser (1953). Data on direct determination of these values in Glirids are lacking but we know that these animals hibernate with short periods of awakening (Pohl, 1967; Kayser, Stussi & Richert, 1969). Hence the proportion of sleep and periods of awakening, as well as differentiation of the metabolic rate in the calculation of energy budgets for the *Gliridae*, were assumed to be identical with that of ground squirrel.

During winter dormice consume energy reserves accumulated before hibernation. Assuming that the whole reserve consists of fat having the caloric value of 9 kcal/g, it should be 60 g in the fat dormouse and 17 and 19 g, respectively, in common and forest dormice. Although under laboratory conditions Pohl (1967) observed that fat dormice sometimes consume food, after awakening, this is unlikely to occur in natural conditions. Thus it should be assumed that for the entire period between October and March, *Gliridae* accumulate sufficient body tissues reserves. The costs of autumn fat deposition should be added to the calculations. These costs are not high and amount to 3.1 kcal/g of deposited tissue (cf. Table 3), hence they are within 2–3% of the annual budget.

The considerable differentiation of energy requirements during the year observed in hibernating rodents constitutes a basic difference between them and non-hibernating rodents having relatively small *DEB* seasonal fluctuations (Gębczyński, 1966; Grodziński & Górecki, 1967; Górecki, 1968, 1969). Although in certain periods of the year these two groups of small mammals act as similar links in the energy flow chain, their significance in the yearly energy balance is different. From the bioenergetic standpoint is important that energy consumption by dormice is very small in winter, and — even more important — that in this period they utilize reserves accumulated in autumn since they are excluded from their biotopes energy flow then.

In the general energy flow balance the *Gliridae* may play a considerable role in the biotopes where larger numbers of them live, but of course only in the active period of their life. For example, in linden-oak forests of central Russia the numbers of *M. avellanarius* reach 3.5 individuals per ha (Likhachev, 1954). Hence in this case the energy flow through this species approximates 6,000 kcal/ha per year. All these data emphasize the necessity of taking *Gliridae* into consideration in studies of energy flow through a mammal population.

Acknowledgement: The authors are indebted to Dr. G. L. Dryden for revising the English text.

REFERENCES

1. Angermann R., 1963: Zur Ökologie und Biologie des Baumschläfers, *Dryomys nitedula* (Pallas, 1779) in der Waldsteppenzone. Acta theriol., 7, 18: 333—367.
2. Drożdż A., 1968a: Digestibility and assimilation of natural foods in small rodents. Acta theriol., 13, 21: 367—389.
3. Drożdż A., 1968b: Studies on digestibility and assimilation of foods in rodents. Ekol. pol., B, 14, 2: 147—159 [In Polish with English summ.].
4. Drożdż A., Górecki A., Grodziński W. & Pelikan J., 1971: Bioenergetics of water voles (*Arvicola terrestris* L.) from southern Moravia. Ann. zool. Fennici 8: 97—103.
5. Eisentraut M., 1946: Der Winterschlaf mit seinen ökologischen und physiologischen Begleiterscheinungen. Gustav Fischer: 1—160. Jena.
6. Gębczyński M., 1963: Apparatus for daily measurements of oxygen consumption in small mammals. Bull. Acad. pol. Sci., Cl. II, 11, 9: 433—436.
7. Gębczyński M., 1966: The daily energy requirement of the yellow-necked field mouse in different seasons. Acta theriol., 11, 17: 391—398.
8. Gębczyński M., 1969: Social regulation of body temperature in the bank vole. Acta theriol., 14, 29: 427—440.
9. Golodushko B. S. & Padutov E. E., 1961: Materialy k ekologii lesnoj soni v Belovežskoj pušče. Fauna i ekol. nazeřn. pozvon. Belorussii: 49—70. Minsk.
10. Górecki A., 1968: Metabolic rate and energy budget in the bank vole. Acta theriol., 13, 20: 341—365.
11. Górecki A., 1969: Metabolic rate and energy budget of the striped field mouse. Acta theriol., 14, 14: 181—190.
12. Grodziński W., 1971: Energy flow through populations of small mammals in the Alaska taiga forest. Acta theriol., 16, 17: 231—276.
13. Grodziński W. & Górecki A., 1967: Daily energy budgets of small mammals. [In: »Secondary productivity of terrestrial ecosystems«, ed. K. Petruszewicz]. Państw. Wyd. Nauk.: 295—314. Warszawa—Kraków.
14. Holišova V., 1968: Notes on the food of dormice (*Gliridae*). Zool. Listy, 17, 2: 109—114.
15. Kaczmarek F., 1966: Bioenergetics of pregnancy and lactation in the bank vole. Acta theriol., 11, 19: 409—417.
16. Kalabukhov N. I., 1960: Comparative ecology of hibernating mammals. Bull. Mus. comp. Zool., 124: 45—74.
17. Kalabukhov N. I., 1969: Periodičeskie i godičnye izmenenija v organizme gryzunov, ih pričiny i posledstvija. Izd. Nauka: 1—248. Leningrad.
18. Kayser Ch., 1939: Les échanges respiratoires des hibernants réveillés. Ann. physiol. physicochim. biol., 15: 1087—1219 (after Kayser, 1965).
19. Kayser Ch., 1940: Les échanges respiratoires des hibernants à l'état de sommeil hivernal. Ann. Physiol., 16: 127—221 (after Kayser, 1961).
20. Kayser Ch., 1953: L'hibernation des mammifères. Année biol., 29: 105—150 (after Kayser, 1965).
21. Kayser Ch., 1961: The physiology of natural hibernation. Pergamon Press: 1—325+VII. Oxford—London—New York—Paris.
22. Kayser Ch., 1965: Hibernation. [In: »Physiological Mammalogy«, eds. W. V. Mayer & R. G. van Gelder]. Academic Press: 179—296. New York—London.

23. Kayser Ch. & Hildwein G., 1966: Le rythme nycthémeral de la consommation d'oxygène du Loir (*Glis glis*) à l'état réveillé et actif en autonome. C. r. Séanc. Soc. Biol., 160, 5: 1068—1071.
24. Kayser Ch., Stussi T. & Richert R., 1969: La consommation d'oxygène du Loir (*Glis glis*) on cours de l'hibernation. C. r. Séanc. Soc. Biol., 163, 1: 212—214.
25. Kowalski K. (ed.), 1964: Klucze do oznaczania kręgowców Polski. V. Ssaki — *Mammalia*. Państw. Wyd. Nauk.: 1—280. Warszawa—Kraków.
26. Likhachev G. N., 1954: Razmnoženie i čislennost' orešnikovoj soni. Zool. Ž., 33, 5: 1171—1182.
27. Likhachev G. N., 1965: Materialy po sutočnoj aktivnosti i letnej spiačkie orešnikovoj soni. Bjul. Mosk. Obšč. Ispyt. Prir., Biol., 70, 2: 5—17.
28. Ludwick R. L., Fontenot J. P. & Mosby H. S., 1969: Energy metabolism of the eastern gray squirrel. J. Wildl. Mgmt., 33, 3: 569—575.
29. Migula P., 1969: Bioenergetics of pregnancy and lactation in European common vole. Acta theriol., 14, 13: 167—179.
30. Morrison P. R. & Grodziński W., 1968: Morrison respirometer and determination of ADMR. [In: »Methods of Ecological Bioenergetics«, eds. W. Grodziński & R. Klekowski]. Polish Acad. Sci.: 153—163.
31. Nevo E. & Amir E., 1960: Biological observations on the forest dormouse *Dryomys nitedula* Pallas in Israel (*Rodentia*, *Muscardinidae*). Bull. Res. Counc. Israel, Zool., 9B, 4: 200—201.
32. Ostermann K., 1956: Zur Aktivität heimischer Muriden und Gliriden. Zool. Jb., Zool. Physiol., 66, 2/3: 355—388.
33. Pohl H., 1967: Circadian rhythms in hibernation and the influence of light. [In: »Mammalian Hibernation III«, eds. K. C. Fisher, A. R. Dawe, C. P. Lyman E. Schönbaum & F. E. South, Jr.]. Oliver & Boyd: 140—151: Edinburgh—London.
34. Pielowski Z. & Wasilewski A., 1960: Haselmäuse in Vogelnistkästen. Ztschr. Säugetierkde, 25: 74—80.
35. Rosický B. & Kratochvíl J., 1955: Drobní ssavci Tatranského národního parku. Ochrana Přírody, 10, 2: 3—16.
36. Saint Girons M. C., 1960: Les variations saisonnières du rythme nycthémeral d'activité chez un Lérot femelle (*Eliomys quercinus*) en captivité. *Mammalia*, 24: 177—189.
37. Saint Girons M. C., 1965: On the persistence of circadian rhythms in hibernating mammals. [In: »Circadian Clocks«, ed. J. Aschoff]. North-Holland Publ. Co.: 321—323. Amsterdam.
38. Saint Girons M. C. & Lenkiewicz Z., 1965: Variations annuelles de l'activité chez *Dryomys nitedula* (Pallas, 1778) en captivité. *Folia biol.*, 13, 1: 23—39. Kraków.
39. Smirnov P. K., 1964: O sutočnoj aktivnosti lesnoj soni. Vestn. Leningrad. Univ., 9, 2: 125—127.
40. South F. E. & House W. A., 1967: Energy metabolism in hibernation. [In: »Mammalian Hibernation III«, eds. K. C. Fisher, A. R. Dawe, C. P. Lyman, E. Schönbaum & F. E. South, Jr.]. Oliver & Boyd: 305—324. Edinburgh—London.
41. Trojan P. & Wojciechowska B., 1967: Resting metabolism rate during pregnancy and lactation in the European common vole — *Microtus arvalis* (Pall.). *Ekol. pol.*, A, 15, 44: 811—817.

42. Vietinghoff-Riesch A., 1960: Der Siebenschläfer (*Glis glis* L.). Gustav Fischer: 1—196. Jena.
43. Walhovd H., 1971: The activity of a pair of common dormice *Muscardinus avellanarius* in conditions of captivity. *Oikos*, 22: 358—365.

Accepted, May 20, 1972.

Marek Gębczyński
Mammals Research Institute,
Polish Academy of Sciences,
Białowieża.

Andrzej Górecki, Andrzej Drożdż
Department of Animal Genetics
and Organic Evolution,
Jagiellonian University,
Kraków 2. Krupnicza 50.

Marek GĘBCZYŃSKI, Andrzej GÓRECKI i Andrzej DROŹDŹ

METABOLIZM, ASYMLACJA POKARMU I BIOENERGETYKA
TRZECH GATUNKÓW GLIRIDAE

Streszczenie

Na przełomie wiosny i lata oraz jesienią zmierzono zużycie tlenu u popielicy *Glis glis* (Linnaeus, 1766), koszatki *Dryomys nitedula* (Pallas, 1779) i orzesznicy *Muscardinus avellanarius* (Linnaeus, 1758). Dzięki dobowym pomiarom możliwe było nie tylko poznanie średniej wartości zużycia tlenu w różnych sezonach (Tabela 1), ale także dało się ocenić dobowy rytm aktywności u poszczególnych gatunków (Ryc. 2, 3, 5, 6). Zmierzono również u wszystkich trzech badanych gatunków wielkość termoregulacji chemicznej (Ryc. 1, 4). Poza tym na wiosnę oszacowano współczynnik strawności i wielkość wykorzystania pokarmu przez popielice (Tabela 2) a na tej podstawie obliczono zależność pomiędzy asymilacją energii a wzrostem ciężaru ciała (Ryc. 7) oraz bilans energetyczny popielic karmionych orzechami i marchwią (Tabela 3).

Wszystkie te uzyskane dane posłużyły do oznaczenia wielkości dobowego budżetu energetycznego badanych gatunków na wiosnę i jesienią (Tabela 5). W dalszej kolejności dokonano próby skalkulowania rocznego budżetu energetycznego *Gliridae* (Tabela 7), przy czym wartość metabolizmu w czasie hibernacji przyjęto według danych z literatury (Tabela 6).

Stwierdzono, że ogromne zróżnicowanie zapotrzebowania energetycznego w ciągu roku, jakie obserwuje się u gryzoni hibernujących stanowi podstawową różnicę między nimi a gryzoniami nie zapadającymi w sen zimowy, u których sezonowe wahania tej wartości są względnie małe. Choć więc latem obie te grupy drobnych ssaków działają jako podobne ogniwa w łańcuchu przepływu energii, to w przekroju rocznym znaczenie ich jest inne. Z bioenergetycznego punktu widzenia ważne jest nie tylko to, że zimą zużycie energii przez *Gliridae* jest małe, gdyż nie osiąga nawet 10% całej wartości rocznej, ale istotny jest fakt, że w tym czasie spalają one zapasy nagromadzone jesienią. Zwierzęta te są więc zimą wyłączone z przepływu energii w zamieszkiwanym przez nie biotopie.