

Marek GĘBCZYŃSKI

**Seasonal and Age Changes in the Metabolism and Activity  
of *Sorex araneus* Linnaeus 1758\*)**

[With 6 Figs. &amp; 4 Tables]

The oxygen consumption of the Common shrew, *Sorex araneus* L. was measured in 70 daily runs, using a closed-circuit respirometer. The shrews were divided into five groups covering the whole life cycle of these animals: young adults (summer, autumn, winter) and old adults (spring, summer). In young adults the average daily metabolic rate is 9.91 cc O<sub>2</sub>/g hr (daily requirement — 8.847 kcal per animal) in summer, 9.67 (8.533) in autumn, 9.66 (7.478) in winter and in old adults 9.29 (9.953) in spring and 8.28 (11.093) in summer. The seasonal fluctuations in the metabolism of shrews are smaller than in rodents and cannot be investigated in abstraction from the age of animals. Oxygen consumption was measured in 8—12 shrews at temperatures of 7, 10, 15, 20, 25, 30, and 35°C in summer and in winter. The values for summer are higher than those for winter. In the winter the thermoneutral zone lies within limits of 10—15°C, whereas in the summer it ranges from 15 to 20°C. The results support the opinion of the authors who claim that the metabolism of shrews is higher than it might be inferred from the general interrelations between the animal size and its metabolism. In the author's opinion this fact results both from the relation between the weight and the surface area of the body, which is more unfavourable than in bigger animals, and from the specific dynamic action of food.

Short cycles, connected with the frequency of food intake, change with season and, in *S. araneus*, last from about one hour and a half in winter to about 2½ hours in summer. The pattern of daily activity (traced on the basis of the rhythm of oxygen consumption) is also dependent on the animal age and on season. It is bimodal in autumn, winter, and spring and unimodal in young adults in summer. Old adults are nearly uniformly active in the daytime and at night in the summer.

## I. INTRODUCTION

The unusual agility and the huge food requirement of shrews drew attention of investigators to the metabolism and activity of these animals fairly long ago.

\*) In memory of Professor A. Dehnel.

As early as in their first paper on the metabolism of shrews, Morrison & Pearson (1945) stated that the oxygen consumption of the masked shrew *Sorex cinereus* Kerr, 1792 is very high and amounts on the average to more than 15 cc/g hr. These data have been confirmed by the next works (Pearson, 1947; Morrison, 1948). Pearson (1948) set forth the supposition that metabolism in shrews is higher than in other mammals similar in size and body weight. He attempted to explain these differences by tissular metabolism, which, however, has not been corroborated afterwards (Redmond & Layne, 1958).

After universal studies on the physiological indices of *S. cinereus*, Morrison et al. (1953) confirmed the opinion that its metabolism is greater than it might be judged from the size of animal. This time, however, they tried to explain this phenomenon by the specific dynamic action of food. Pfeiffer & Gass (1962) found that *Cryptotis parva* (Baird, 1858), too, has a high oxygen consumption. Also Buckner (1964) supported the results obtained by the previous investigators in his paper on the metabolism of four shrew species: *S. cinereus*, *Sorex arcticus* Kerr, 1792, *Microsorex hoyi* (Baird, 1858), and *Blarina brevicauda* (Say, 1823).

The opinions disagree as to the size of metabolism in shrews though. There are authors who claim that no such differences exist between shrews and other mammals. Having carried out experiments by means of a differential calorimeter, Hawkins et al. (1960) arrived at this very conclusion in contradistinction to all the above-mentioned papers based on the results of respirometric studies. The authors examined a number of shrew species, including *S. araneus*, and compared the results with the data for the white mouse. They failed to show that the metabolism of shrews differs significantly from that of mice or voles. Later, determining the magnitude of food consumption, Hawkins & Jewell (1962) corroborated their own earlier results.

Tupikova (1949) and Crowcroft (1954; 1957) studied the daily activity of shrews, including *S. araneus*, under laboratory conditions. On the other hand, Janský & Hanák (1960) investigated the daily activity of shrews under field conditions, catching them from April to November, and found that the daily activity pattern varies with season.

The data concerning the metabolism and daily activity of shrews were collected without regard to the specific properties of their biology. And yet the seasonal changes in the organism of shrews, combined with the age changes, undoubtedly exert an influence on the indices mentioned above. Young shrews leave the nest (June — October) physically fully developed and completely adapted to the self-reliant ways of life (Dehnel, 1949). The young usually winter as sexually immature individuals and it is only in the spring of the next year that they are fit for reproduction. They live till December at the longest or the maximum length of life of *S. araneus* is about 18 months, but old adults form a small proportion of the population, starting from the July—August period. Thus the young adult stage lasts 5—9 months in particular specimens, and the old adult stage 6 months at most. A singular phenomenon of seasonal morphological variation, discovered by Dehnel (1949) is connected with life cycle. Dehnel (l.c.) found out that the braincase heights of *Sorex araneus* Linnaeus, 1758, *Sorex minutus* Linnaeus, 1766, and *Sorex caecutiens* Laxman, 1788 change with season and age. Their value is the greatest in June. In July the skull begins to flatten and reaches the minimum in February. Then the process gets reversed and starting from March the skull height increases, but not so much as to reach the normal size of young adults. These observations were next corroborated by many investigators (for references see

Pucek, 1963). This last author confirmed the occurrence of the phenomenon of seasonal and age morphological variation in many species of the genus *Sorex* from the Palaearctic. The brain weight changes parallel to the skull height (Caboń, 1956; Bielak & Pucek, 1960) (Fig. 1). In the spring the growth of particular inner organs contributes to the rapid growth of the body weight (Pucek, 1965).

In addition, there is a correlation between the processes bringing about the changes in the skull height and the changes of the parathyroids. The resorption of bones (Pucek, 1957) is accompanied by an inhibition of the parathyroid secretion, whereas at the time when the bones are being reconstructed the gland becomes active (Dzierżkraj-Rogalska, 1952). The suprarenal cortex is the most thin in the winter months (Siuda, 1964). An atrophy of the thymus, which occurs in autumn, 6 months before the animal attains sexual maturity (Bazan, 1952), is also a peculiar fact. It has been found as well that the number of erythrocytes of the shrew changes remarkably with season and so does the haemoglobin content of an erythrocyte (Kunicki-Goldfinger & Kunicka-Goldfinger, 1964).

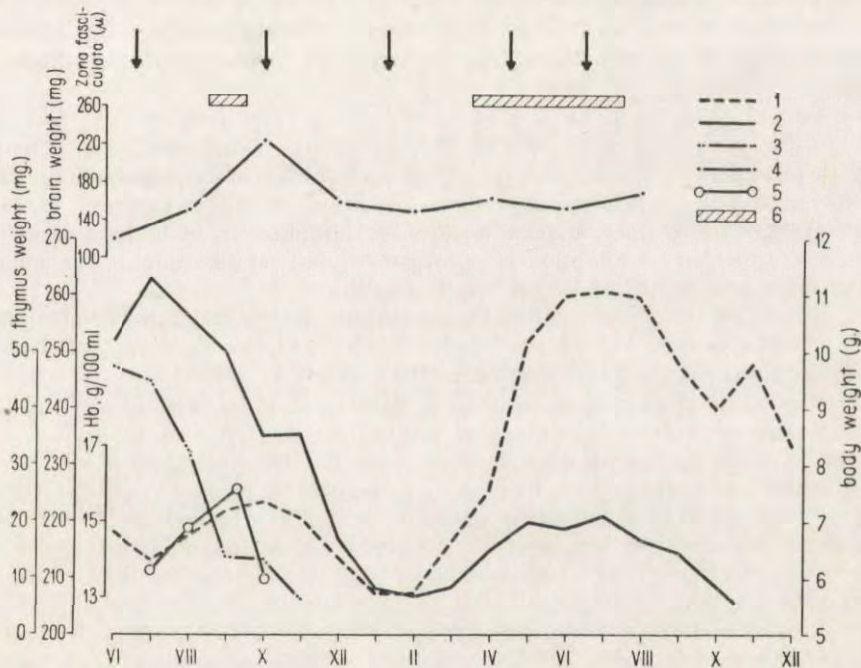


Fig. 1. Seasonal and age changes in some morphological indices of *S. araneus*. 1 — body weight (after Pucek, 1955), 2 — brain weight, 3 — thymus weight (2—3 — after Pucek, 1965), 4 — thickness of *zona fasciculata* of the adrenal cortex ( $\sigma\sigma$ ) (after Siuda, 1964), 5 — haemoglobin concentration in blood (Hb. g/100 ml) (after Kunicki-Goldfinger & Kunicka-Goldfinger, 1964), 6 — periods of height activity of the parathyroids (after Dzierżkraj-Rogalska, 1952). The arrows indicate the periods when animals were caught for experiments.

The diversity of opinions as to the magnitude of metabolism in shrews as well as the disregarding of the phenomenon of seasonal morphological variation in the studies carried out on metabolism and activity so far

induced me to take up the investigation of these phenomena in the seasonal and life cycles of *S. araneus*.

## II. MATERIAL AND METHOD

Common shrews *Sorex araneus* Linnaeus, 1758 were caught in the Białowieża National Park, mainly in the *Glycerietum maximae* Rusk, 1931 and *Circaeo-Alnetum* Oberdorfer, 1953.

When brought to the laboratory, the shrews were weighed and placed in wooden cages with peat and moss litter. The temperature of the laboratory room ranged from 10 to 18°C and the humidity from 60 to 95%. Twice a day the animals were fed minced meat with an addition of germinating wheat and vitamins (Pucek, 1964). The 24-hour experiments were started 1—4 days after the capture. Experiments on chemical thermoregulation were made later, when the shrews had stayed in the laboratory for 11—19 days.

The experiments were carried on from March 1963 till February 1964 (Table 1). The arrows in Figure 1 indicate the periods of life cycle or, in other words, the seasons when animals were caught for experiments.

In a total of 70 specimens of *S. araneus* metabolism was measured in full daily runs (25—26 hrs) at a temperature of 20°C (Table 1). Measurements of chemical thermoregulation were made on 8—12 specimens, which were examined many times for this purpose at temperatures of 5 (only in winter), 7 (only in summer), 10, 15, 20, 25, 30, and 35°C. Each measurement took 35—45 minutes. In both these cases only the values of oxygen consumption were measured, without determining the amounts of discharged CO<sub>2</sub>, which was absorbed by NaOH.

The 24-hour cycles of metabolism were examined in the respirometer of a closed system (Gębczyński, 1963) modelled after Skvartsov's modification (1957) of the apparatus designed by Kalabukhov (1951).

The chamber of the apparatus having a capacity of 14.4 l. and measurements of 40×20×18 cm was divided into a nest and a pen. In the nest there was some cotton-wool, whereas the pen possessed vessels for food and water, which were always offered in excess, and a treadmill. It should be made clear at once that shrews rarely run in the treadmill in contradistinction to rodents (Smirnov, 1957) and consequently it was impossible to record their locomotor activity in this manner. The floor of the chamber was of wood. The length of the light phase was constant in all seasons and amounted to 12 hours (from 7 a.m. till 7 p.m.). The passage from daylight to darkness and reversely was by switching off or on the light. In the summer the dark phase was 4 hours longer than the night under natural conditions, whereas in the autumn there was hardly any difference. On the other hand, in the winter the real night was 4 hours longer than the dark phase in the experiment and, on the contrary 2 hours shorter in the spring.

The pattern of 24-hour activity was determined on the basis of the daily rhythm of oxygen consumption.

The same apparatus but with a small chamber, having a capacity of 1 l. was used for experiments on chemical thermoregulation. A shrew was placed in a small cage of wire net, 6×3.5×3.5 cm. The size of the cage let the animal turn fairly easily. During these experiments the shrews were not given any food. The runs were made always at the same time of day, i.e. between 9 a.m. and 2 p.m. in an artificial light.

In both these experiments the animals were weighed before and after the run.

Mean values from two measurements were used for calculation. The volume of oxygen consumed was calculated for normal conditions and expressed in cc/g hr.

### III. DAILY METABOLIC RATE AND BIOENERGETICS

The daily metabolic rate of the Common shrew was studied in five age groups, which were at the same time seasonal groups (Fig. 1, Table 1). The average daily metabolic rate (ADMR), which expresses the 24-hour oxygen consumption converted to averages per hour (Grodziński, MS.) was used as the basis of comparison between these groups. These values made it possible to calculate the magnitude of the 24-hour energetic requirement in kcal per day (kcal/animal/day). However, the respiratory quotient (*R.Q.*) of *S. araneus* is not exactly known. Buckner (1964) calculated the values of *R.Q.* for a few species of shrews, these being 0.88 for *S. cinereus*, 0.81 for *S. arcticus*, 0.85 for *Microsorex hoyi*, and 0.78 for *Blarina brevicauda*. For their calculations Hawkins and his co-workers (1960) adopted an *R.Q.* equal to 0.82. In the present investigation it has been

**Table 1.**  
Daily metabolism and bioenergetics of shrews.

Season — age	n	Body weight (g)	S. D.	ADMR cc/g hr	S. D.	Kcal/animal per day	%
21.VI.—13.VII.1963 young adults	19	7.75	0.70	9.91	0.74	8.347	100.0
3.X.—6.XI.1963 young adults	12	7.66	0.89	9.67	0.83	8.533	96.4
4.I.—19.II.1964 young adults	14	6.72	0.58	9.66	0.45	7.478	84.5
10.IV.—10.V.1963 old adults	16	9.31	1.59	9.29	0.71	9.953	112.5
21.VI.—11.VII.1963 old adults	9	11.63	1.42	8.28	0.14	11.093	125.4

assumed that the *R.Q.* approximates to 0.8, at which the calorific value of oxygen is 4.8 kcal/1 l. O<sub>2</sub>. Such an accuracy is sufficient for bioenergetic calculations, the more so because the value of *R.Q.* is not entirely constant. It has been found out that for an *R.Q.* of 0.85 the value of energy consumption expressed in kcal/animal/day in *S. araneus* is higher by 1.3% than the value obtained with an *R.Q.* of 0.8. However, when the *R.Q.* equals 0.82 the difference decreases to 0.5%. In both cases the difference is therefore small, and for this reason the value of 4.8 kcal/1 l. O<sub>2</sub> was used in all calculations for simplification.

#### 1. Young Adults from Summer

This group (19 specimens) was examined at the end of June and at the beginning of July. In this period shrews little differ in age and they have lived self-reliant lives for only 3—5 weeks. The morphological indices

have their maximum values (Fig. 1) and the parathyroids are characterized by intense activity.

In the summer, young adult shrews exhibit a high rate of metabolism. The *ADMR* amounts to  $9.91 \pm 0.74$  cc O<sub>2</sub>/g hr at a temperature of 20°C and is the highest of all the values for other seasons.

The *ADMR* was converted to a value expressed in kcal/animal/day (Table 1), which made the more direct comparison of values for various groups possible, because it included the factor of body weight.

Figure 2 shows the daily requirements of energy for all the specimens of young adult shrews in summer as well as for all the other groups. These values are variable and, to a high degree, dependent upon the body weight

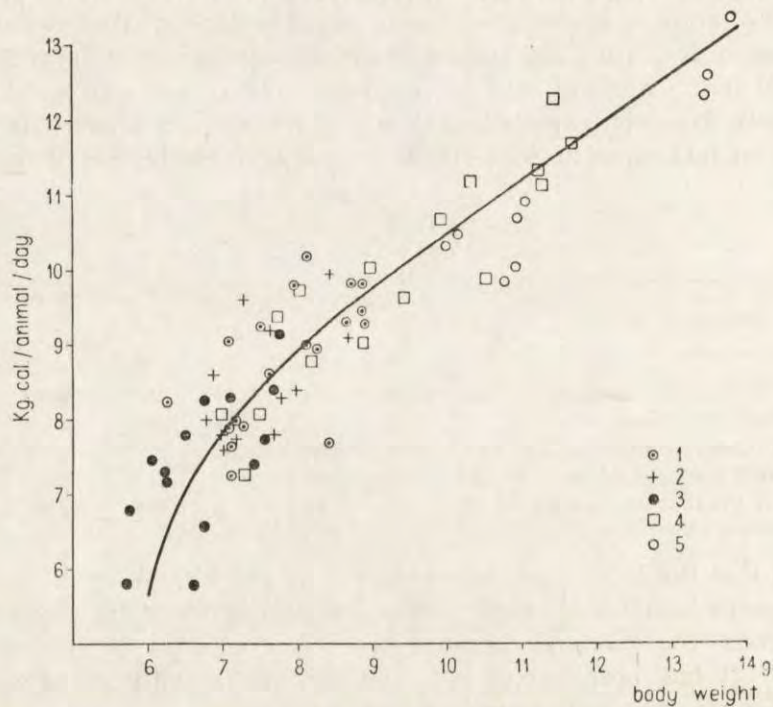


Fig. 2. Dependence of energy requirement in shrews on body weight and season. The curve is based on the empirical data. 1 — young adults from summer, 2 — young adults from autumn, 3 — young adults from winter, 4 — old adults from spring, 5 — old adults from summer.

of the animal. The dots indicating the daily requirements of the members of the summer group are distributed before the middle of the curve (Fig. 2).

Similarly, when plotting the value of the *ADMR* on the curve representing the course of morphological variation resulting from season and age, it becomes clear that this value is characterized not only by the highest

average, but also by the highest level of the maximum and the minimum values of oxygen consumption for the whole group (Fig. 3).

## 2. Young Adults from Autumn

Twelve specimens were examined in the autumn, i.e. in October and November (Table 1). In this period there is a significant drop in all the morphological indices in comparison with the summer time (Fig. 1). Besides, the age of the specimens was more differentiated than in the previous group, which was due to two facts: 1. The autumn catches include both specimens from the first litters of the year, and then of an age of 4 months, and those from the later litters, e.g. 4 weeks old. 2. On account of difficulties in catching shrews the experiments were prolonged over about 5 weeks, which also contributed to the age differentiation of the group.

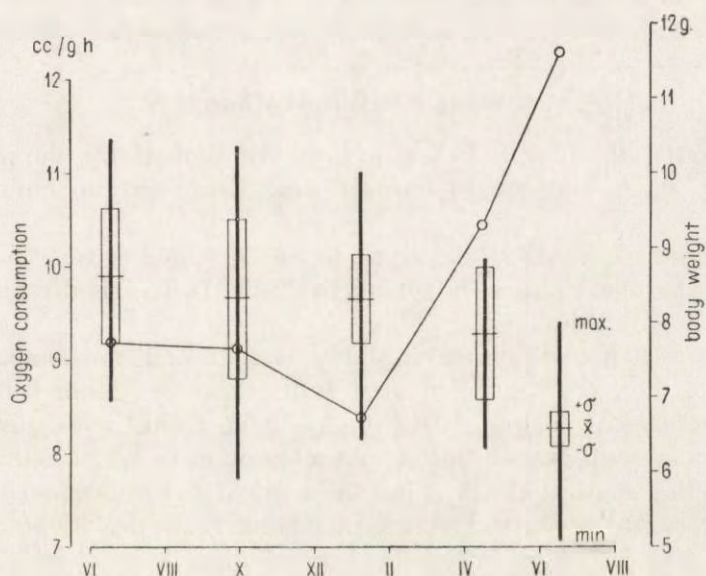


Fig. 3. Seasonal and age changes in daily metabolism rate (*ADMR*) of shrews at 20°C.

The *ADMR* of the specimens of this group amounts to  $9.67 \pm 0.83$  cc/g hr and is smaller than that of young adult shrews from summer, although their body weight is somewhat smaller (7.66 g) (Table 1). The relatively high level of the metabolic rate in shrews in the autumn seems to have been brought about by the fact that part of the specimens were probably young. An exact division of the autumn group into younger and older animals was impossible. A lower body weight in younger specimens may be, to some extent, a differential characteristic. Out of the total of 12 shrews under examination, eight specimens with an average weight of

7.93 g had their *ADMR* equal to 9.12 cc/g hr, and the four others, the average body weight of which was 7.15 g, had an *ADMR* of 10.77 cc/g hr. However, such a difference in magnitude of the *ADMR* between the two sub-groups seems to have been caused not only by different weights but, above all, by differences in age. Young specimens are much more active than the older ones. This phenomenon is known to ethologists as "overflow activities". *Slonim* (1963) explained it by a difference in accumulation of energetic substances in the musculature of animals dependent on their age and exemplified his opinions by frolics of young rodents. The energetic potential of muscles is the highest in still growing young specimens. Therefore, they are more active than adult and, especially, ageing specimens.

The split of the autumn group into two sub-groups is also visible in the magnitude of the daily calorie requirements (Fig. 2). The young adult shrews from autumn are characterized by a high standard deviation and a great difference between the maximum and the minimum values (Fig. 3).

### 3. Young Adults from Winter

In the winter the morphological indices are marked by the minimum values (Fig. 1). A total of 13 shrews were examined in January and February.

In this group the *ADMR* amounts to  $9.66 \pm 0.45$  cc/g hr. The shrews from winter had the smallest body weight (Table 1). The smallest specimen weighed 5.70 g and the largest 7.70 g.

On account of the difference in body weight and the comparatively low value of the *ADMR* as compared with that for summer, the daily calorie requirement is low. It differs by 15.5% from the requirement of the young summer shrews (Table 1). At a temperature of 20°C this difference is not the smallest at all. It has been calculated preliminarily on the basis of measurements of the resting metabolism rate (*RMR*) at different temperatures (see section IV) that at low (7, 10°C) and high (25, 30°C) temperatures the daily energy requirement would be about 30% lower than in the summer (Table 2, page 313).

The values of the daily requirement for the young adults from winter are grouped in the lower part of the diagram (Fig. 2). In this period the standard deviation is lower than in the groups discussed above (Fig. 3).

### 4. Old Adults from Spring

The period of depression in the winter months is followed by the growth of particular organs of body in shrews, which brings about a rapid increase in the body weight of these animals (9.31 g) (Fig. 1).



In this group the *ADMR* is somewhat lower and amounts to  $9.29 \pm 0.71$  cc/g hr, but the daily calorie requirement increases (Table 1). The dots indicating the daily energy consumption of a shrew are amassed within a range from 8.5 to 12 kcal/animal/day (Fig. 2). The difference between the maximum and the minimum values decreased considerably, although the results were not very uniform, which is revealed by the standard deviation (Fig. 3).

#### 5. Old Adults from Summer

This group of shrews and the young adults from summer were experimented on at nearly the same time, that is, at the end of June and at the beginning of July.

In the summer the *ADMR* of old adult shrews amounts to  $8.28 \pm 0.14$  cc/g hr. This value is, therefore, the smallest of all age groups, whereas the daily energy requirement is the highest. The change in both these values is connected with the very high average body weight of this group (11.63 g) (Table 1). The dots representing the energy consumption in particular specimens are distributed in the upper part of the diagram, above the spring group (Fig. 2). This group is characterized by a very small standard deviation (Fig. 3), which is probably due to the comparatively small number of the members of this group, but it also seems that a decrease in activity and some equalization of it occur in old specimens.



A comparison of the *ADMR* values with the average body weight shows that there is a differentiation in the metabolic rate between the groups discussed above (Fig. 4). Negative correlation between the body weight and the metabolic rate calculated for a unit of body weight is a widely known phenomenon. This relation is expressed by the equation  $M = KW^b$ , where  $M$  is the total metabolic rate and  $W$  the body weight. The constant  $K$  is distinctive of the given species and ranges from 10 to 12 in mammals (Prosser & Brown, 1961), but according to Grodziński (1961) in rodents it is lower and lies between 8 and 10. The value of  $b$  is about 0.73 in mammals (Prosser & Brown, 1961). It is generally assumed that with a 100% increase in the body weight the metabolic rate increases only by 70% (Davis & Golley, 1963).

Since all the five groups of shrews differ from each other in body weight, it is not possible to compare their *ADMR* values directly. For this reason in Figure 4 the average values of *ADMR* are presented as functions of body weight. If we draw a straight line inclined according to the rule 1 : 0.7, the *ADMR* value of the group of young adults from autumn and old adults from summer will lie on it and the value of the metabolic rate of

the group of young adults from summer and old adults from spring will be above this line. It will be seen from this graph that the young adult shrews in winter have the lowest daily metabolic rate, whereas the young adult shrews from summer and the old adult shrews from spring reach the highest values. Thus, the *ADMR* varies with season. It should be emphasized that it is not only a function of body weight but is also modified by the seasonal and age changes occurring in the organism of the shrew, as will be seen from the graph of daily energy requirement for shrews with various body weights, which is not a straight line (Fig. 2).

It was found by means of Student's test that the difference in daily energy requirement between the young adult shrews from summer and those from autumn is not statistically significant, whereas between all the successive groups these differences are significant.

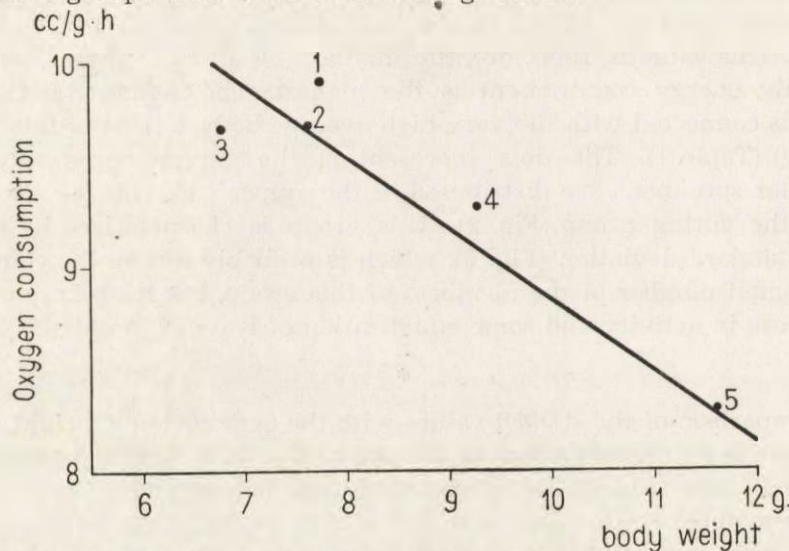


Fig. 4. Dependence of average daily metabolic rate of shrews on body weight. 1 — young adults from summer, 2 — young adults from autumn, 3 — young adults from winter, 4 — old adults from spring, 5 — old adults from summer.

The measurements of *ADMR* at a temperature of 20°C and the measurements of *RMR*, among others those at 20°C, for summer and winter were compared and the bioenergetics of shrews was calculated from both (Tables 1 and 2). The *RMR* is always higher than the *ADMR*, showing that in short runs shrews are more active in small cages than in large ones, if we take averages for 24 hours (periods of sleep). For this reason the value in kcal/animal/day calculated from the *RMR* is higher than that calculated from the *ADMR*. Hence it follows that the results of the 24-hour runs should rather be used in bioenergetic studies, whereas a suitable correction should be applied for calculations from the short runs.

## IV. CHEMICAL THERMOREGULATION

The values of chemical thermoregulation of young adult shrews from summer (second half of July) were compared with those of young adults from winter (second half of January). It was found that the metabolism rate at the same temperature is higher in summer than in winter. The differences are not the same for all temperatures (Table 2, Fig. 5).

The close determination of chemical thermoregulation in the Common shrew is difficult because of the very great agility of this animal. During the runs the shrews were inactive for only short periods, lasting a few minutes. It is also impossible to immobilize these animals for the time of measurements. For this reason they were placed in such cages (see section II) that their mobility was restricted, though they could turn round.

Table 2.

Resting metabolism rate of young adult shrews from summer and winter at various temperatures. Metabolism has also been calculated in kcal/animal/day. The results of comparison between metabolism for summer and that for winter are expressed in percentages, assuming 100% for summer values.

Temperature in °C	Summer				Winter				%
	n	Body weight (g)	RMR	Kcal/animal per day	n	Body weight (g)	RMR	Kcal/animal per day	
7	8	8.20	17.93	16.937	8	7.21	14.10	11.711	69.1
10	12	8.13	15.12	14.161	10	7.22	11.84	9.847	69.5
15	12	8.09	11.95	11.163	12	6.86	11.86	9.372	84.2
20	12	8.08	11.63	10.825	12	7.22	10.35	8.608	79.5
25	12	8.17	10.24	9.637	8	6.98	8.44	6.786	70.4
30	8	8.20	8.61	8.133	8	6.90	7.33	5.826	71.6
35	8	7.80	7.74	6.954	7	6.90	7.77	6.176	88.8

Generally, the activity of *S. araneus* decreased, as the temperature went up. On account of the change in mobility in dependence on the temperature, a relative picture of chemical thermoregulation was obtained.

The curve of chemical thermoregulation for summer as well as for winter can be divided into three sections differing from each other in the magnitude of oxygen consumption in relation to the gradient of temperature (Fig. 5). In the summer group the change in metabolism is the most intense for temperatures from 7 to 15°C, and then it comes to 0.75 cc O<sub>2</sub>/g hr/1°C (4.2%/1°C). The middle section, covering a range of temperatures from 15 to 20°C, is characterized by the almost complete lack of change in the intensity of metabolism, for the difference amounts only to 0.3 cc O<sub>2</sub>/g hr/5°C. The third section of the curve stretches from 20 to 35°C and in this case the metabolism rate lowers fairly uniformly. The

decrease occurs at a rate of  $0.26 \text{ cc O}_2/\text{g hr}/1^\circ\text{C}$  ( $2.2\%/1^\circ\text{C}$ ). The curve of chemical thermoregulation of young adult shrews in winter looks similar (Fig. 5). It, too, can be divided into three sections, which will differ from each other in their courses. This curve lies below the values of the young adults from summer, but it is almost parallel to them. The most conspicuous change in the rate of oxygen consumption per  $1^\circ\text{C}$  falls within a range of temperature from  $5$  to  $10^\circ\text{C}$  and amounts to  $0.45 \text{ cc O}_2/\text{g hr}$  ( $5.3\%/1^\circ\text{C}$ ). A change in temperature within a range from  $10$  to  $15^\circ\text{C}$  does not cause any lowering of metabolism, but there is even a slight rise. However, between  $15$  and  $30^\circ\text{C}$  the oxygen consumption drops on the average by  $0.30 \text{ cc/g hr}/1^\circ\text{C}$  ( $2.5\%/1^\circ\text{C}$ ).

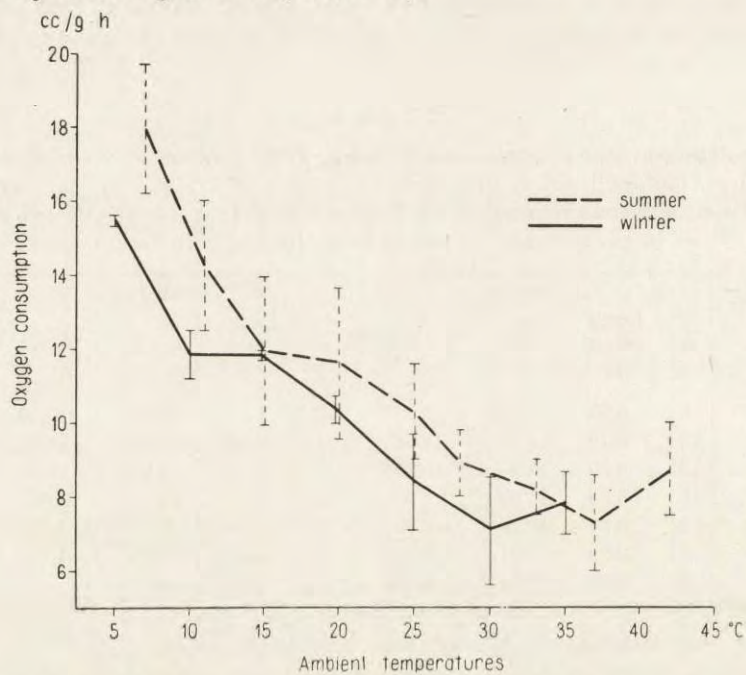


Fig. 5. Chemical thermoregulation in shrews in winter and in summer. The magnitude of standard deviation at particular temperatures is determined.

The point of rise in the metabolism rate in the group of young adults from summer is  $37^\circ\text{C}$  and in the winter group as low as  $30^\circ\text{C}$ . Nevertheless, it seems hardly probable that the temperatures of  $37^\circ\text{C}$  in summer and  $30^\circ\text{C}$  in winter mark the limits of the zone of chemical thermoregulation. They are rather critical points; the more so because they do not delimit the beginning of the lethal zone; it has been found that shrews are fairly resistant to high temperatures. In summer at a temperature of  $42^\circ\text{C}$  death occurs after 20—45 minutes (three specimens were put to such experiments).

The zones of neutral temperatures are, in all probability, within a range from 15 to 20°C in the summer group and from 10 to 15°C in the winter group (Fig. 5). In both these cases it is a range of temperatures at which the metabolism rate undergoes no changes. In winter the neutral zone is lower than in summer.

The supposition that the neutral zone in shrews lies in relatively low temperatures is supported also by the fact that *S. araneus* inhabits damp and cool environments. Similar results have been obtained by Mezhzherin (1964), who found that shrews eat the least food at a temperature of 17–20°C.

#### V. DAILY ACTIVITY RHYTHM

The recording of changes in oxygen consumption at different times of day makes it possible to get indirect knowledge of the daily activity rhythm. In rodents about 9 to 20% of energy dissipated by the animal is used for locomotor activity (McNab, 1963). Since *S. araneus* was examined in different seasonal and age groups, perhaps it is worth while to try to investigate the daily activity rhythm in this aspect. The daily activity rhythm was presented at 2-hour intervals (Aschhoff, 1957). The night/day ratio expresses the relation of the average oxygen consumption per hour in the night to the average oxygen consumption per hour in the daytime.

##### 1. Young Adults from Summer

The group of young adult shrews from summer has the highest level of energetic transformations ( $ADMR = 9.91$  cc/g hr). This suggests that the activity level is the highest as well. The daily activity pattern differs from that in the other groups (Fig. 6 A).

The daily pattern of activity is characterized by one peak, which whole falls in the night. The maximum takes place from 10 p.m. to 2 a.m., whereas the minimum extends from midday to 4 p.m. (Fig. 6 A). In experiments the length of artificial night was 12 hours, but at that time of year the real night lasted about 7 hours and a half and despite those artificial light conditions it was just during the real night that the shrews exhibited intense activity.

The shape of the curve of daily activity is closely connected with the day length. The increment of activity does not occur till after sunset and the decrease at sunrise (Fig. 6 A — arrows indicate sunrise and sunset). This indicates at the same time that the short (1–4 days) keeping of shrews in the laboratory does not, as a rule, disturb their activity pattern. The great stability of the daily activity pattern in shrews under laboratory conditions was observed by Ingles (1960) in *Sorex vagrans obscurus*

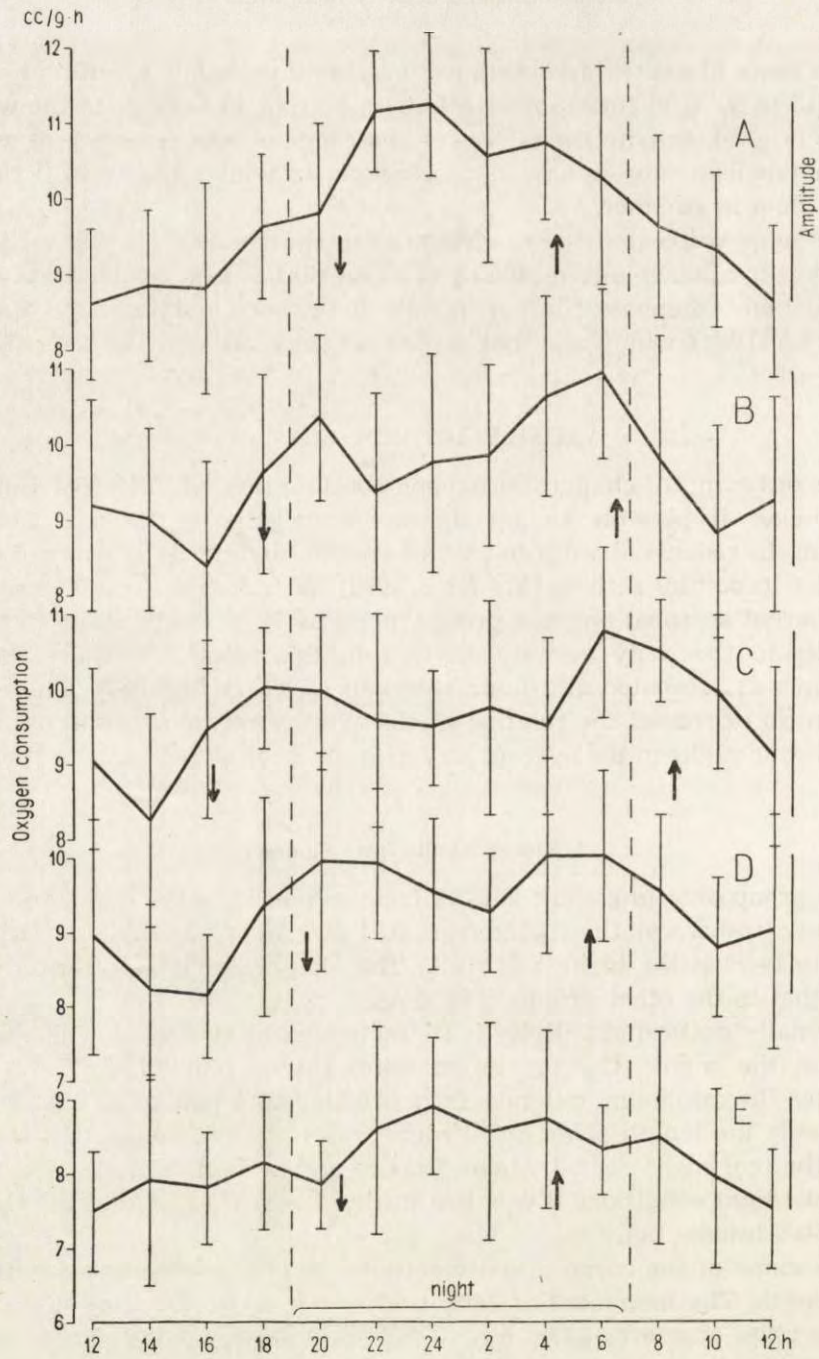


Fig. 6. Daily activity of shrews. A — young adults from summer, B — young adults from autumn, C — young adults from winter, D — old adults from spring, E — old adults from summer. Arrows indicate sunset and sunrise. The magnitude of standard deviation of oxygen consumption is marked.

Merriam, 1891. In his opinion even the eight-month stay in the laboratory does not change the type of the pattern significantly in comparison with the specimens experimented on directly after their arrival from the field.

In *S. araneus* the period of the poorest activity comes to an end 3 hours before sunrise. However, the actual increase in activity is not observed till sunset. Instead, the subsidence of activity after sunrise is not so fast (Fig. 6 A).

The ratio of the metabolism rate in shrews in night hours to that in the daytime (the night/day ratio) is 1.14. As has been established by McNab (1963) for warm-blooded animals with nocturnal ways of living, the differences between the maximum and the minimum of metabolism and the day/night ratio are high, whereas in animals with diurnal ways of living they are lower. As *S. araneus* is active throughout the day and the night, this activity being somewhat intenser at night (Crowcroft, 1954, 1957; Janský & Hanák, 1960), like *S. cinereus* (Morrison et al., 1959) and *S. vagrans obscurus* (Ingles, 1960) it has its night/day ratio lower than in species characterized by nocturnal activity, but higher than in those active in the daytime.

### 2. Young Adults from Autumn

In the autumn period the metabolism of shrews is slightly lower than in the summer ( $ADMR = 9.67$  cc/g hr), and hence there is a small difference in the levels of general activity, but the daily activity pattern has been completely changed. It is bimodal nocturnal in this period (Fig. 6 B). The first, lower, peak of activity falls at 8 p.m. and reaches 10.34 cc/g hr. The other peak (at an interval of 10 hours from the first one) occurs at 6 a.m. when the oxygen consumption comes up to 10.90 cc/g hr. The period of increasing activity is shifted and begins at sunset, and the first peak takes place as early as about 2 hours later. The second peak falls within the last hours of the night. It begins about 2 hours and a half before sunrise and the maximum is attained 30 minutes before sunrise. Thus in this case, too, increased but rapidly subsiding activity extends over the dawn period. The minimum of activity occurs from 10 a.m. to 4 p.m. The night/day ratio amounts to 1.11 and so it is lower than in young adult shrews in the summer.

### 3. Young Adults from Winter

In this period shrews have the lowest level of energetic transformations ( $ADMR = 9.66$  cc/g hr; 7.478 kcal/animal/day) and thus certainly the lowest level of general activity).

The daily activity pattern of this group is similar to that of the young

adult shrews from autumn. It is therefore bimodal nocturnal (Fig. 6 C). The lower and more extensive peak occurs at 6 p.m. reaching 10.05 cc O<sub>2</sub>/g hr. The other, higher and more compact, peak is formed at 6 a.m. (10.72 cc/g hr). Thus, the peaks are 12 hours apart, which makes 2 hrs more than in the autumn group. The length of night in winter exceeds 16 hours. The increment in activity begins after sunset, though in experimental conditions it is still the phase of daylight, whereas the second peak occurs 2 hours and a half before sunrise. In addition to this difference between the periods of time intervening between the peaks, the pattern of the winter group differs somewhat from that of the autumn group in having both peaks of activity defined less clearly than in the autumn. Activity at night is proportionally lower than in autumn, the night/day ratio being 1.09.

#### 4. Old Adults from Spring

The metabolism rate of this group is higher than in the other groups except for the young adults from summer (Fig. 4). General activity is also high in this period. It is the breeding season in shrews, during which the level of activity rises.

In this period the daily activity pattern undergoes some changes, although it still remains bimodal nocturnal (Fig. 6 D). The modification of the pattern is connected both with the rise in the activity level and with the decrease in the night length, which in spring lasts about 10 hours.

The first peak of activity takes place between 8 and 10 p.m., the other between 4 and 6 a.m., the distance between the periods of increased activity being 6 hours. The first peak of activity attains the level of 9.95 cc O<sub>2</sub>/g hr and the second 10.00 cc O<sub>2</sub>/g hr. The difference in the heights of the peaks is therefore very slight. Besides, both these periods are uniformly extensive, whereas in shrews from autumn and winter there was an evident difference between the heights and extensivities of the peaks. The first of them was always smaller than the other. This character distinguishes the activity of the old adults from spring from the two above-mentioned groups fairly conspicuously (Fig. 6 B, C, D).

In spring the increase in activity of shrews begins as early as 6 p.m. and the nocturnal lowering between the peaks (from midnight to 2 a.m.) is smaller than in the previous groups with the same pattern and it lasts shorter. The decrease in activity (the end of the second peak) comes at 8 a.m. Consequently, both the beginning of the rise of the second peak and its decline fall within the day hours. Not only the final periods have been shifted to the daytime, but also the maximum of the second elevation coincides with the phase of dawn and sunrise. The night/day ratio amounts to 1.10.



### 5. Old Adults from Summer

In this period the old adults are characterized by a low level of oxygen consumption, their *ADMR* being 8.28 cc/g hr. The daily activity pattern is completely different from that in the other groups (Fig. 6 D). It resembles the unimodal pattern of young adult shrews from summer to some degree (Fig. 6 A). It is very easy to compare these groups, as they were investigated at the same time and so the differences in their levels and patterns of activity may be ascribed only to the age differentiation of the material examined.

The old adults from summer have their increment of nocturnal activity poorly marked. Consequently, in opposition to the young adult shrews there are slight differences here between the daytime and the night in activity level. Naturally, in this group, too, the sunset is the stimulus that brings about an increase in activity. This has not one clear-cut peak, which is so distinctly defined in the group of young adults from summer, as is also indicated by the lower night/day ratio, amounting to 1.07.

### 6. Short Cycles in Particular Groups

Shrews are active both in the daytime and at night. This is undoubtedly connected with their frequent intake of food reflected by short cycles of increased activity (Morrison, 1948; Tupikova, 1949; Crowcroft, 1954; Blagosklonov, 1957; Ingles, 1960). Daily runs of oxygen consumption in *S. araneus* were analysed in all groups examined and the existence of short cycles was corroborated. The calculation of the

**Table 3.**  
Length of short cycles in particular groups of shrews.

	Young adults			Old adults	
	Summer	Autumn	Winter	Spring	Summer
Body weight in g	7.75	7.66	6.72	9.31	11.63
Short cycle in minutes	118	123	106	157	192

lengths of these cycles consisted in plotting the data concerning oxygen consumption, noted every 5—30 minutes during experiments, on profile paper. In this manner 6—8 daily records of single shrews were traced in each group and next the lengths of short cycles were summed up to calculate the mean value for the group. Young adult shrews from summer and autumn have cycles averaging 2 hours in length. In the group of young adults from winter the cycles are shorter and last less than 2 hours.

On the other hand, the short cycles of old adults in spring are prolonged and the longest cycle occurs in old adults in summer (Table 3).

As will be seen from Table 3 the length of short cycles may be related to the body weight (Tupikova, 1949). In heavier specimens the cycle becomes prolonged and less distinct. The short cycles may be connected also with the ambient temperature. In winter at low temperatures the animal runs out more frequently than in the other seasons, but, probably, for a shorter time.

## VI. DISCUSSION

### 1. Metabolism

Morrison & Pearson (1946), in their first work on the metabolism of shrews, studied the magnitude of oxygen consumption in *S. cinereus* (3.5 g). The metabolism rate turned out very high and its maximum equal to 1.72 kcal/g/day. However, they failed to measure the basal metabolism rate (BMR) owing to the great agility of this species of shrews.

Naturally, such a great energy requirement must be satisfied with a suitable amount of food. Many investigators found surprisingly high food consumption both in American shrew species (Hamilton, 1930; Morrison et al., 1957; and others) and in Euroasiatic ones (Tupikova, 1949; Blagosklonov, 1957, Hawkins & Jewell, 1962; Mezhhzherin, 1964; and others). The daily food requirement of the *Soricidae* is so high that the weight of food eaten by an animal during a day forms 100—420% of its body weight, which is obviously dependent upon its size and the ambient temperature.

Pearson (1948) found that metabolism in shrews is higher than it might be expected in view of the general correlation between the size of animal and its metabolism. He put forward the hypothesis that this difference is connected with the higher level of cellular metabolism of shrews and, consequently, with the higher body temperature than in other small mammals. This supposition was supported by Morrison (1948). Nevertheless, the body temperature in shrews has not been ascertained higher than in other mammals (Morrison et al., 1953; Morrison et al., 1959; Layne & Redmond, 1959). Neither has this hypothesis been confirmed by studies on oxygen consumption in tissues in vitro (Redmond & Layne, 1958). Redmond & Layne (l.c.) examined hepatic, pulmonary, diaphragmatic and renal tissues of *Cryptotis parva* (Say, 1823) and compared them with the tissues of the same organs of the white mouse, white rat, rabbit, mole *Scalopus aquaticus* (Linnaeus, 1758) and *Reithrodontomys humulis* (Audubon & Bachman, 1841). It appeared there were no significant differences between these species.

Morrison et al. (1959) checked the physiological indices of *S. cinereus* once again, measuring, among other things, the value of oxygen consumption. Its minimum value was determined for 3 specimens in 10 measurements and it turned out to be 9.0 cc/g hr. The value, calculated theoretically for a homiotherm organism of a weight of 3 g, should amount to 2.7 cc/g hr. The authors suggest that such a remarkable rise in metabolism is due to the specifically dynamic action of food (*SDA*). However, this interpretation seems hardly probable, as the *SDA* increases metabolism by about 40% at most, and the difference calculated by Morrison et al. (1959) for *S. cinereus* is greater than threefold. So great a difference cannot be caused only by the action of the *SDA*.

The oxygen consumption determined for *Cryptotis parva* (Pfeiffer & Gass, 1962) and the measurements of oxygen consumption, carbon dioxide production, and urinary nitrogen excretion in *S. cinereus*, *S. arcticus*, *Microsorex hoyi*, and *Blarina brevicauda* agree with the results obtained by all of the above-mentioned authors (Buckner, 1964).

Hawkins et al. (1960) examined shrews in the differential calorimeter and arrived at the conclusion that their metabolism is not usually higher than that of the white mouse. Then Hawkins & Jewel (1962) measured food consumption in many shrew species. They corroborated the fact of huge food requirement in shrews, but the calorific value of their food appeared very small owing to its high water content (about 70%), whereas in the food of rodents, in this case of the white and the house mouse (10–15 g) and of the harvest mouse *Micromys minutus* (Pallas, 1771) (7.2 g), water forms 15% at most. According to these authors, it is the only reason why shrews consume considerably more food in weight units. Shrews make better use of food than rodents, since they excrete only 7% of the energy contained in the food in faeces, whereas in rodents this value is as great as 25% of the energy (Hawkins & Jewell, 1962). However, in rodents the coefficient of digestibility amounts to 10–12% of food of high nutritive value and for this reason the value determined by the named authors seems to be too high.

Surely the difference in opinions on the magnitude of metabolism in shrews is not so great as it has been supposed so far. Table 4 offers the results obtained by particular authors. Although the experiments were carried out on various species, by various methods, in various seasons and at various temperatures, the results do not differ from each other so much as to be placed in two opposite groups. The existing differences are big, which does not permit the ascertainment of perfect conformity of the results but, on the other hand, they provide no grounds to regard them as opposed to each other. Only the data for *S. minutus* and *S. araneus* obtained by Hawkins & Jewel (1962) using the food method are

conspicuously higher than the others. Probably this method is not very accurate in relation to very small mammals, because also Morrison et al. (1957) obtained higher results for *S. cinereus* and *Blarina brevicauda* than those calculated from oxygen consumption.

**Table 4.**  
Metabolism rate of shrews after different authors.

Species	n	Body weight (g)	Temperature, °C	Kcal/g/day <sup>1)</sup>
<i>Sorex cinereus</i> <sup>2)</sup>	1	3.6	26—27	1.80
<i>S. cinereus</i> <sup>3)</sup>	15	3.6	5—14?	1.69
<i>S. cinereus</i> <sup>4)</sup>	3	3.0	?	1.04
<i>S. vagrans vagrans</i> <sup>1, 5)</sup>	3	5.0	24	0.92
<i>S. pacificus sonome</i> <sup>1, 5)</sup>	2	10.2	24	1.11
<i>S. arcticus</i> <sup>3)</sup>	33	5.4	5—14?	1.29
<i>S. trowbridgii</i> <sup>5)</sup>	1	6.7	24	0.84
<i>S. minutus</i> <sup>6)</sup>	1	4.8	26	0.86
<i>S. minutus</i> <sup>7)</sup>	2	4.2	16—23	3.12
<i>S. minutus</i> <sup>8)</sup>	2	3.0	20	1.43
<i>S. araneus</i> <sup>6)</sup>	1	8.1	28—30	0.53
<i>S. araneus</i> <sup>7)</sup>	5	8.60	14—16	2.04
<i>S. araneus</i> <sup>9)</sup>	70	8.6	20	1.08
<i>S. araneus</i> <sup>10)</sup>	12	8.1	15	1.46
<i>S. araneus</i> <sup>10)</sup>	12	8.2	25	1.25
<i>S. araneus</i> <sup>11)</sup>	12	6.9	15	1.73
<i>S. araneus</i> <sup>11)</sup>	8	7.0	25	1.20
<i>Microsorex hoyi</i> <sup>3)</sup>	1	3.5	9—14?	1.90
<i>Cryptotis parva</i> <sup>12)</sup>	3	5.7	25—27	1.44
<i>Neomys anomalus</i> <sup>13)</sup>	6	13.6	20	0.75
<i>N. fodiens bicolor</i> <sup>6)</sup>	2	13.1	28—30	0.45
<i>N. fodiens bicolor</i> <sup>7)</sup>	2	13.5	11—19	1.22
<i>N. fodiens</i> <sup>13)</sup>	12	15.8	20	0.64
<i>Crocridura cassiteridum</i> <sup>6)</sup>	1	7.6	28—30	0.66
<i>C. cassiteridum</i> <sup>7)</sup>	1	8.0	17	1.85

<sup>1)</sup> Author's conversions; <sup>2)</sup> Morrison & Pearson, 1946 — oxygen consumption, 1 l chamber, daily runs, autumn; <sup>3)</sup> Buckner, 1964 — oxygen consumption + carbon dioxide production + urinary nitrogen excretion, daily runs; <sup>4)</sup> Morrison, Ryser & Dawe, 1959 — oxygen consumption, short runs, inactive shrew; <sup>5)</sup> Pearson, 1948 — oxygen consumption, 1 l chamber, inactive shrew, two-hour runs; <sup>6)</sup> Hawkins, Jewell & Tomlinson, 1960 — differential calorimeter, inactive shrew, several-minute runs, data for *S. araneus*, *N. fodiens bicolor* and *C. cassiteridum* calculated by author; <sup>7)</sup> Hawkins & Jewell, 1962 — food consumption, several day experiments, early spring and autumn; <sup>8)</sup> Author's experiments (unpubl. data), oxygen consumption, ten-hour runs, 14.4 l chamber, summer; <sup>9)</sup> Author's own experiments — oxygen consumption, daily runs, 14.4 l chamber, all seasons; <sup>10)</sup> Author's own experiments — oxygen consumption, 1 l chamber, 35—45 minutes runs, summer; <sup>11)</sup> As above — winter; <sup>12)</sup> Pfeiffer & Gass, 1960 — oxygen consumption, several-minutes runs; <sup>13)</sup> Gębczyńska & Gębczyński, 1965 — oxygen consumption, daily runs, 14.4 l chamber, *N. anomalus* only in autumn, *N. fodiens* in autumn and winter.

The results obtained in the present investigations support the supposition that metabolism in shrews is higher than it might be expected on the basis of the known correlation between the size of animal and the metabolism rate. In the author's opinion, the cause of this fact is complex:

1. The body weight/surface area ratio in mammals of a weight of less than 8 g seems to be more disadvantageous than in bigger animals, which brings about an increase in heat loss. Pearson (1948) found that the line illustrating the dependence of metabolism on the body weight in mammals is curved just for the values from 8 to 10 g. In the common shrew this line is bent between 7 and 9 g (Fig. 2) and has a tendency to rise. For this reason, metabolism is increased in rodents and, especially, in shrews, which are the smallest mammals (e.g. *Sorex minutissimus* weighs 1.5 g — Judin, 1964).

2. An additional increase in metabolism in shrews is connected with the kind of food consumed. Shrews are "carnivorous". In the Białowieża National Park *S. araneus* feeds mainly on myriapods, insects, and snails (Kisielewska, 1963) and, consequently, on high-protein food. Also water-shrews *Neomys* Kaup, which are placed close to the genus *Sorex* L. in the system, feed on flesh; for instance, *Neomys fodiens* (Pennant, 1771) eats frogs, snails and small fish (Buchalczyk & Pucek, 1963). On the contrary, rodents live chiefly on vegetable food. A comparison of the ADMR of *Neomys anomalus* Cabrera, 1907 (13.57 g) with that of the European pine vole *Pitymys subterraneus* (13.66 g), examined by the same method at a temperature of 20°C, showed that the ADMR of water-shrews is about 22% higher (Gębczyński, 1964; Gębczyńska & Gębczyński, 1965). This difference is surely caused only by the stronger action of the SDA, because the food of water-shrews contains more protein than that of rodents.

As Hawkins & Jewell (1962) demonstrated, the food of shrews has a low calorific value. Since the energy requirement of these animals is high, it necessitates the acquisition of large amounts of food. A foraging Common shrew covers long distances at a high speed, digs in the litter, and takes only the food it comes across (Dehnel, 1951). Dehnel (l.c.) investigated also the postnatal development of shrews and found that, leaving the nest, the young are quite grown up and self-reliant. On the basis of the specific features of the postnatal development in the species of the genera *Sorex* and *Neomys*, Dehnel (1951) concluded that they surely differ from other mammals in respect of their physiology. This view is fully supported by the results obtained in the present study and by the data of American authors.

The sort of food and the manner in which it is acquired by shrews demand intense activity, which is closely connected with their increased

metabolism. A peculiar balance between the amount of food indispensable for a shrew to keep alive and the cost of its acquisition arose as a necessary result of these conditions. An interesting concept has been put forward by Mezhzherin (1964), who claims that the winter drop in body weight allows a remarkable decrease in general energy requirement in spite of its relative growth resulting from the fall in the shrew size. Such an interpretation of the phenomenon of seasonal variation seems sensible. It explains the decrease of bioenergetics accompanied by a relatively small reduction in metabolism. The seasonal adaptation of the shrew, therefore, consists mainly in morphological changes, in which it differs from most mammals, whose adaptation is based, above all, on functional changes (Kalabukhov, 1946).

In many species this adaptation is expressed by seasonal changes in their metabolism. The highest level of metabolism in non-hibernating animals falls in the spring. During the summer and autumn it lowers by degrees to reach the minimum in the winter, whereas in rodents the level rises somewhat in the autumn in comparison with the summer, but its minimum takes place in the winter as well (Slonim, 1961).

The seasonal variation of metabolism was also found in the Common shrew, but here it is closely connected with the animal's life cycle. The young begin their independent life in June and they live (under conditions provided by the Białowieża National Park) as long as December of the next year at most, or about 18 months. Analysing the catches made for 11 years in the Białowieża National Park (9241 specimens) Pucek (1959) found that in June old adults form nearly 30% of the specimens caught and in July only 10%. The actual longevity of shrews is therefore much smaller.

The value of the *ADMR* in young adults of *S. araneus* is the highest in the summer, it goes down a little in the autumn to reach its minimum in the winter. A conspicuous rise in the *ADMR*, as compared with the winter level, is observed in the spring, whereas in the summer it drops again in old adults (Fig. 4). The summer lowering in old adults is particularly well visible in comparison with the young adults from the same season. The metabolism rate increases twice in shrews, in summer (young adults) and in spring (old adults), and it drops twice as well, in winter (young adults) and in summer (old adults). Seasonal variation in metabolism differs from that in other mammals examined so far (Slonim, 1961). This is expressed by the relatively slight lowering of metabolism in the winter, and the seasonal changes are connected with the shrew's life cycle.

The cycle of changes in metabolism is associated with the specific variation in morphological indices of shrews, e.g. the brain weight (Bielak & Pucek, 1960). Seasonal changes are evident in the parathyroid

(Dzierżykraj-Rogalska, 1952), suprarenal cortex (Siuda, 1964), and a weight of inner organs (e.g., heart, liver, spleen, kidneys) (Pucek, 1965). Particularly important are here the changes in the weight indices for kidneys and heart, which, according to Schwarz (1962), well reflect the changes in metabolism and activity of the species examined. The cycle of changes in the number of erythrocytes and in the haemoglobin content in the shrew is somewhat different (Kunicki-Goldfinger & Kunicka-Goldfinger, 1964). According to Kunicki-Goldfinger & Kunicka-Goldfinger (l.c.) the blood indices show low values in the spring, reach the maximum in September, and drop again in the autumn. It is a pity that their results were obtained on relatively poor materials ( $n = 27$ ).

A seasonal change in chemical thermoregulation was observed in shrews as well (Fig. 5). In the winter the thermoneutral zone lowers by  $5^{\circ}\text{C}$  as compared with the summer values ( $15\text{--}20^{\circ}\text{C}$ ). The phenomenon of lowering of the neutral zone has been observed also in other mammalian species; for example, in the fox *Vulpes fulva alascensis* Merriam, 1900, this zone is  $8^{\circ}\text{C}$  in summer and  $-13^{\circ}\text{C}$  in winter, and in *Erethizon dorsatum myops* (Merriam, 1900)  $7^{\circ}\text{C}$  in summer and  $-12^{\circ}\text{C}$  in winter (Irving et al., 1955). These differences are associated with seasonal changes in the insulating properties of the fur. The negative correlation between the magnitude of oxygen consumption and the insulating properties of the coat has been already found by Hart & Heroux (1953) in *Peromyscus*. The same type of correlation seems possible also in the Common shrew. In the summer the coat of a shrew lets pass  $3.43\text{ mcal/sq. cm sec.}$ , in winter  $2.82\text{ mcal/cm sec.}$ , i.e., 18% less (Gębczyński & Olszewski, 1963).

Hart & Irving (1959) arrived at the conclusion that seasonal acclimatization in small mammals is reflected, above all, by changes in metabolism. Instead, in large mammals it is rather expressed by a change in physical thermoregulation (increase in insulating properties of fur, a drop in the temperature of peripheral tissues), which, in consequence, leads to a reduction in the heat loss rate.

There is a large increment in the insulating properties of the fur of the Common shrew as well. A relatively small decrease in metabolism rate in the winter, demonstrated in this study, is probably connected with this increment.

## 2. Activity

The first studies on the daily activity of the shrew were carried out by Tupikova (1949) under laboratory conditions. It appeared that *S. ara-*

*neus* is active throughout the day and the night, though the periods of activity at night are more frequent and longer than those in the daytime. Long periods of resting (inactivity), which are so characteristic of many rodent species, are lacking both in the daytime and at night. Crowcroft (1954) observed, also under laboratory conditions, that in the autumn the activity pattern of the shrew (daylight from 5 a.m. to 5 p.m.) is bimodal with a higher peak between 8 p.m. and 4 a.m. and a lower one between 7 a.m. and 11 a.m. On the other hand, Janský & Hanák (1960) conducted investigations on activity under field conditions. On the basis of the number of catches at various times of the day they examined activity from April to November. These authors found that in the spring and autumn shrews are characterized by two peaks of activity. The first, lower, peak takes place in the evening, the second, higher than the first one, is formed in the hours of dawn. In summer (May—July) there is one, very distinctly marked, peak at night.

The present studies, which were also made in various seasons, confirm the results obtained by Janský & Hanák (1960) concerning the changes in the pattern in particular seasons, for it has been shown that the type of the activity pattern is the same in the winter as in the autumn and spring. The differences existing between the patterns in autumn, winter, and spring are only those in intervals between the peaks and in the extensivity of peaks. The intervals between the peaks are probably associated with night length, for the longer the night the longer the interval was, irrespective of the length or dark periods in the laboratory room. The sunset was generally a stimulus inciting the animals to increase their night activity, followed next by a night break and another rise before the sunrise. In spring, however, when the night was short and the general activity of shrews increased in connection with breeding season, the period of increased activity extends partly over the day phase as well.

Owing to the division of shrews caught into young adults and old adults it was possible to demonstrate that in the same season, i.e., in the summer, the activity of young adults (3—5 weeks old) differs from that of old adults (9—13 months old) (Fig. 6 A, E). The activity pattern seems to be the same type in both these groups, but the old adults are evidently less active than the young adult shrews, which is indicated by the great difference between the maximum and the minimum of activity in the young adults, whereas in the old adults this difference is less conspicuous.

In most shrew species, activity is somewhat more intense and its duration longer at night than in the daytime. This is true of *S. araneus*, *S. minutus*, *Neomys fodiens*, *Crocidura suaveolens* (Tupikova, 1949; Crowcroft, 1954; Janský & Hanák, 1960), *S. fumeus* (Hamilton, 1940), *S. cinereus* (Morrison & Pearson, 1946), *Blarina bre-*



*vicauda talpoides* (Mann & Stinson, 1957) and *S. vagrans obscurus* (Ingles, 1960). However, in *S. cinereus* from Alaska examined in the period when the night lasts there 2 hours and a half the difference between night and day activity is great (Grodziński, MS), whereas in *S. tscherskii* (Blagosklonov, 1957) activity is the same at night and in the daytime, or even somewhat more intense in morning hours. The lack of differentiation between the day and the night activity is due to the fact that such a small shrew (the specimen under examination weighed only 2.4 g) must take food very often, on the average every 10 minutes. The longest interval between two successive "repasts" was 55 minutes (Blagosklonov, 1957). These are the shortest "short-term cycles" found in mammals.

The short cycles of *S. cinereus* were 1.4 hr (Morrison & Pearson, 1946) or 1.5 hr (Pearson, 1947). In *S. vagrans obscurus* there were 9 to 15 periods of activity alternating with resting periods (Ingles, 1960). In the Common shrew and the Pygmy shrew the short cycles, however, last about 2 hrs (Crowcroft, 1954). The present study has shown that the length of the short cycle of the Common shrew differs with season. This cycle is the shortest in the winter, and the longest in the summer in old adults (Table 3). The length of short cycles is associated with the size of the specimen and so in heavier specimens it is greater than in lighter ones.

The night/day ratio is also differentiated in the Common shrew according to the age of the animal. In younger shrews, more active than older specimens, the greater part of activity takes place at night. It seems that an increment in activity may occur only in the night.

#### REFERENCES

1. Aschoff J., 1957: Aktivitätsmuster der Tagesperiodik. *Naturwiss.*, 44: 361—367.
2. Bazan I., 1952: Morphohistologische Veränderungen des Thymus im Lebenszyklus von *Sorex araneus* L. *Ann. Univ. M. Curie-Skłodowska*, C 7, 5: 253—304 (In Polish with German & Russian summ.).
3. Bielak T. & Pucek Z., 1960: Seasonal changes in the brain-weight of the common shrew (*Sorex araneus araneus* Linnaeus, 1758). *Acta theriol.*, 3, 13: 297—300.
4. Blagosklonov K. N., 1957: O pitanii i haraktere sutočnoj aktivnosti krošečnoj burozubki (*Sorex tscherskii* Ogniev). *Zool. Ž.*, 36, 3: 465—467.
5. Buchalczyk T. & Pucek Z., 1963: Food storage of the European water shrew, *Neomys fodiens* (Pennant, 1771). *Acta theriol.*, 7, 19: 376—379.
6. Buckner C. H., 1964: Metabolism, food consumption, and feeding behaviour in four species of shrews. *Canad. J. Zool.*, 42: 259—279.
7. Cabań K., 1956: Untersuchungen über die saisonale Veränderungen des Gehirnes bei der kleinen Spitzmaus (*Sorex minutus minutus* L.). *Ann. Univ. M. Curie-Skłodowska*, C 10, 5: 93—115.

8. Crowcroft P., 1954: The daily cycle of activity in British shrews. Proc. zool. Soc. Lond., 123: 715—729.
9. Crowcroft P., 1957: The life of the shrew. Reinhard: 1—166. London.
10. Davis D. E. & Golley F. B., 1963: Principles in mammalogy. Reinhold: 1—335. New York—London.
11. Dehnel A., 1949: Studies on the genus *Sorex* L. Ann. Univ. M. Curie-Skłodowska, C 4: 17—102 (In Polish with English summ.).
12. Dehnel A., 1951: Studies on the genus *Neomys* K a u p. Ann. Univ. M. Curie-Skłodowska, C 5, 1: 1—63 (In Polish with English & Russian summaries).
13. Dzierżykraj - Rogalska I., 1952: Histomorphologische Veränderungen der Schilddrüse in Lebenszyklus *Sorex araneus araneus* L. Ann. Univ. M. Curie-Skłodowska, C 7, 4: 213—252 (In Polish with German & Russian summ.).
14. Gębczyńska Z. & Gębczyński M., 1965: Oxygen consumption in two species of water shrews. Acta theriol., 10, 13: 209—214.
15. Gębczyński M., 1963: Apparatus for daily measurements of oxygen consumption in small mammals. Bull. Acad. Pol. Sci., Cl. II, 11, 9: 433—436.
16. Gębczyński M., 1964: Effect of light and temperature on the 24-hour rhythm in *Pitymys subterraneus* (de Sél. - Long.). Acta theriol., 9, 9: 125—137.
17. Gębczyński M. & Olszewski J., 1963: Katathermometric measurements of insulating properties of the fur in small mammals. Acta theriol., 7, 19: 399—402.
18. Grodziński W., 1961: Metabolism rate and bioenergetics of small rodents from the deciduous forest. Bull. Acad. Pol. Sci., Cl. II, 9, 12: 493—499.
19. Grodziński W., 1964 (MS): Energy flow through the populations of small mammals in the alaskan taiga forest.
20. Hamilton W. J., 1930: Food of the *Soricidae*. J. Mamm., 2: 26—39.
21. Hamilton W. J., 1940: The biology of the smoke shrew (*Sorex fumeus fumeus* Miller). Zoologica, N. Y. Zool. Soc., 25, 4: 473—492.
22. Hart J. S. & Heroux O., 1953: A comparison of some seasonal and temperature induced changes in *Peromyscus*: cold resistance, metabolism, and pelage insulation. Canad. J. Zool., 31: 528—534.
23. Hart J. S. & Irving L., 1959: The energetics of harbor seals in air and in water with special consideration of seasonal changes. Canad. J. Zool., 37: 447—457.
24. Hawkins A. E. & Jewell P. A., 1962: Food consumption and energy requirements of captive British shrews and the mole. Proc. zool. Soc. Lond., 138, 1: 137—155.
25. Hawkins A. E., Jewell P. A. & Tomlinson G., 1960: The metabolism of some British shrews. Proc. zool. Soc. Lond., 135: 99—103.
26. Ingles L. G., 1960: A quantitative study on the activity of the dusky shrew (*Sorex vagrans obscurus*). Ecology, 41, 4: 656—660.
27. Irving L., Krog H. & Monson M., 1955: The metabolism of some alaskan animals in winter and summer. Physiol. Zoöl., 28, 3: 173—185.
28. Janský L. & Hanák V., 1960: Aktivität der Spitzmäuse unter natürlichen Bedingungen. Säugetierkunde Mitt., 8, 1/2: 55—63.
29. Judin B. S., 1962: Ekologija burozubok (rod *Sorex*) Zapadnoj Sibirii: Tr. biol. In-ta, 8: 33—134.
30. Judin B. S., 1964: The geographical distribution and interspecific taxonomy of *Sorex minutissimus* Zimmermann, 1780 in West Siberia. Acta theriol., 8, 10: 167—179 (In Russian with English & Polish summ.).

31. Kalabukhov N. I., 1946: Sohranene energetičeskogo balansa organizma kak osnova processa adaptacii. Ž. obšč. Biol., 7: 417—432.
32. Kalabukhov N. I., 1951: Metodika eksperimentalnyh issledovanij po ekologii nazemnyh pozvonočnyh. Izd. „Sov. nauka”: 1—176. Moskva—Leningrad.
33. Kisielewska, K., 1963: Food composition and reproduction of *Sorex araneus* Linnaeus, 1758 in the light of parasitological research. Acta theriol., 7, 9: 127—153.
34. Kunicki-Goldfinger W. & Kunicka-Goldfinger W., 1964: Seasonal variations of some haematological values in small mammals living in natural conditions. Acta theriol., 9, 11: 149—163.
35. Layne J. N. & Redmond J. R., 1959: Body temperatures of the Least shrew, *Cryptotis parva floridana* (Merriam, 1895). Säugetierkunde Mitt., 7: 169—172.
36. Mann P. M. & Stinson R. H., 1957: Activity of the short-tailed shrew. Canad. J. Zool., 35: 171—177.
37. McNab B. K., 1963: A model of the energy budget of a wild mouse. Ecology, 44, 3: 521—532.
38. Mezhzherin V. A., 1964: Dehnel's phenomenon and its possible explanation. Acta theriol., 8, 6: 95—114 (In Russian with English & Polish summ.).
39. Morrison P. R., 1948: Oxygen consumption in several small wild mammals. J. cell, comp. Physiol., 31: 69—96.
40. Morrison P. R. & Pearson O. P., 1946: The metabolism of a very small mammal. Science, 104, 2700: 287—292.
41. Morrison P. R., Pierce M. & Ryser F. A., 1957: Food consumption and body weight in the masked and short-tailed shrews. Am. Midland Nat., 57, 2: 493—500.
42. Morrison P. R., Ryser F. A. & Dawe A. R., 1953: Physiological observations on a small shrew. Federat. Proc., 12: 100—101.
43. Morrison P. R., Ryser F. A. & Dawe A. R., 1959: Studies on the physiology of the masked shrew, *Sorex cinereus*. Physiol. Zoöl., 32, 4: 256—271.
44. Pearson O. P., 1947: The rate of metabolism of some small mammals. Ecology, 28: 127—134.
45. Pearson O. P., 1948: Metabolism of small mammals, with remarks on the lower limit of mammalian size. Science, 108, 2794: 44.
46. Pfeiffer C. J. & Gass G. H., 1962: Oxygen consumption in the small, short-tailed shrew (*Cryptotis parva*). Trans. Ill. State Acad. Sci., 55, 2: 130—132.
47. Prosser C. L. & Brown F. A., 1961: Comparative animal physiology. Saunders Co: 1—688, Philadelphia—London. II ed.
48. Pucek Z., 1955: Untersuchungen über die Veränderlichkeit des Schädels im Lebenszyklus von *Sorex araneus araneus* L. Ann. Univ. M. Curie-Skłodowska, C 9, 4: 163—211.
49. Pucek Z., 1957: Histomorphologische Untersuchungen über die Winterdepression des Schädels bei *Sorex* L. und *Neomys* K a u p. Ann. Univ. M. Curie-Skłodowska, C 10, 15: 299—428.
50. Pucek Z., 1959: Some biological aspects of the sex-ratio in the Common shrew (*Sorex araneus araneus* L.). Acta theriol., 3, 4: 43—73.

51. Pucek Z., 1963: Seasonal changes in the braincase of some representatives of the genus *Sorex* from the Palearctic. *J. Mamm.*, 44, 4: 523—536.
52. Pucek Z., 1964: Morphological changes in shrews kept in captivity. *Acta theriol.*, 8, 9: 137—166.
53. Pucek Z., 1965: Seasonal and age changes in the weight of internal organs of shrews. *Acta theriol.*, 10, (in print).
54. Redmond J. R. & Layne J. N., 1958: A consideration of the metabolism rates of some shrew tissues. *Science*, 128: 1508.
55. Schwarz S. S., 1962: Morfologičeskie i ekologičeskie osobennosti zemlerook na krajnem severnom predele ih rasprostranjenja. AN SSSR, Ural. Filial., Tr. In-ta Biol., 29: 45—51.
56. Siuda S., 1964: Morphology of the adrenal cortex of *Sorex araneus* Linnaeus, 1758 during the life cycle. *Acta theriol.*, 8, 7: 115—124.
57. Skvortzov G. N., 1957: Ulutšennyj metod opredelenija potreblenija kisloroda gryzunami i drugimi melkimi životnymi. Sb. „Gryzuny i borba s nimi”, 5: 124—132.
58. Slonim A. D., 1961: Osnovy obščej ekologičeskoj fizjologii. AN SSSR: 1—430. Moskva—Leningrad.
59. Slonim A. D., 1963: Modern problems of physiological studies of instinct. *Ž. obšč. Biol.* 24, 5: 313—323 (In Russian).
60. Smirnov P. K., 1957: Novoe prisposoblene dlja registracii i količestvennoj ocenki podvižnosti melkih gryzunov. *Vestn. Leningrad. Univ.*, 15: 137—139.
61. Tupikova N. V., 1949: Pitane i harakter sutočnoj aktivnosti zemlerook srednei polosy SSSR. *Zool. Ž.*, 28, 6: 561—572.

Polish Academy of Sciences,  
Mammals Research Institute,  
Białowieża, woj. Białystok.

---

M. GĘBCZYŃSKI

SEZONOWE I WIEKOWE ZMIANY METABOLIZMU I AKTYWNOŚCI  
*SOREX ARANEUS* LINNAEUS, 1758

Streszczenie

W respirometrze typu zamkniętego zmierzono 70 dobowych przebiegów zużycia tlenu ryjówki aksamitnej, *Sorex araneus*. Ryjówki badano w pięciu grupach obejmujących pełny cykl życiowy tych zwierząt: młode (lato, jesień, zima), przezimki (wiosna, lato) (Ryc. 1). Średni metabolizm dobowy u młodych latem wynosi 9,91 cm<sup>3</sup> O<sub>2</sub>/g godz. (dobowe zapotrzebowanie energetyczne — 8,847 Kcal/zwierzę), jesienią 9,67 (8,533), zimą 9,66 (7,478), u przezimków wiosną 9,29 (9,953 i latem 8,28 (11,093) (Tabela 1). Wahania sezonowe metabolizmu ryjówek są mniejsze niż u gryzoni i nie dają się badać w oderwaniu od wieku zwierzęcia (Ryc. 2, 3, 4).

Latem i zimą mierzono zużycie tlenu na 8—12 ryjówkach w temperaturze 7, 10, 15, 20, 25, 30 i 35°C. Uzyskane wartości są latem wyższe niż zimą. Strefa termoneutralna zimą leży w granicach 10—15°C, latem 15—20°C (Tabela 2, Ryc. 5).

Potwierdzono zdanie tych autorów, którzy uważają, że metabolizm ryjówek jest wyższy niż wynikałoby to z ogólnej zależności pomiędzy wielkością zwierzęcia a jego metabolizmem (Tabela 4). Przyczyną tego jest, zdaniem autora, zarówno (1) bardziej niekorzystny niż u zwierząt większych stosunek ciężaru ciała do jego powierzchni (Ryc. 2), jak też (2) Działanie specyficznie-dynamiczne pokarmu.

Krótkie cykle, związane z częstotliwością pobierania pokarmu, zmieniają się zależnie od sezonu i trwają u *S. araneus* od ponad 1½ (w zimie) do około 2½ godziny (latem) (Tabela 3). Wzorec aktywności dobowej (wykreślony na podstawie dobowego rytmu zużycia tlenu) również zależy od wieku zwierzęcia i sezonu. Jest on dwudzielny jesienią, zimą i wiosną a jednoszczytowy u młodych latem. Przezimki latem są prawie jednakowo aktywne w dzień jak i w nocy (Ryc. 6).