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# Effect of Light and Temperature on the 24-Hour Rhythm in *Pitymys subterraneus* (de Sél.-Long.)

## Wpływ światła i temperatury na rytm dobowy *Pitymys subterraneus* (de Sél.-Long.)

[With 3 Figs. & 2 Tables]

## I. INTRODUCTION

Light (photoperiods — lengths of days and nights) and temperature are climatic factors which control the seasonal changes occurring in animal organisms in an essential manner. Similarly, the 24-hour rhythm depends, above all, upon these very factors.

The 24-hour rhythm is reflected, among other things, by changes in activity, metabolism, and body temperature (Kleitman, 1949). Measurements of the 24-hour metabolism rhythm make it possible to get acquainted with the activity rhythm of animals examined (Pearson, 1947; Morrison, 1948; Hart, 1950; Aschoff, 1962), for the total value of metabolism varies with the level of activity and the level of specific dynamic action (SDA) of food.

The opinion prevails that in most vertebrates the length of day rules the basic pattern of activity (Kowalski, 1951; Ostermann, 1956; Bünning, 1958; Saint Girons, 1960, 1961; Smirnov, 1960; Erkinaro, 1961; Aschoff, 1962; Grodziński, 1963). Temperature, like light, exerts influence upon activity (Ščeglova, 1953; Sweeney & Hastings, 1960) and controls, above all, the sum of activity.

The purpose of the present study was to investigate the 24-hour rhythm of oxygen consumption in various conditions of light and temperature. The investigation made it also possible to grasp the 24-hour activity rhythm and its dependence upon the joint action of light and temperature.

The animal used in this study was the European pine vole, *Pitymys subterraneus* (de Sélys - Longchamps, 1835). This species is very common in Western Europe, in Poland it inhabits the northern edge of its range (Wasilewski, 1960). *P. subterraneus* lives underground and feeds on fairly substantial food (bulbs, rhizomes) available all the year round. It is a nocturnal animal; 75.47% of its activity falls in the night (Smirnov, 1962). In connection with its ways of living, light and temperature exert lesser influence on it as compared with the other members of the *Microtidae*. Owing to this fact the European pine vole breeds all the year and the intensity of reproduction is only slightly smaller in winter than in spring (Wasilewski, 1960). *P. subterraneus* was rarely used as an object for study. Smirnov (1962) carried out ecological and physiological experiments on European pine voles from the central regions of the European part of the U.S.S.R. (Belgorodskaya oblast). He measured the metabolism and chemical thermoregulation, the temperature in a few points of body at various environmental temperatures, and the 24-hour activity rhythm.

## II. MATERIAL AND METHOD

European pine voles used for experiments were derived from the laboratory stock of the Mammals Research Institute of the Polish Academy of Sciences at Białowieża (Buchalczyk, 1961). The animals were divided into four experimental groups (Table 1), which were kept under different conditions of light and temperature for 2—5 months:

*A.* long (18 hrs.) periods of illumination at an ambient temperature of 20°C corresponding to long summer days
*B.* short (6 hrs.) periods of illumination at 20°C
*C.* long (18 hrs.) periods of illumination at 5°C
*D.* short (6 hrs.) periods of illumination at 5°C corresponding to short winter days.

The particular groups of animals were examined in such conditions as they had been adapted for. The period of adaptation of the animals to the given conditions of light and temperature was long and lasted 120 days in the case of groups *A* and *B* and 45 days for groups *C* and *D*.

The animals were fed oats, beetroots and carrots. In the period of adaptation and during the experiments the animals of all the groups were provided with the same kind of food, which made it possible to avoid differences in activity between the groups caused by the quality of food (Grodziński, 1962) and to equalize the specific dynamic action of food to some degree in all the specimens examined.

Experiments were carried out using a respirometer of the closed circuit type. The construction of this respirometer (Gębczyński, 1963) is based on the principle of the apparatus of Kalabukhov (1951) modified by Skvortzov (1957). In this case the oxygen consumption was measured, and carbon dioxide was absorbed by soda-lime. The dimensions of the apparatus chamber are 40 cm by 20 cm by 18 cm. Inside the chamber there are some nest material and an activity wheel. Food was offered in excess before starting the experiment. Each run, lasting usually for 25—26 hours, covered a day and a night. The experiments were started between 9 a.m. and 4 p.m. The changes of days into nights and vice versa were brought about by switching the lamp off or on. The intensity of illumination reaching the bottoms of the cages was 150 luxes.

The animals under study were weighed before and after the experiment, and the mean from these two measurments was used for further calculations. It should be added that the rise/drop in body weight after the experiment was small and did not exceed ±0.25 gms. The volume of oxygen consumed was reduced to the value for standard conditions (0°C, 760 mm of mercury) and converted into cc $O_2$/gm/hr. The average daily metabolic rate (*ADMR*) was used for comparisons between the groups.

It is the average value for 1 hour obtained from measurements of the 24-hour metabolism (Grodziński, msc.). The statistical significance of differences was determined by the *t* test of Student for the difference between averages for two independent groups.

## III. RESULTS

### 1. Effect of Light

The 24-hour rhythm in the groups examined under conditions of long day is presented in Fig. 1. The curve illustrating the average oxygen consumption for the group with summer day (*A*) has one peak in the night time (Fig. 1 A). A small rise in the level of metabolism is also perceptible 2 hours before the end of the daytime. The average oxygen consumption in night hours is higher by 26% than it is in the daytime. As early as the first hour of night the oxygen consumption for the whole group increases by 17.9% as compared with the previous hour, i.e., the last hour of day. The metabolism reaches its maximum rate at midnight, amounting then to 6.73 cc $O_2$/gm/hr against the minimum rate of 4.25 cc $O_2$/gm/hr at 10 a.m. Such a rhythm of metabolism conforms to the reversed bimodal activity pattern (Aschoff, 1957). At the same time, it is a mixed pattern, because the first, smaller, peak falls in the daytime and the maximum at night.

The group exposed to long cold days (*C*) shows the 24-hour rhythm of oxygen consumption more clearly than the previous group (Fig. 1 C). As in group *A*, the maximum occurs in the night time, but it is marked very strongly. There is also another, smaller peak in the afternoon hours. Group *C*, therefore, has a mixed and reversed bimodal activity pattern, as well. However, these groups differ in that the peaks of group *A* are separated by an interval of 6 hours, whereas in group C the interval amounts to 12 hours.

The maximum oxygen consumption occurs at 4 a.m. (11.38 cc $O_2$/gm/hr) and the minimum at 8 a.m. (6.15). Nights in both these groups fall in somewhat different hours and thus the dependence of the course of the curve upon light is visualized more conspicuously.

In the case of the two groups exposed to short days the 24-hour rhythm differs from that in the groups used in experiments with long days. In the group used with short warm days (*B*) the curve of the average daily oxygen consumption has two peaks (Fig. 2 B). They both occur at night. The first peak falls in the first night hours (6 p.m.) and reaches the maximum 3—4 hours after dark. The second peak takes place from 4 to 6 a.m. and is considerably lower than the first one. A drop in the level of metabolism comes before the break of day. The maximum rate of oxygen consumption occurs at 6 p.m., amounting to 7.43 cc $O_2$/gm/hr and is 57% higher than the minimum rate equal to 4.75 cc $O_2$/gm/hr (10 a.m.). The activity pattern of this group can be defined as a typical simple (nocturnal) bimodal one.

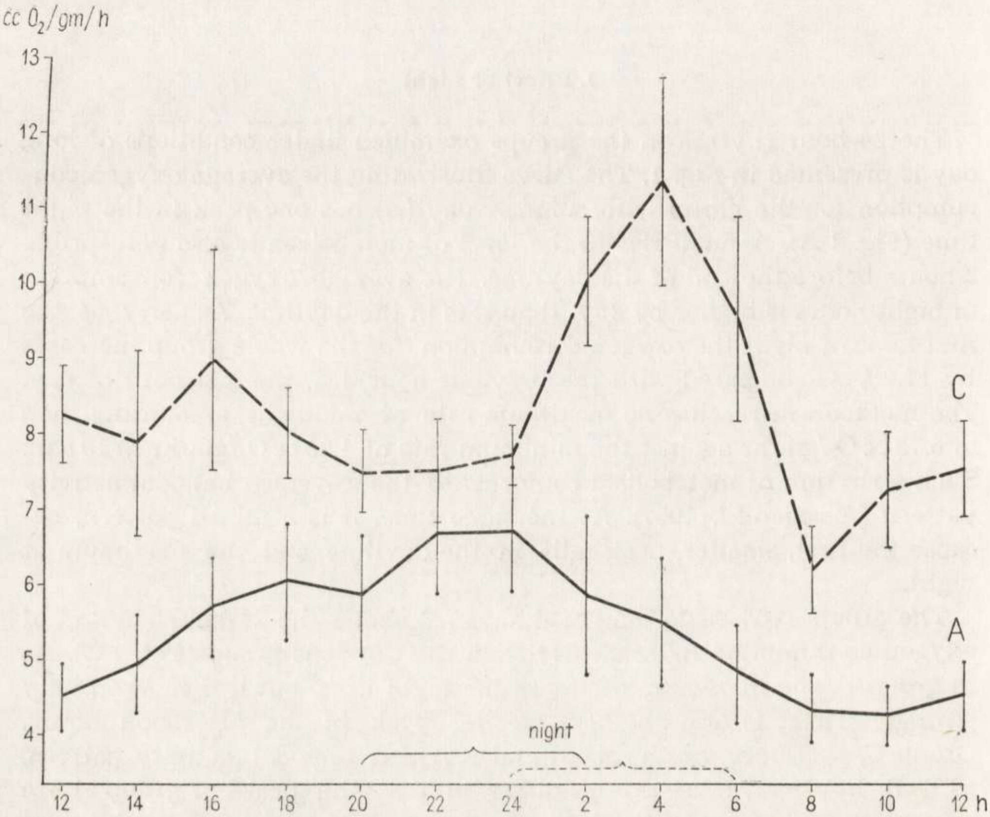


Fig. 1. The 24-hour rhythm of oxygen consumption in the groups placed in long day at temperatures of 20°C (*A*) and 5°C (C). The data are given at two-hour intervals.

The same pattern is revealed by the group kept before experiments and examined under winter day conditions (*D*). The rhythm of oxygen consumption is very like that of group *B* (Figs. 2 B, D). It also has two peaks, the first being higher than the second. The maximum rate takes place at 6 p.m. and it is 11.04 cc $O_2$/gm/hr, the minimum reaches 6.23 cc $O_2$/gm/hr at 10 a.m.

There was a supposition based on the knowledge of the life history of *P. subterraneus* that this animal is not sensitive to light (Wasilewski, 1960). On the other hand, Langenstein-Issel (1950) ascertained on the basis of field observations and the number of catches in particular hours of day that the European pine vole is active day and night. However, the results of the present study suggest decidedly that it avoids light (Figs. 1, 2, and 3). This fact is responsible for the close dependence of the 24-hour activity pattern upon the length of day. In the experiments with short 6-hour nights the animals are active all the night time. There is one peak covering the whole period of darkness (Fig. 1). Another small additional

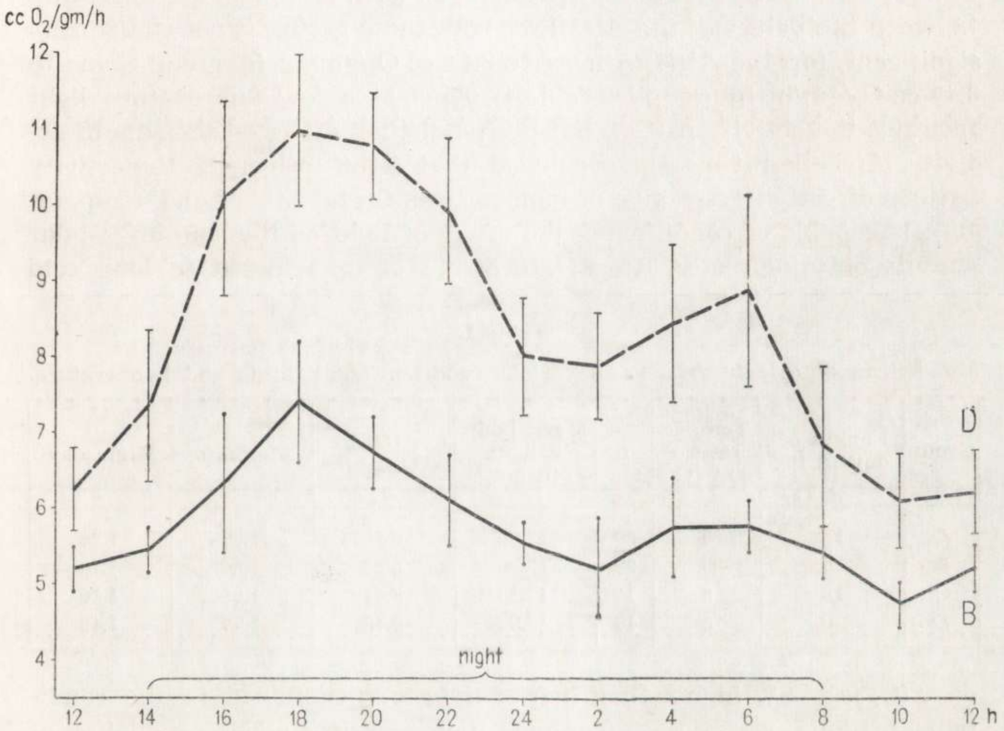


Fig. 2. The 24-hour rhythm of oxygen consumption in the groups placed in short day at temperatures of 20°C (*B*) and 5°C (*D*). The data are given at two-hour intervals.

peak occurs in the day time. With long 18-hour nights, the pattern is alike in both groups irrespective of temperature. It has two clear-cut maxima separated by a drop in the middle of the night (Fig. 2). It should be added that both in long night and in short night conditions *P. subterraneus* as a rule begins its activity after darkness. Before the break of day its activity decreases.

### 2. Effect of Temperature

The 24-hour rhythm of metabolism and activity in the conditions of long warm day (*A*) differs evidently from that in the experiments with warm but short days (*B*). The two groups vary also in their values of the *ADMR*, which amount to 5.39 cc $O_2$/gm/hr in group *A* and to 5.82 cc $O_2$/gm/hr in group *B* (Table 1). The difference is statistically significant. This fact indicates that at 20°C light not only modifies the type of activity pattern a little, but also governs the sum of 24-hour activity.

The groups examined in the conditions of winter day (*D*) and long cold day (*C*) have different 24-hour patterns, as well. However, the difference between the values of the *ADMR* of both these groups is not statistically significant, for the *ADMR* comes to 8.41 cc $O_2$/gm/hr in group *C* and to 8.48 cc $O_2$/gm/hr in group *D* (Table 1). Thus, at a low temperature light modifies the activity pattern but has no distinct effect on the sum of activity. And then it may be concluded that light influences the activity pattern directly irrespective of temperature. On the other hand, temperature is capable of conditioning the effect of light on the sum of 24-hour activity only indirectly. The *ADMR* of the group exposed to long cold

**Table 1.**

Metabolism of *P. subterraneus* in various conditions of lighting and temperature.

| Group | Length of day in hr. | Temperature in °C | n | Mean body weight in gm | *ADMR* cc $O_2$/gm/hr | Max/min | Night/day |
|---|---|---|---|---|---|---|---|
| *A* | 18 | 20 | 20 | 13.66 | 5.39 | 1.58 | 1.26 |
| *B* | 6 | 20 | 20 | 12.30 | 5.82 | 1.56 | 1.18 |
| *C* | 18 | 5 | 16 | 13.35 | 8.41 | 1.85 | 1.30 |
| *D* | 6 | 5 | 16 | 12.82 | 8.48 | 1.77 | 1.42 |

days (*C*) is 55.9% higher than that of the group examined in the conditions of long warm days (summer days, group *A*). The calculation of chemical thermoregulation (between 5 and 20°C) reveals that the metabolism changes by 3.7% per 1°C. The difference between the group used with short cold days (winter days, *D*) and that with short warm days (*B*) diverges a little from the previous one: the *ADMR* of group *D* is 45.7% higher than the *ADMR* of group *B*, which gives 3.0% per 1°.

At a temperature of 5°C the difference between the maximum and the minimum is also higher than it is at 20° (Table 1). This proves that temperature may have an effect on the magnitude of activity amplitude. The night/day ratio varies somewhat with temperature (Table 1).

### 3. The 24-Hour Rhythm of Individual Specimens

The 24-hour rhythm of metabolism conditioned by short and long days as well as by temperature is presented in Figs. 1 and 2. In the case of groups *A* and *B* it is the average course from 20 specimens, in groups *C* and *D* from 16 specimens (Table 1). The 24-hour rhythm of each individual examined deviates a little from the average for the whole group. To illustrate this fact the typical course of a daily cycle of oxygen consumption in 2 specimens of group *B* is exemplified in Fig. 3. In this case, however, the values of oxygen consumption are given at 1-hour intervals to show the individual features of the rhythm more clearly, while in the graphs illustrating the rhythm of the whole groups the intervals are 2-hour ones (Fig. 1 and 2).

For comparison, the average for the whole group *B* is also plotted in Fig 3. The specimens selected for illustration have their *ADMR* nearly equal to the *ADMR* of the whole group. It amounts to 5.88 cc $O_2$/gm/hr

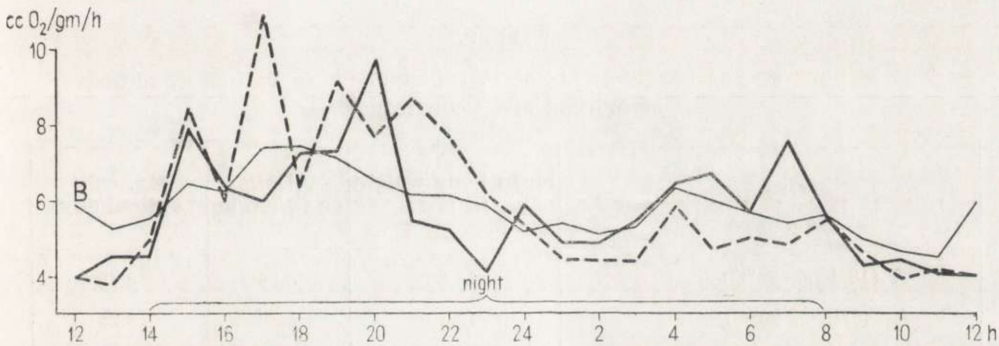


Fig. 3. The 24-hour oxygen consumption of two individual specimens. Length of day — 6 hrs, temperature — 20°C. The data are given at one-hour intervals for better illustration of individual variation.

for the first specimen (body weight — 12.05 gms) and to 5.75 cc $O_2$/gm/hr for the second (weight — 11.60 gms) against the average for the whole group *B* equal to 5.87 cc $O_2$/gm/hr (body weight — 12.30 gms).

A distinctive feature of the behaviour of particular specimens is that in some periods they reach a high level of oxygen consumption (they are polyphase). The phases of activity last usually for 5—10 minutes, but occasionally they may go on for as much as 60—90 minutes. Such a long period of activity falls mostly in the first hours of darkness (Fig. 3). The oxygen consumption rate reaches 11—12 cc $O_2$/gm/hr in this period. At that time the animal runs in the activity wheel. It is also characteristic that besides the night time European pine voles run in the activity wheel just after they have been put in the chamber or while the apparatus is being dismantled after an experiment. Thus, in the daytime they run only if disturbed (they "run away"). The long-lasting period of intense activity (60—90 minutes) is characterized by the following behaviour of the animal: after going away from the feeding place the vole searches the chamber and next begins to run in the wheel. It runs generally for a few minutes, then stops running, calls at the feeding place and runs again. In such a period of increased activity the animal calls at the feeding place 4—10 times in all and during the remaining breaks in running it searches the chamber.

## IV. BIOENERGETICS OF *P. SUBTERRANEUS*

The 24-hour energy requirements of the European pine vole in dependence on temperature and light (Table 2) has been calculated from the data offered in Table 1. It was assumed for calculations that the respiratory quotient (*RQ*) equals 0.8, at which the caloric value of 1 l. of $O_2$ is 4.8 kg. cal.

**Table 2.**

The 24-hour energy requirements of *P. subterraneus* in various conditions of lighting and temperature.

| Group | Mean body weight in gm | *ADMR* gc $O_2$/gm/hr | Kg. cal./ animal/day |
|---|---|---|---|
| *A* (18 hrs., 20°C) | 13.66 | 5.39 | 8.48 |
| *B* (6 hrs., 20°C) | 12.30 | 5.82 | 8.25 |
| *C* (18 hrs., 5°C) | 13.35 | 8.41 | 12.93 |
| *D* (6 hrs., 5°C) | 12.82 | 8.48 | 12.52 |

The 24-hour energy consumption of *P. subterraneus* expressed in kg. cal./animal/day is governed, above all, by temperature. At the same time, however, it is observed that the length of daylight period has some effect on this value. At a temperature of 20°C the difference between group *A* (18 hrs) and group *B* (6 hrs) is small, though the difference between these groups in their values of *ADMR* is statistically significant. This is due to a difference in the mean body weights, amounting to 1.36 gms.

If we theoretically reduce the mean body weights to the same value in both these groups, the requirements of group *B* are higher than those of group *A* by about 0.7 kg. cal./animal/day. The difference between group *C* (18 hrs) and group *D* (6 hrs) is 0.41 kg. cal./animal/day at a temperature of 5°C (Table 2). However, these groups, too, show a difference in their mean body weights, amounting to 0.53 gms. The reduction of the mean body weights to the same value reveals that the requirements in group *D* are higher by 0.1 kg. cal./animal/day.

Thus, in so far as the European pine vole is concerned, light may control the value of the daily energy requirements, but only to a low degree. In the case of long nights the requirements are higher, but even this difference is influenced by temperature, for at 20°C it amounts to 0.7 kg. cal./animal/day (8.4%) and at 5°C only to 0.1 kg. cal./animal/day (0.8%).

## V. DISCUSSION

Smirnov (1962) studied European pine voles late in summer and early in autumn. He found that in this period *P. subterraneus* is a nocturnal animal. In the daytime it leaves the nest for periods of 3—10 minutes only every 3—4 hours. At night, however, the periods of resting are short and those of activity last for 50—65 minutes. These observations are corroborated by the present study. The European pine voles now examined show very similar periods of activity. The results obtained by Langenstein-Issel (1950) are somewhat different. She ascertained on the basis of her observations and the results from day-and-night catches that *P. subterraneus* is as active by day as it is at night. These results do not seem to be inconsistent with each other, because the appropriate appraisal of the length and intensity of activity periods cannot be based on visual observations and data obtained from catches. In the daytime voles may be caught during their short and rare stays out on the surface. Langenstein-Issel (1950) classified the data obtained from catches at intervals of 4 hours and it was just every 3—4 hours that these animals were observed coming out for a short time (Smirnov, 1962). It should be added that, basing on the results of her catches, the authoress found the activity of males far intenser than that of females, their ratio being as 3:2. The present study has not shown any significant differences between males and females in any of the groups examined.

*Pitymys pinetorum scalopsi* (Aud. & Bachman, 1841) and American members of the genus *Pitymys* in general (Pearson, 1947; Morrison, 1948; Odum, 1959) show a different pattern of activity. Short alternating periods of activity and resting are independent of the time of day or night. This is connected with the ways of living of these voles (Benton, 1955). In contrast with typical nocturnal *P. subterraneus* the American species are polyphase animals.

The 24-hour activity pattern of *P. subterraneus* is fairly stable and little changes under the influence of temperature and light. This pattern is always bimodal, simple or reversed.

The remarkable stability of the 24-hour rhythm can be explained by the hardly changing environmental conditions of the European pine vole. Under experimental conditions the pattern of activity does not change much and undergoes only some modifications.

The reversal of the activity pattern in relation to the pattern observed with short days occurs in experiments with long days. Besides, in the groups examined in the conditions of long days (*A* and *C*) the second, smaller peak falls in the daytime, the whole period of night being covered by one peak (Fig. 1). And then the modification of the 24-hour activity pattern depends on the length of the day light period. No dependence of the 24-hour activity rhythm on temperature was found. This result is compatible with the general presumption that one of the features of biologic rhythms is their independence of temperature (Folk et al., 1958). De Coursey (1961), using *Glaucomys volans* as an example, confirmed the independence of the 24-hour activity pattern from temperature.

The stability of the activity pattern of *P. subterraneus* differs it from *Clethrionomys glareolus* (Schreber, 1780), *Microtus agrestis* (Linnaeus, 1761) and *Apodemus agrarius* (Pallas, 1771), (Grodziński, 1962). In the three above-mentioned species of rodents the 24-hour rhythm changes with season. Erkinaro (1961) indicated that in spring months the activity of *M. agrestis* is a typical polyphase one. In summer the activity pattern is unimodal, nocturnal. In autumn it becomes polyphase again and in winter months a bimodal diurnal pattern develops. A similar close connection of the activity pattern with season is observed in *C. glareolus* (Ostermann, 1956; Saint Girons, 1960; 1961).

The statistically significant differences between the *ADMR* of the group with summer day and that of the group with short warm day as well as the lack of such differences in the groups placed in winter days and long cold days may be explained by the fact that the temperature of 20°C little differs from the thermoneutral zone. Smirnov (1962) ascertained that in summer in *P. subterraneus* this zone lies about 28°C. In this period the oxygen consumption at 20° compared with that at 28°, increases by 20% or by 2.5% per 1°C (calculated by the author from the data of Smirnov, 1962). The increase of metabolism brought about by a drop in temperature (chemical thermoregulation) being so small, the energy consumption is not very great. Under favourable lighting conditions the European pine vole may be active for long. Therefore, there is a possibility of additional energy outgo. With short nights this outgo of energy is smaller owing to the shortened period of activity.

At a low temperature (5°C) the increase of metabolic rate in comparison with that in the thermoneutral zone is threefold (by 199.5%, Smirnov, 1962). Calculated for 1°C it is 8.7%. In these hard thermic conditions the maintenance of stable body temperature requires large amounts of energy. The possibility of additional energy outgo is smaller. This is probably responsible for the lack of difference in the amount of oxygen consumed between the group examined in long days (*C*) and that in short days (*D*). Consequently, there are no differences in the total activity between these groups.

Light seems to have a decisive effect on the activity pattern in animals with distinct diurnal or nocturnal ways of living. In these species light may also control the magnitude of total activity, to some degree, and then probably the sum of activity, under thermic conditions which do not compel the animal organism to intensive metabolism.

## VI. SUMMARY

The 24-hour rhythm of metabolism of *Pitymys subterraneus* was examined in the conditions of long (18 hrs) and short (6 hrs) days and at temperatures of 5 and 20°C.

1. *P. subterraneus* is a nocturnal animal showing a simple or reversed bimodal activity pattern.
2. This pattern is stable and undergoes no changes even when animals are kept in changed environmental conditions for a long time.
3. Some modification of the activity pattern is dependent on light.
4. The rate of 24-hour energy consumption and, consequently, the rate of activity depend on the joint action of light and temperature. In favourable thermic conditions the length of the light period influences the activity of the animal so that the difference between the values of the *ADMR* of the groups placed in long and short days is statistically significant. On the other hand, at a low temperature there are no differences between these values.

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## STRESZCZENIE

Badano rytmikę dobową metabolizmu darniówki, *Pitymys subterraneus* (de Sélys-Longchamps, 1835) w dniu długim (18 godz.) i krótkim (6 godz.), oraz przy temperaturze 5 i 20°C (Tabela 1). Stwierdzono, że:

1. *P. subterraneus* jest zwierzęciem nocnym, o wzorcu aktywności dwudzielnym prostym lub odwróconym.

2. Wzorzec ten jest stały i nie ulega zmianom nawet po długotrwałym trzymaniu zwierząt w zmienionych warunkach środowiskowych.

3. Pewne modelowanie (odwrócenie) wzorca aktywności uzależnione jest od światła.

4. Wielkość dobowego zużycia energii, a więc i wielkość aktywności zależy od wzajemnego oddziaływania światła i temperatury. W sprzyjających warunkach termicznych długość fazy świetlnej wpływa tak na aktywność zwierzęcia, że metabolism (*ADMR*) grupy z dnia długiego i krótkiego różni się w sposób istotny statystycznie. Natomiast w niskiej temperaturze nie ma różnic pomiędzy metabolizmem grupy z dnia długiego i krótkiego (Tabela 1, 2).