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

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Social Regulation of Body Temperature in the Bank Vole*

[With 3 Tables & 3 Figs.]

Social regulation of oxygen consumption rate was measured in the bank vole, *Clethrionomys glareolus* (S c h r e b e r, 1780), kept in groups of various numbers and in different ambient temperatures. Daily measurements of oxygen consumption in groups consisting of 3 and 5 voles were carried out at 3, 14 and 25°C. In a more numerous group the efficiency of social temperature regulation was higher than in smaller one. The magnitude of this thermoregulation depends on ambient temperature. At lower temperatures the change of oxygen requirement was less intensive than at higher ones. Oxygen consumption during one-hour measurements was studied in groups consisting of 2, 3 and 5 specimens. At 5, 10 and 15°C the lowest oxygen consumption, expressed in ccm/g per hr was found in larger groups. At 20 and 25°C this effect decreased, and at 30°C oxygen consumption by single voles was the same as in groups. Therefore one can conclude that at 30°C social thermoregulation was not observed in this species.

I. INTRODUCTION

Both the poikilothermic and homeothermic animals are able of lowering the heat losses by aggregation (huddling). This phenomenon is known as social temperature regulation (B r o d y, 1945; K l e i b e r, 1961) or effect of aggregation (P r y c h o d k o, 1958) or group effect (P e a r s o n, 1960). Such type of thermoregulation was found to exist in many Vertebrates, among others in frogs (P o n u g a e v a, 1960) and birds (K l e i b e r & W i n c h e s t e r, 1933). However, majority of data are relevant to mammals (P r y c h o d k o, 1958; P e a r s o n, 1960; P o n u g a e v a, 1960; W i e g e r t, 1961; G ó r e c k i, 1968; 1969; T r o j a n & W o j c i e c h o w s k a, 1968; G ę b c z y ń s k a, 1969). In some species of mammals an increase of metabolism rate after aggregation was also described (P o n u g a e v a, 1960).

Reduction in the rate of heat loses in these species of mammals which decrease their metabolism after huddling depends on many factors, such as: number of animals in a group (P r y c h o d k o, 1958; T r o j a n & W o j c i e c h o w s k a, 1968), intensity of light (P o n u g a e v a, 1960), temperature of the environment (P r y c h o d k o, 1958; P o n u g a e v a, *l.c.*).

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Ponugaeva (1960) reported an increase of oxygen consumption computed per unit of body weight in the bank vole after huddling. On the other hand, Górecki (1968) observed that voles kept in groups of two decrease their oxygen consumption by 12.7%, and in groups of four by 13.9% in comparison with voles examined individually. Hence, the effect of aggregation on oxygen consumption in these rodents should be reinvestigated.

The aim of undertaken experiments was to measure oxygen consumption in the bank vole kept in groups of various numbers and in different ambient temperatures. Moreover, the efficiency of social thermoregulation in relation to the time of exposure to different temperatures was evaluated since the determinations of oxygen consumption were carried out both in daily measurements and in one-hour runs.

II. MATERIAL AND METHODS

The bank vole, *Clethrionomys glareolus* (Schreber, 1780), was used in the experiments. The rodents derived from the laboratory stock (Buchalczyk, 1969) and were kept for at least one week in such group as intended to be used in a subsequent experiment. On the whole 39 daily measurements (see Table 1) and 256 one-hour measurements (see Table 3) were completed. Every group was used several times in the experiment. Between successive experiments the animals were kept for 10 days in the laboratory. Groups consisting of 3 and 5 voles included animals of one sex only. On the other hand half of groups consisting of two specimens contained a male and a female, while the remaining groups contained individuals of one sex only. Since no statistically significant differences were found between groups of various sex composition they were used jointly in calculations. Also in case of individual voles the proportion of males and females was similar and no differences were observed.

The experiments were carried out mainly in winter between December and March, and only a few additional experiments with individual voles and groups consisting of two animals were completed in June.

Temperature in a room where the animals were reared ranged from 16 do 20°C with 12 hours period of mixed artificial-natural light. The animals were fed with oats and beets *ad libitum* and supplied with water. Measurements of oxygen consumption during 24 hr were carried out in a modified Morrison respirometer in chambers of 9 l in volume according to the accepted technique (Morrison & Grodziński, 1968). The nest material consisted of cotton wool. The animals had a possibility to move freely and built the nest from attainable materials. Before and after every experiment the animals were separately weighed and their rectal temperature determined with an electric thermometer. A set of one-hour measurements was carried out by means of a Kalabukhov-Skvortzov apparatus Kalabukhov, 1951; Skvortzov, 1957). In this case glass chambers of approximately 3 l were employed. The floor in the chamber was made of wood but no nest material was supplied. During these measurements the animals were left without food and water.

III. RESULTS

1. Daily Metabolism Rate in Groups of Various Size

Daily measurements of oxygen consumption in groups consisting of 3 and 5 voles were carried out at 3, 14 and 25°C (Table 1). The lowest daily metabolism rate was found for voles in groups of 3 individuals at 25°C. It amounts barely to 2.85 ccm/g/hr and is slightly below the value recorded for the group of 5 voles (Table 1). On the other hand, at 14 and 3°C oxygen consumption expressed in ccm/g/hr is higher in smaller groups in comparison with larger groups. The relationship between the rate of oxygen consumption by groups of various numbers and the ambient temperature is well illustrated by the following calculation.

Table 1.

Average daily oxygen consumption in the vole in relation to the group size and ambient temperature.

Temp. °C	Groups of 3 voles				Groups of 5 voles			
	n	Mean weight of group	ccm/g/hr ± S.D.	kcal/kg$^{3/4}$ per hr[1])	n	Mean weight of group	ccm/g/hr ± S.D.	kcal/kg$^{3/4}$ per hr[1])
25	8	53.5	2.85±49	6.56	6	79.9	2.99±53	7.59
14	6	53.6	3.92±27	9.08	6	77.8	3.67±44	9.26
3 A[2])	5	53.5	4.48±39	10.32	5	72.3	4.21±29	10.43
3 B[3])	2	51.1	5.79	13.14	1	73.8	5.41	13.50

n — number of measurements, [1]) For expressing oxygen consumption in calories the *RQ* value was assumed to be 0.82 and that corresponds to caloric equvalent of oxygen = 4.8 kcal per l, [2]) Mean values for 24 hr period, [3]) Mean values for the first 10 hours of experiments.

When oxygen consumption at 25° is assumed to be 100% the increase of this value at 14° in groups of 2 animals is equal to 37.5%. Hence the rate of change of oxygen consumption amounts to 3.4% per 1°C, whereas in the range of temperature between 3 and 14° this rate is smaller and equal to 1.8% per 1°C. Similarly calculated values for groups of 5 voles correspond to 2.1% and 1.6% per 1°C, respectively (see Figs 1 & 2).

There is no doubt that in more numerous groups the efficiency of social thermoregulation is higher, because the rise of oxygen consumption is less pronounced that in smaller groups. One can also conclude that the magnitude of this thermoregulation depends on temperature. At lower temperatures the change in oxygen requirement is less intensive than in higher ones. However, this is complicated by the nest effect increasing at lower temperatures (Pearson, 1960).

The comparison of metabolism in particular groups is difficult due to their different average weight. To accomplish such comparison the obtained results of oxygen consumption were expressed in calories computed for metabolic body size, *i.e.* $kg^{3/4}$ (Kleiber, 1961). Generally observed uniformity of metabolism refers to basal conditions and in approximation is equal to 70 $kcal/kg^{3/4}$ (Kleiber, *l.c.*). The employed calculations allow to compare also other metabolic parameters such as average daily metabolism rate (Gębczyński, 1969). For computation of oxygen consumption in relation to the metabolic body size of a group one has to assume that the reaction of this group to the effect of cold is similar as in individual specimens. Due to these assumptions it was possible to compare the metabolism of voles assembled in groups of various size and examined in different conditions.

After expressing oxygen consumption in $kcal/kg^{3/4}$ per hr it appears that the lowest metabolism was found also in groups consisting of three specimens and studied at 25°C. At the same temperature groups of 5 voles show the metabolism significantly higher (at $P = 0.05$, Student *t*-test) in comparison to 3 voles (Table 1). At lower temperatures these differences decrease and groups of 5 voles exhibit only slightly higher oxygen consumption than groups of 3 animals (Table 1). The differences in metabolism in these cases are statistically not significant, when significance level $P = 0.05$ is accepted. Hence at 3 and 14°C the metabolism expressed in $kcal/kg^{3/4}$ is slightly higher in more numerous groups in contrast to the metabolism expressed as oxygen consumption in ccm/g per hr.

The observed differences in the metabolism of groups consisting of various numbers, particularly significant at 25°, are certainly related to the increased activity of animals in larger groups comparing to smaller ones. In groups of three the voles stayed often in the nest and behaved as a compact group. On the other hand, with 5 voles kept at 25°C very often two separate groups were formed or the animals remainded entirely independent for a long time. In some cases 4 voles stayed together whereas the fifth animal was active. All these facts undoubtedly contributed to the enhanced metabolism observed in larger groups.

Observations of behaviour of voles during these experiments indicate that at lower temperatures the activity of animals decreases. They stay aggregated in their nest and leave it rarely for feeding. The time spent out of the nest was not measured but a marked decrease of activity with the fall of ambient temperature was apparent. This is in agreement with the observations of Ščeglova (1953) who found that for the bank vole time of staying out of the nest amounts to 300 min during 24 hr at 20°C and becomes reduced to 100 min at —5°.

It was difficult to establish average daily metabolism rate at 3° since some animals died during the experiment. The death of a member of group resulted in elimination of the whole group from subsequent calculations. In such way two groups of 3 voles and one consisting of 5 animals were eliminated. However, since all these groups survived in experimental conditions for at least 10 hr, oxygen consumption in initial period of measurements was calculated (Table 1). Average metabolism for 10 initial hours was higher than in groups which survived the whole day in experimental conditions (Table 1, 3°C, A). Only one of these groups built the nest whereas two others were not able to make it. Of course all the groups which survived 24 hr at 3° built the nest.

2. Changes of Body Weight and Temperature During Daily Measurements

The voles were weighed and their body temperature determined before and after every experiment. The results are presented in Table 2. Changes of body weight were small and only at 3° a certain decrease (by 2.3% on average) is visible in the two types of groups. At 14° groups containing 3 individuals slightly decreased their body weight

Table 2.

Changes of body weight (*Bw*) and rectal temperature (*Tb*) during daily measurements of oxygen consumption.

(—) indicates a decrease of average weight of the studied groups whereas (+) indicates an increase of weight. Average body temperature of all studied bank voles was equal to 36.9°C before the experiments (n = 84).

No. of voles in groups	25°C		14°C		3°C	
	Bw, g	*Tb*, °C	*Bw*, g	*Tb*, °C	*Bw*, g	*Tb*, °C
3	+0.1	36.9	—0.4	37.1	—1.1	36.4
5	+0.4	37.2	+0.6	36.8	—1.7	36.2

whereas the reverse reaction occurred with 5 animals. At 25° an increase of body weight during the measurements was negligible (Table 2).

Before the experiments body temperature was similar in all the animals and equal to 36.9°C on the average with variations between 36.6 and 37.4° (n = 84). After daily runs body temperature of voles showed some variations in particular groups but only at 3° was significantly lower (Table 2).

3. Daily Rhythm of Oxygen Consumption

The rhythm of oxygen consumption is presented separately for individual groups and for various temperatures (Fig. 1).

Daily course of oxygen consumption in voles examined at 25 and 14° shows only slight differentiation in particular periods of a day. The voles kept in groups exhibit less marked daily rhythm in comparison with specimens examined individually. In this latter case variations in oxygen consumption during 24 hr are rather strong and at night the voles consume up to 20% more oxygen than in daily hours (G ó r e c k i, 1968). Differences between groups and single specimens result undoubtedly from the fact that in groups the periods of increased activity and quietness are not so clearly separated as in individual voles. It was observed that members of a group take food successively and at this time other specimens are aggregated together.

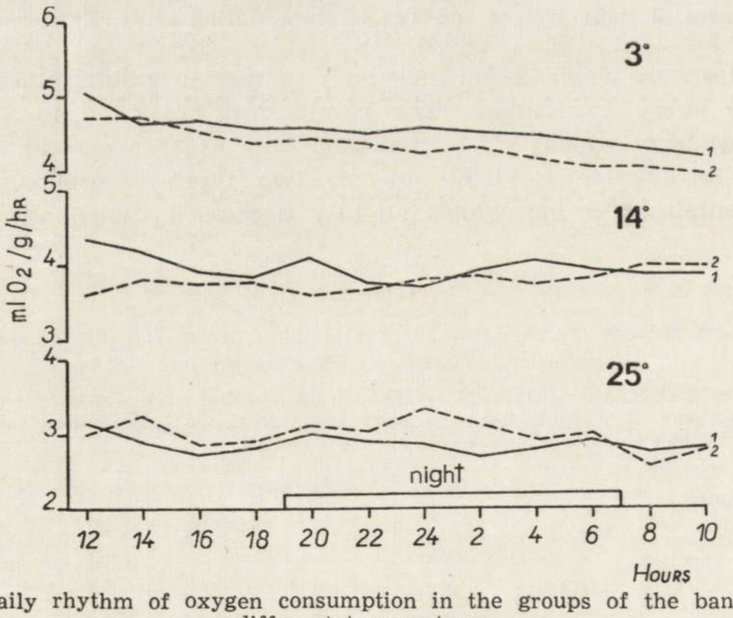

Fig. 1. Daily rhythm of oxygen consumption in the groups of the bank vole at different temperatures.
1 — group of 3 voles, 2 — group of 5 voles.

A certain degree of reduction of oxygen consumption rate occurred during last few hours of the experiment at 3° (Fig. 1). This fact may be related to lowering of body temperature in the animals after the experiment and hence to a decrease of metabolism rate.

4. One-hour Measurements of Oxygen Consumption at Different Temperatures

Oxygen consumption during one-hour runs was studied in groups consisting of 2, 3 and 5 animals but for comparison the determinations were also made with single voles (Table 3). At 5, 10 and 15° the lowest oxygen consumption expressed in ccm/g per hr was found in larger groups and the highest one in groups of two animals. On the other hand, at higher temperatures groups consisting of 5 voles show increased

Table 3.

Oxygen consumption during one-hour measurements in the bank vole in relation to the group size and ambient temperatures.
n — number of measurements.

No. of voles	Temp. °C	Mean weight of group, g	ccm/g/hr	± S.D.	kcal/kg$^{3/4}$ per hr	n
Single specimens	5	19.6	8.88	.82	16.06	12
	10	18.8	7.31	.91	13.19	16
	15	19.1	5.67	.21	10.40	20
	20	19.8	5.56	.16	9.97	32
	25	20.3	4.52	.63	8.15	12
	30	19.2	3.70	.50	6.60	14
Groups of 2	5	41.8	6.96	.53	14.85	12
	10	42.6	6.22	.41	13.39	10
	15	41.0	5.23	.62	11.19	10
	20	39.6	4.32	.74	9.12	10
	25	42.5	3.96	.48	8.55	8
	30	43.1	3.88	.69	8.45	8
Groups of 3	5	62.6	6.15	.70	14.78	8
	10	63.1	5.34	.61	12.84	6
	15	62.2	4.88	.44	11.75	10
	20	61.6	3.82	.52	9.14	10
	25	62.2	3.63	.73	8.74	8
	30	61.8	3.75	.40	8.97	7
Groups of 5	5	93.4	5.80	.31	15.38	6
	10	92.2	5.15	.46	13.64	8
	15	88.9	4.64	.57	12.15	7
	20	91.1	4.18	.62	11.08	10
	25	92.0	4.03	.59	10.64	8
	30	90.9	4.76	.83	12.50	4

metabolism in relation to smaller groups (Fig. 2). Hence the relationship between the group size and oxygen consumption is clearly visible. The presented data indicate that at lower temperatures large groups consume proportionally less oxygen. As an example, at 5° oxygen consumption in a group of two voles is lower by 21.6% in comparison to single animals, and that in groups of 3 and 5 specimens is lower by 30.7 and 34.7%, respectively (Table 3). This effect becomes reduced with an increase of ambient temperature and at 30° oxygen consumption by single animals is the same as in groups of two or three voles. Therefore one can conclude that at 30° social thermoregulation was not observed in the bank vole. A characteristic feature depends on the increase of metabolism in groups of 5 voles at 30°. It looks that some additional

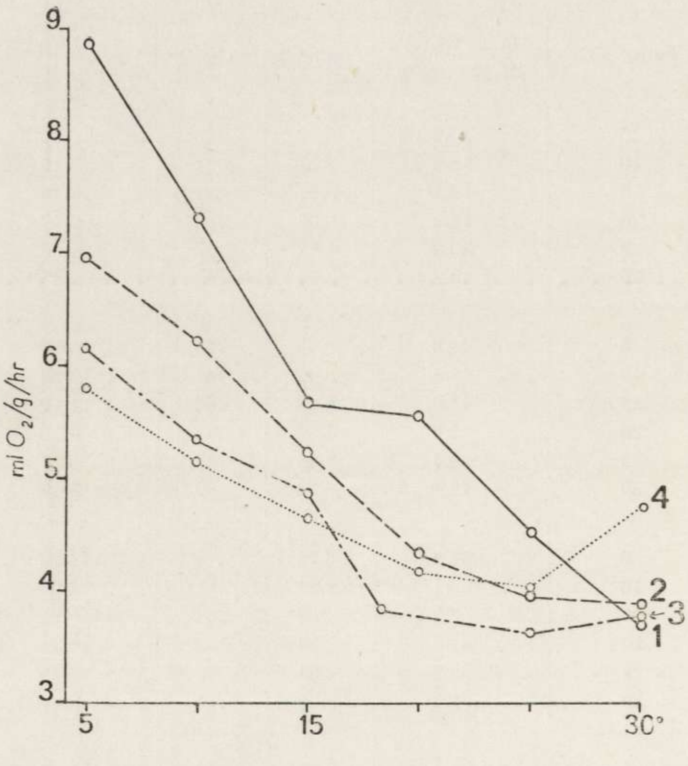

Fig. 2. One-hour oxygen consumption at different temperatures in groups in comparison to single individuals.
1 — single voles, 2 — group of 2 voles, 3 — group of 3 voles, 4 — group of 5 voles.

enhancement of activity occurs in that case, probably due to a relatively small chamber.

Intensity of social thermoregulation is best evaluated by computation of changes of oxygen consumption in relation to the environmental temperature. The lowest level of metabolism (Fig. 2) was assumed as 100% and its increase expressed in per cent per 1°C. In single specimens oxygen consumption went up by 5.6% with lowering of ambient temperature by 1°C. The lowest increase of oxygen consumption was observed in groups consisting of 5 voles (2.5%/1°) and the highest one in groups of three (3.4%/1°). The voles kept in groups of two increased oxygen consumption by 3.2% with a fall of temperature by 1°C. These differences indicate that in groups the rate of heat losses is much lower in comparison with single individual.

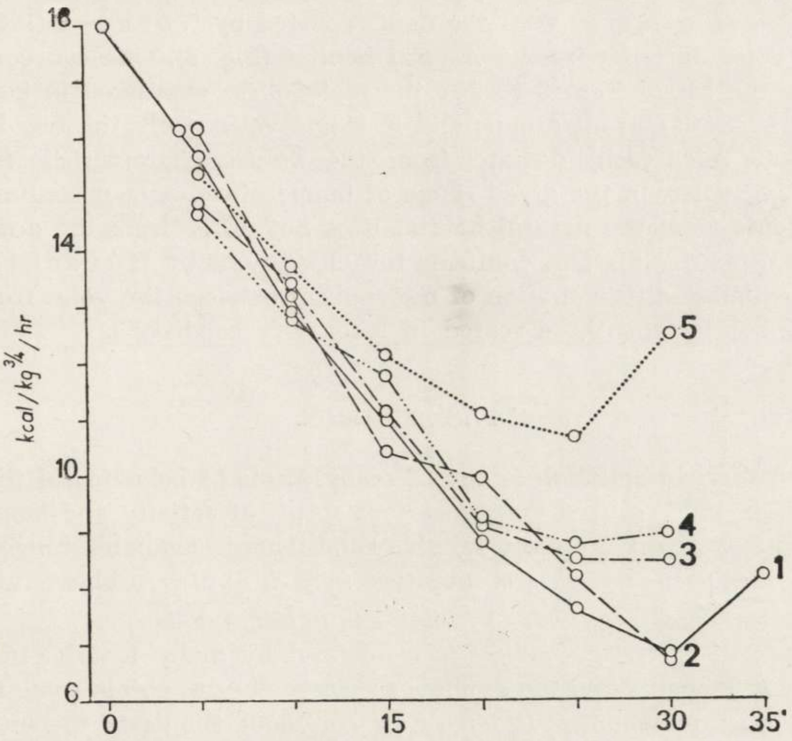

Fig. 3. Metabolism of voles aggregated in groups or as single individuals from the laboratory stock and as single individuals from the natural habitat.
Data for the vole from the natural habitat after Górecki (1968), additional data on the body weight were also supplied by this author. 1 — single from natural habitat, 2 — single from laboratory stock, 3 — groups of 2, 4 — groups of 3, 5 — groups of 5.

After computation of oxygen consumption for metabolic unit of body size it appears that in groups of 3 voles the effect of social thermoregulation is most marked (Table 3). In such groups the rate of heat losses is relatively lowest. It should be emphasized, however, that at lower temperatures (5, 10, 15°) energy requirement computed for $kg^{3/4}$ is similar independently of the group size. Also the requirement in single individuals does not deviate from the data obtained for various groups. At 25 and 30° oxygen consumption expressed per unit of weight significantly increases in more numerous groups. The explanation of this phenomenon is probably similar to that with daily measurements. In small groups the animals are more quiet and less active in contrast to larger groups. This is particularly visible during the comparison of groups with single specimens.

The obtained results of oxygen consumption, computed for kcal/kg$^{3/4}$ per hr, were compared with the data reported by Górecki (1968) for single voles deriving from a natural habitat (Fig. 3). One can conclude that in the range from 5 to 20° the metabolism expressed in kcal/kg$^{3/4}$ per hr is similar in all groups and in single voles. Only the two largest groups (5 voles each) deviate from the values characteristic for the remaining voles. In the given range of temperature oxygen consumption by rodents from the natural habitat does not differ from the described results (Fig. 3). This fact confirms the obserations by Górecki (1966) on a negligible differentiation of metabolism between the voles from the natural habitat and those reared in laboratory conditions.

IV. DISCUSSION

Social thermoregulation is one of many forms of behavioural thermoregulation. It is realized due to various forms of activity and hence the animals may select the most suitable conditions in available range. Species living normally in communities may in unfavourable situations reduce the rate of heat losses by aggregation in groups.

This form of energy saving is influenced by many factors. In some cases it is enough when the animals see each other to obtain some reduction in their metabolism (Ponugaeva, 1960). Similarly the intensity of light allow to reduce oxygen consumption by a group. There is no doubt, however, that the number of animals in a group is more important factor (Prychodko, 1958; Gębczyńska, 1969; Górecki, 1969). The significance of group size has been particularly well demonstrated in the case of common vole, *Microtus arvalis* (Trojan & Wojciechowska, 1968). These authors found that in groups consisting of two or three animals oxygen consumption at 20°C remained constant. Social thermoregulation occurred only in more numerous groups and with 6 specimens the effect amounted to 39.1%. In the bank vole oxygen consumption computed per unit of body weight was also lower in more numerous groups.

The efficiency of social thermoregulation depends mainly on the ambient temperature as already demonstrated by Prychodko (1958) for the laboratory mouse. Also in the bank vole the energy saving is most marked in the range of low temperatures (Fig. 2). In the cold environment the voles always form a compact group and spend most of time in the nest. Hence the energy saving includes also the insulating value of the nest used efficiently at low temperatures (P e a r s o n, 1960). In the temperature above 20°C the rodents significantly increased their activity and reduced the time of staying in the group or even did not aggregate at all. This resulted in the disappearance of huddling effect. Hence the existence of social thermoregulation is produced by definite conditions and appears mainly at low temperatures. It seems that the term of »social thermoregulation« or »social temperature regulation« is better than the »group effect« since the animals kept together reduce their metabolism only in certain conditions.

When the animals were exposed to 3°C for 24 hr the rate of heat losses was so high that even the specimens forming compact groups and staying most time in the nest decreased slightly their body temperature (Table 2). This in turn resulted in the reduction of the rate of oxygen consumption (Fig. 1). It should be added that with a long exposure to 3° accompanied by lack of food the bank voles may reduce their body temperature even to 34°C (G ę b c z y ń s k i, unpubl. data).

Oxygen consumption determined during 24 hr is lower than in one-hour measurements. The difference results, among others, on the lack of the nest in case of short runs. Moreover, the short-term measurements do not include usually periods of sleep and total rest. Change of oxygen consumption related to temperature amounts in groups of three individuals to 2.6% per 1°C (between 3 and 25°) whereas in one-hour measurements is equal to 3.4%/1°C (between 5 and 25°C). Similarly in groups of 5 voles this change amounts to 1.9% and 2.2% per 1°C, respectively.

After expressing oxygen consumption in calories per $kg^{3/4}$, the values obtained in one-hour measurements for groups of various numbers are similar and depend mainly on temperature (Fig. 3). With an intensive cooling the animals utilize the maximum possibilities of reducing heat losses and the value becomes correlated to the total weight of a group raised to the $^3/_4$ power, independently of the number of animals. However, in temperatures close to the thermoneutral zone, more numerous groups show higher rate of oxygen consumption, computed for such unit of body weight, than less numerous groups of smaller body weight (cf. Fig. 3).

On an example of the bank vole one can state that at low temperatures the eficiency of social thermoregulation is a function of body weight of the whole group, independently of its numbers. In conditions when heat losses are not high the increased number of animals in the group enhances the metabolism in comparison with smaller groups. In this case the explanation should be sought probably in the social composition of a group. A tendency to aggregation of animals and utilization of this effect for thermoregulation depends also on the age and size of animals. Mount & Holmes (1969) found that piglets weighing 20 kg aggregate more readily than older pigs of 60 kg body weight.

The results obtained for the bank vole remain in agreement with the data reported by Górecki (1968). He found that at 20°C daily oxygen consumption of voles assembled in groups of two amonuts to 3.20, and in groups of four to 3.29 ccm/g/hr. These values exceed those presented above daily means obtained for 14 and 25°C. However, Ponugaeva (1960) reported that oxygen consumption in vole males kept in a group went up by 17%. Unfortunately she did not specify the group size and details of experiments so any comparison of results becomes difficult. Still it seems that the increase of metabolism in groups studied by Ponugaeva (1960) results from the fact that the measurements were carried out at temperature close to the thermoneutral zone. In this range of temperatures the voles do not form a compact group and show enhanced activity that leads to increased oxygen consumption. Certain confirmation of this assumption derives from the fact that in present experiments a group consisiting of 5 voles consumed more oxygen at 25 and 30°C than less numerous groups. An increased metabolism in a group studied by Ponugaeva (*l.c.*) may also result from eventual lack of period of accustoming animals to each other before the measurements.

The data presented above allow a conclusion to be drawn that social thermoregulation in the bank vole staying in the nest for the most time out of 24 hr plays an important function in modelling the energy budget, especially at lower temperatures. Above 15° the magnitude of social thermoregulation may be calculated from oxygen consumption of individual specimens and the total weight of a group. Oxygen consumption should be earlier computed for metabolic body size (cf. Fig. 3).

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TERMOREGULACJA ZESPOŁOWA U NORNICY RUDEJ

Streszczenie

Zmierzono zużycie tlenu u nornic trzymanych w grupach o różnej liczebności, w różnych temperaturach otoczenia. Ogółem wykonano 39 pomiarów całodobowych (Tabela 1) i 256 jednogodzinnych (Tabela 3). Dobowe oznaczenia zużycia tlenu przeprowadzono w grupach składających się z 3 i 5 nornic, w temperaturach 3, 14 i 25°C (Tabela 1). W grupach o większej liczebności zużycie tlenu wyrażone w cm^3/g na godzinę jest mniejsze niż w zespołach mniej licznych. Jest to szczególnie widoczne w temperaturach niższych. Temperatura ciała badanych gryzoni oraz ich ciężar ciała nie ulegał w czasie tych doświadczeń większym wahaniom (Tabela 2). Dobowy cykl zużycia tlenu przez zespoły, wykazuje tylko niewielkie wahania (Ryc. 1), w odróżnieniu od cyklu dobowego właściwego osobnikom badanym pojedynczo.

Zużycie tlenu w ciągu godzinnych pomiarów badano u grup składających się z 2, 3 i 5 osobników oraz dla porównania wykonano pomiar na nornicach trzymanych pojedynczo (Tabela 3). W temperaturze 5, 10 i 15°C zużycie tlenu (cm^3/g na godzinę, jest wyraźnie niższe w grupach liczniejszych, w porównaniu do grup mniej licznych oraz do osobników pojedynczych (Ryc. 2). Wraz ze wzrostem temperatury obniża się efektywność termoregulacji zespołowej i przy 30°C w ogóle nie obserwuje się tego zjawiska. Po przeliczeniu uzyskanych wyników na metaboliczną wielkość ciała ($kg^{3/4}$), wartości uzyskane w pomiarach jednogodzinnych, w zakresie od 0 do 20°, są podobne u wszystkich grup, niezależnie od ich liczebności (Ryc. 3).