

Roman TERTIL

**The Effect of Behavioural Thermoregulation on the Daily
Metabolism of *Apodemus agrarius* (Pallas, 1771)**

[With 2 Tables & 3 Figs.]

Studies were made of the effect of social thermoregulation and use of the nest on the metabolism of *Apodemus agrarius*. Measurements of daily oxygen consumption were carried out at 5°C and 20°C for single animals and groups of two or three individuals. The metabolic rate of mice in groups was always from 12 to 32% lower than that in single animals. Use of the nest also causes a reduction in oxygen consumption of 8 to 31%. The two effects occur very distinctly at 5°C, at which temperature transformation of daily activity rhythm takes place from single-period nocturnal (20°C) to two-period nocturnal pattern. Group thermoregulation and the effect of use of the nest exert the most marked effect during the day, when the animals' activity decreases. Use of the nest is the chief thermo-regulating mechanism in this case. The energy required for the active period was calculated from oxygen consumption by single mice at a temperature of 5°C outside the nest. Energy dispersal during the animals' resting period was calculated from the metabolism of the group of mice at 20°C. The daily energy budget for *Apodemus agrarius* calculated on the basis of these data for the winter period was 0.511 kcal/g.

I. INTRODUCTION

The evolutionary development of vertebrates which led to the development of homoiothermic animals, was linked with the creation of several thermoregulating systems in these animals. The following forms of thermoregulation can be distinguished among these mechanisms: chemical, also known as metabolic, physical, consisting in variations in resistance to the stream of heat and finally behavioural. We include in the last kind of thermoregulation certain modifications in behaviour which make a more economic heat balance possible for the animals under unfavourable temperature conditions. The following effects have been distinguished here: reduction in metabolism as the result of huddling

together in a group (social thermoregulation, group effect), adopting an appropriate pose, building and using nests and places of shelter and variations in daily activity.

Studies so far made of these phenomena have proceeded in two main directions. The first of these consisted of bioenergetic studies on various manifestations of behavioural thermoregulation — the effect of grouping on growth and survival of rodents (Vetulani, 1931; Sealander, 1952) and on changes in the metabolism of animals living in groups (Prychodko, 1958; Ponugaeva, 1960; Trojan & Wojciechowska, 1968; Gębczyński, 1969; Fedyk, 1971). Examination was also made of the effect of the combined action of group thermoregulation and use of the nest (Gębczyńska & Gębczyński, 1971) and also the metabolic results of gathering in groups with simultaneous studies of the circadian activity rhythm (Wiegert, 1961). In addition the bioenergetic trend in research also includes a number of studies in which examination was made of manifestations of behavioural thermoregulation when drawing up energy budgets for small mammals. In these studies behavioural thermoregulation was only one of the parameters — usually studied within a narrow range and in relation to a small amount of material (Pearson, 1960; Górecki, 1968, 1969; Hannson & Grodziński, 1970). A large number of studies were also made on variations in the daily rhythm of mammals depending on changes in habitat conditions (Smirnov, 1960; Erkinaro, 1961; Grodziński, 1963; Gębczyński, 1964).

The second trend in research on phenomena considered as coming within the scope of behavioural thermoregulation covers studies on the borderline between ecology and animal psychology, which interpret grouping, construction of nests and variations in activity as given modifications of behaviour, without taking into consideration their energy aspect (Aschoff, 1957; Barnett, 1963).

Thus data on different forms of behavioural thermoregulation have been presented from different aspects, for different animals which, combined with their scattered character, makes full use of them difficult. Under these circumstances it was decided to undertake investigation as a whole of manifestations of behavioural thermoregulation in relation to one species. By obtaining data of this kind it would be possible to construct a model of their energy budget which would come far closer than has hitherto been the case in field conditions under which the animals live.

The species chosen for the studies was *Apodemus agrarius*, which is one of the numerical dominants among rodents living in field ecosystems in Central Europe. The present study is intended as an attempt at find-

ing a reply to the question — what effect is exerted by thermoregulating modifications of the animals' behaviour on their daily metabolism?

II. MATERIAL AND METHODS

A total of 52 individuals of *Apodemus agrarius* (Pallas, 1771) caught in the Kraków district were used for the studies. The animals were divided at random into groups of 3 animal, and then kept in these groups in captivity. They were fed on oats, carrot and water *ad libitum*. All the mice were toe-clipped according to a cypher key for identification purposes.

The animals were taken singly, or in twos and threes, for the experiments, but mice from different cages were never placed together. The animals were acclimatized to laboratory conditions for at least a week, and one day before the start of the experiment were transferred to cages in which respirometric measurements were later carried out, keeping the animals under the conditions of the given series of measurements for 24 hours.

Investigations of group thermoregulation and use of the nest were based on determination of daily oxygen consumption by means of the Morrison system automatic respirometer (Morrison & Grodziński, 1968) in 9-litre chambers, at 20°C and 5°C. This permitted calculation of the average daily metabolic rate (ADMR). The times at which measurements were begun were staggered over the whole of the 24-hour period in order to obtain the most accurate picture possible of the animals' daily rhythm.

In all 141, 24-hour measurements were made of ADMR in four series as follows (Table 1):

Series I — (20N) — temp. 20°C, — the animals' cage contained a wooden nesting box, nest material (cotton wool) and food (oats, carrot) *ad libitum*.

Series II — (20NN) — 20°C — no wooden box or nest material, amount of food enough to support life — approx. 3 g of oats per animal.

Series III (5N) — 5°C — other conditions as in series I.

Series IV (5NN) — 5°C — other conditions as in series II.

In all four series the animals were observed either singly, or in twos and threes, this being indicated within each series (*e.g.* 20N—1, 20N—2 *etc.*).

In experiments at 5°C the cages were supplied with wooden floors to isolate the animals from the metal wire netting.

The mice were weighed before and after each experiment: average body weight was used for calculations. The average value is used in elaboration of the results obtained, and average standard error and variance coefficient in percentages. Student's *t* test was used for assessing significance of differences.

III. RESULTS

1. Effect of Social Thermoregulation on Daily Metabolism

1.1. Daily Metabolic Rate at 20°C

Of the mice examined at 20°C, with a nest (20N), highest metabolic rate was exhibited by animals kept singly, the average value being 5.04 ccm O₂/g hr (Table 1). In comparison with such animals groups of two

mice reduced metabolic rate by 27%, and groups of three animals by 32% (Fig. 1). This reduction was statistically significant in both cases in relation to single animals ($P < .01$), but the metabolic rate of groups of two or three animals did not significantly differ from each other.

In other experiments at this temperature (20NN) the animals were deprived of nesting box, and in this case single animals exhibited highest metabolic rate — 5.49 ccm O₂/g hr (Table 1). This value was significantly reduced for groups of two and three animals by 15% and 12% ($.01 < P < .05$) respectively.

Social thermoregulation is distinctly intensified by possession of a nest, but with groups of this size (two and three animals) no reduction in metabolic rate was found depending on the number of mice in the group.

Table 1

Average daily metabolic rate of *Apodemus agrarius* depending on temperature, numbers of animals in the group and possession of a nest. For explanation of symbols denoting series of measurements see »Material and method«.

Series	No. of measurements (animals)	Body wt., g	ccm O ₂ /g hr ± S.E.	C.V. %	kcal/kg ^{0.75}
20N—1	29 (29)	17.9	5.04 ± 0.14	14.7	9.00
20N—2	18 (36)	19.7	3.66 ± 0.10	11.5	6.51
20N—3	10 (30)	20.5	3.38 ± 0.08	8.0	6.26
20NN—1	16 (16)	20.0	5.49 ± 0.16	11.9	9.94
20NN—2	6 (12)	22.9	4.65 ± 0.16	8.6	8.62
20NN—3	8 (24)	22.4	4.82 ± 0.23	13.7	8.84
5N—1	12 (12)	20.6	6.18 ± 0.30	16.9	11.11
5N—2	8 (16)	22.6	5.88 ± 0.44	21.4	10.81
5N—3	5 (15)	23.3	4.45 ± 0.27	13.5	8.44
5NN—1	12 (12)	24.0	8.25 ± 0.34	14.1	15.57
5NN—2	10 (10)	24.0	7.17 ± 0.17	7.5	13.55
5NN—3	7 (21)	24.4	6.51 ± 0.14	5.7	12.27

In the case of animals without a nest there was even a very slight increase in metabolic rate when data for groups of two and three mice were compared.

1.2. Daily Metabolic Rate at 5°C

When measurements were made at 5°C for animals with a nest (5N) it was found that metabolic rate was highest in animals kept singly — when it was on an average 6.18 ccm O₂/g hr (Table 1). Mice kept in pairs did not exhibit significant differences in oxygen consumption in relation to single animals, but metabolic rate for mice in groups of three was reduced by 27% in comparison with single animals, which was significant statistically ($P < .01$) (Fig. 1).

In measurements made on animals deprived of a nest (5NN) metabolic rate was again highest for single individuals, *i.e.*, 8.25 cc O_2 /g while that of mice in twos and threes was lower, decrease for the former being 13% ($.01 < P < .05$) and the latter — 21% ($P < .01$).

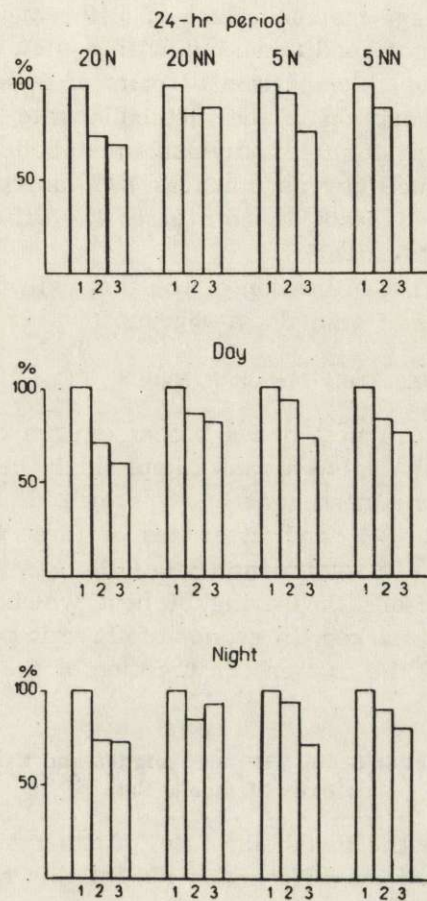


Fig. 1. Effect of group thermoregulation in *Apodemus agrarius* at 20 and 5°C depending on number of animals in a group and possession of nest. Oxygen consumption by single animals was always taken as 100%. For symbols denoting series of measurements see text. 1 — single mice, 2 — groups of two mice, 3 — groups of three mice.

At 5°C also group thermoregulation was found to intensify in animals with a nest, but this only occurred in the case of groups of three animals (Fig. 1).

2. Effect of Use of the Nest on Daily Metabolic Rate

2.1. Daily Metabolic Rate at 20°C

Among animals kept in a temperature of 20°C either singly or in twos or threes, with and without a nest, it was always mice deprived of a nest which exhibited higher metabolic rate (Table 1). Mice kept singly without a nest had an average metabolic rate of 5.49 ccm O₂/g hr, and mice examined under the same conditions, but with a nest, exhibited a value 8% lower ($.01 < P < .05$). Comparison of pairs of mice, with and without a nest, revealed reduction in the metabolic rate of animals with a nest by 21%. In groups of three individuals metabolic rate when a nest was provided was reduced by as much as 29% as compared with the same groups deprived of nests. In both cases the differences were statistically significant ($P < .01$).

It can thus be seen that utilization of the thermal properties of a nest increase in the number of animals in a group.

2.2. Daily Metabolic Rate at 5°C

Animals kept without a nest had a higher oxygen consumption those with a nest (Table 1), the value for mice kept singly being 8.25 ccm O₂/g hr. The presence of the nest reduced this by 25%. In groups of two animals reduction was 18%, and in groups of three 31%. All the differences were statistically significant ($P < .001$).

In all three comparisons the saving of heat which a nest gives the mice is very distinctly marked. In groups of three it permitted the mice to reduce to two-thirds the oxygen consumption of the group of animals deprived of a nest.

3. Combined Effect of Group Thermoregulation and Use of the Nest on Daily Metabolic Rate

In order to compare the metabolic rate of groups of animals kept under varied conditions and differing in weight this rate was converted to a metabolic unit of body measurements — kg^{0.75} (Kleiber, 1961). The total reduction in metabolic rate among mice huddled in a group in a nest was estimated in relation to single animals deprived of a nest. This reduction at 20°C was 37%, which is the result of the combined action of group thermoregulation and use of the nest. At 5°C this reduction is even greater, *i.e.*, 46%, which points to increase in the importance of behavioural thermoregulation at low temperatures (Table 1).

It would, however, appear more interesting to compare the metabolic rate of single animals possessing a nest with the results obtained for

groups of mice deprived of a nest. When this comparison was made for experiments carried out at 20°C it was found that the metabolic rate of single animals in a nest scarcely differs at all from the values characterizing groups of animals deprived of a nest (Table 1). We therefore have here an example of almost complete compensation for lack of a nest by the action of group thermoregulation.

When, however, a similar comparison was made of values of metabolic rate measured at 5°C for single mice with a nest and groups of three without a nest, the rate for groups of animals deprived of a nest was found to rise. In this case group thermoregulation is unable to compensate for the increased loss of heat from animals deprived of a nest.

4. Action of Group Thermoregulation and Use of the Nest During the Day and at Night

Studies made so far on group thermoregulation and use of the nest have not taken into account the fact that the effectiveness of this thermoregulation may be different during the day from that at night. In the

Table 2
Average metabolic rate of *Apodemus agrarius* during day and night hours. In all series (for symbols see: »Material and method«) light phase lasted 12 hours.

Series	Average oxygen consumption, ccm/g hr		
	24-hr period	Day	Night
20N—1	5.04	4.81	5.29
20N—2	3.66	3.40	3.91
20N—3	3.38	2.90	3.87
20NN—1	5.49	5.17	5.85
20NN—2	4.65	4.50	4.97
20NN—3	4.82	4.26	5.44
5N—1	6.18	5.73	6.73
5N—2	5.88	5.42	6.34
5N—3	4.45	4.15	4.79
5NN—1	8.25	8.11	8.38
5NN—2	7.17	6.78	7.58
5NN—3	6.51	6.28	6.73

present study only 24-hour measurements of metabolic rate from continuous recording of oxygen consumption have been used, and it was therefore possible to establish whether the action of thermoregulating mechanisms varies according to the time of day.

Metabolic level was calculated separately for the day and night hours (Table 2) under conditions of 12-hour lighting rhythm. Data illustrating the action of group thermoregulation during the day and at night are

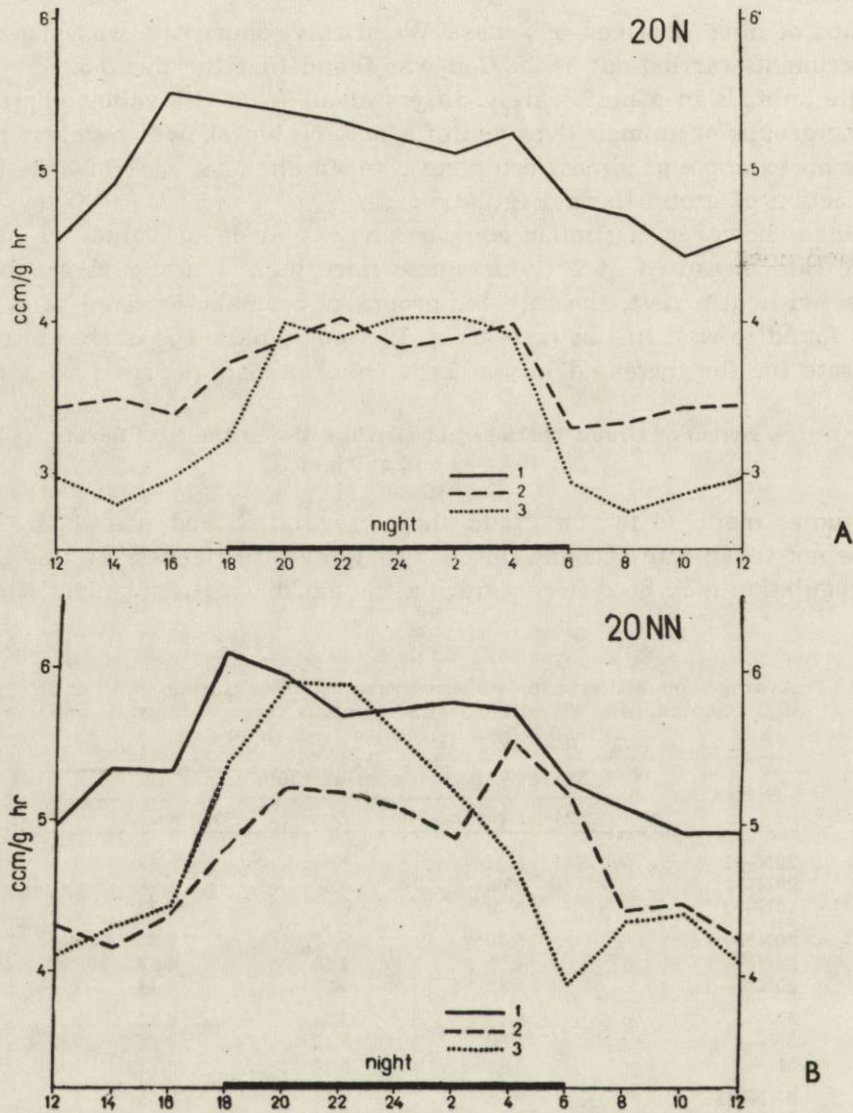


Fig. 2. Daily rhythm of oxygen consumption in *Apodemus agrarius* depending on temperature, number of animals in a group and possession of a nest. For symbols denoting series of measurements see »Material and method«.
1 — single mice, 2 — groups of two mice, 3 — groups of three mice.

given in Fig. 1. The metabolic rate of single animals was always treated as 100% and reduction in this rate with increase in the number of animals in a group calculated in percentages. For example oxygen consumption at 20°C in a group of three mice with a nest was reduced as compared with single animals by as much as 40% during the day, but

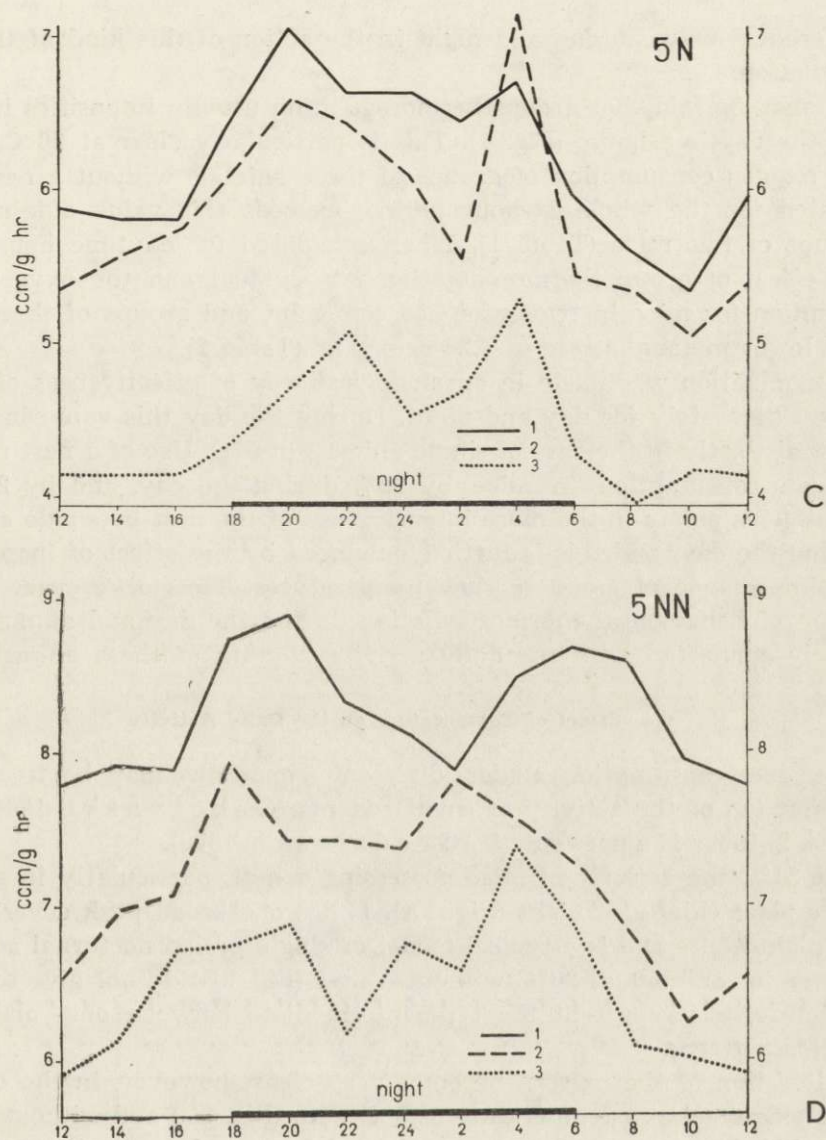


Fig. 2 C, D.

only by 27% at night (Fig. 1). Similar comparison of results for animals without a nest gives reduction in oxygen consumption during the day of 18% for groups of three, and at night of 9%, as compared with mice kept singly.

It must be added that these differences in effectiveness of group thermoregulation occur only at 20°C. At 5°C there are only negligible

differences between day and night in the action of this kind of thermoregulation.

It may be said that group thermoregulation usually intensifies its during the daytime hours (Fig. 1). This is particularly clear at 20°C, when the oxygen consumption of groups of three animals without a nest, calculated for the whole 24-hour period, exceeds this value obtained for groups of two mice (Table 1). When calculated for daytime hours only the effect of group thermoregulation was evident and the oxygen consumption for mice in twos was 4.50 ccm/g hr, and groups of three mice had lower metabolic rate of 4.26 ccm/g hr (Table 2).

Examination was made in an analogical way of effectiveness of using a nest separately for day and night. During the day this value increases most distinctly in the case of single animals at 5°C. Use of a nest reduces oxygen consumption in mice by 29% during the day, and by 20% at night. This points to the more intensive use of the nest by single animals during the day, and this is further enhanced by the effect of increase in the importance of a nest at low temperatures. Thus differences in the action of behavioural thermoregulation during the day and at night are closely connected with the daily activity rhythm of these animals.

5. Effect of Temperature on the Daily Activity

Oxygen consumption under different conditions may be treated as a reflection of the activity of small rodents (Gębczyński, 1964; Górecki, 1968; Hannson & Grodziński, 1970).

At 20°C the activity of mice possessing a nest, particularly in groups, takes place chiefly at night (Fig. 2A). It has one broad peak covering all the night hours and is a typical model of single period nocturnal activity. Curves for animals at 20°C without a nest (Fig. 2B) do not give so clear a picture, but represent the type intermediate between one- and two-period patterns.

Alteration of the pattern becomes very clear, however, in the case of mice examined at a temperature of 5°C with (Fig. 2C) and without a nest (Fig. 2D). The pattern is a typical bimodal one. After the first peak of activity occurring during the first hours of darkness there is distinct slackening, followed by a second distinct peak during the hours before dawn.

IV. DISCUSSION

1. Forms of Behavioural Thermoregulation and Their Interaction

The mechanism of thermoregulation, consisting in animals huddling together for warmth, has been studied in relation to various rodents;

these observations have shown that its effectiveness depends on factors such as temperature, numbers of animals in a group and the possession of a nest.

The effectiveness of group thermoregulation depends to a certain extent on temperature, which is particularly clearly manifested in the bank vole (Gębczyński, 1969), but in the case of *Apodemus agrarius* increase in this effectiveness with decrease in temperature could only be found in the case of animals deprived of a nest — at 5°C reduction in the metabolic rate of mice in groups is greater than that of single animals than at 20°C (Fig. 1). Increase in effectiveness of group thermoregulation applies chiefly to the night hours. At 5°C the animals can be observed to form compact groups not only during the day but also at night, whereas at 20°C the animals are active practically the whole night.

After expressing oxygen consumption in metabolic body size ($\text{kg}^{0.75}$) of the whole group the metabolic values become similar within each group of measurements. When the series were compared with each other it was found that the metabolic rate value calculated in this way depends only on temperature, and always increases at lower temperatures. Similar data for the metabolic rate in groups of similar numbers were obtained by Gębczyński (1969) for voles and Fedyk (1971) for yellow-necked field mouse.

The next factor on which group thermoregulation depends is the number of animals in a group, for instance in the common vole the effect of group thermoregulation is only distinct when groups number at least four individuals (Trojan & Wojciechowska, 1968). Many other authors (Prychodko, 1958; Gębczyński, 1969; Fedyk, 1971) have shown that gradual increase in the number of animals in a group causes intensification of the action of group thermoregulation, this being the greater the lower the temperature. It may be said that in the case of *Apodemus agrarius* this kind of effect of numbers also occurs, particularly at 5°C (Table 1). In experiments made at 20°C in one case (20NN) the metabolism of groups of three was greater than that of groups of two animals. A similar phenomenon of increased metabolic rate at higher temperatures was also described by Gębczyński (1969) and Fedyk (1971), and in this connection it must be emphasised that it occurred in larger groups (4 and 5 animals). It cannot, however, be concluded that in such cases group thermoregulation is not manifested. After dividing results for day and night (Table 2) it was found that group thermoregulation is manifested during the day, and its effect increases with increased numbers (Fig. 1), while at night the metabolic rate of mice in groups of three is higher than in groups of two. It can

be seen from Table 2 that manifestation of the effect of grouping varies during the day and at night, and it may therefore be assumed that if measurements of this effect were made only during short daytime periods the results would be overestimated. It is probable with this form of thermoregulation in *Apodemus flavicollis* (Fedyk, 1971), which is typical a nocturnal animal, the results may be slightly over-estimated. It is likely that the minimum error is contained in short-term daytime measurements for animals with a polymorphic activity pattern, such as *Microtus arvalis* (Trojan & Wojciechowska, 1968) and *Clethrionomys glareolus* (Gębczyński, 1969). It would also seem that some data on increase in metabolic rate in groups (Ponugueva, 1960) may apply to conditions in which the animals are excessively active. This also applies to short-term measurements lasting only a few hours.

In the present study measurements always lasted at least 26 hours, the results for the first two hours of measurement being rejected. This made it possible to reduce to a minimum the effect of preparatory activities (e.g., weighing) on the animals' activity. It is probably impossible to avoid this effect when carrying out short-term measurements, and in addition in making these measurements when there is no nest this undoubtedly contributes to rendering the animals more active and this in turn causes increase in metabolic rate.

When the animals have a nest this causes more distinct occurrence of group thermoregulation. The results obtained (Table 1) show that at 20°C group thermoregulation is fairly weakly expressed, particularly if it is not intensified by the fact of the animals' using the nest. When there is no nest the effect of the fairly great activity of the animals at this temperature is distinct, producing in the group the opposite effect to huddling together. It is sufficient for one animal to begin its active period earlier for it frequently to interrupt the sleep of the other mice in the group during its wanderings round the cage. It has been, however, frequently observed that, when the mice have a nest, the activity of one animal does not affect the behaviour of the others, since the former's wanderings were made chiefly in the rest of the cage, excluding the nest.

Like group thermoregulation, the degree of use of the isolating properties of the nest is a value depending on temperature. This has already been found by Pearson (1960), who applied two corrections for use of nest in summer and winter in the energy budget of *Reithrodontomys*.

If data on use of the nest by single field mice are compared, a distinct difference is evident in oxygen consumption by the animals for measurements made at 20°C and 5°C. Reduction caused by use of the nest is 8% at 20°C, and as much as 25% at 5°C, but with increase in the number

of mice in a group the connection between use of the nest and temperatures use of the nest is intensified by increase in the number of animals in a group.

In comparison with data obtained by Górecki (1969) for *Apodemus agrarius*, in the present studies, which were based on a large amount of material, it was found that the effect of using the nest is not as great as this author states. At 20°C he obtained reduction of as much as 64% in the metabolic rate of single animals in a nest — whereas in the above study reduction of only 8% was found.

Both group thermoregulation and use of the nest, exerting a reducing effect on metabolism when occurring together, do not produce a decrease forming the sum total of these two effects. For example at 20°C group thermoregulation in groups of three mice reduces metabolism in relation to single animals by 32%, and presence of the nest gives a reduction of 29% — but the combined action of these two effects gives a decrease of only 37%. At 5°C group thermoregulation permits reducing metabolism by 27%, and the nest by 31%, but the combined action of these two mechanisms gives a decrease in oxygen consumption of 46%. Similar results are obtained for the combined action of the above thermoregulating mechanisms for the common vole (Trojan & Wojciechowska, 1969) and bank vole (Gębczyńska & Gębczyński, 1971).

It will be seen from the data given here that when group thermoregulation and use of the nest are examined separately an exaggerated estimate of their importance can easily be reached. Under field conditions the animals always make simultaneous use of the nest and advantages of grouping. It was also found that under laboratory conditions rats never occupy singly the several nesting boxes available in the cage, but congregate in one or two, leaving the rest of the boxes empty (Barnett, 1963).

The question of the hierarchy of the two forms of behavioural thermoregulation examined forms a separate problem. In the case of the bank vole (Gębczyńska & Gębczyński, 1971) it was found that the effect of using the nest is a far more important factor, at 4°C almost doubly exceeding the effect of grouping. The results of the present study presented in Table 1 show that in field mice also use of the nest is the chief thermoregulating mechanism, and predominates over group thermoregulation mainly because its action increases more quickly with a drop in temperature. In addition it acts more evenly over the course of the whole 24 hours, even in the case of single animals. The nest, as Daniel (1964) and Cotton & Griffiths (1967) found, is capable of ensuring the animals a fairly constant high temperature, depending to a small degree only on external conditions. At 20°C group thermo-

regulation is capable of taking the place of a nest only when there are at least three field mice. Comparison of oxygen consumption at 5°C by animals able to make use of either huddling together only (5NN—3), or a nest only (5N—1), shows that at this temperature the animal is exposed to lesser heat loss in the nest (Table 1). Thus at a lower temperature reduction in heat loss obtained by huddling together is only a supplementary advantage and cannot provide the animals with the same advantages as the isolation values of a nest.

The experimental conditions in the present study were arranged so as to approach as close as possible to the natural model of »summer« and »winter«. In series 20N the mice were supplied with food *ad libitum*, which is in fact the situation in summer. At 5°C (5NN) food was supplied to the animals in amounts sufficient to support life (Drożdż, 1968), which in turn closely imitates winter conditions.

When comparing the daily oxygen consumption rhythm measured at 20°C and 5°C (Fig. 2 A—D) the same variations in daily activity can be observed as those previously found in field mice by Smirnov (1960). This author described variations in the activity pattern of *Apodemus agrarius* over the yearly cycle. In summer, field mice are characterized by a nocturnal single-period activity pattern, but in winter this changes to two-period nocturnal activity, since the animals' activity slackens in the middle of the night and in consequence there are two peaks of activity. Diagrams of daily oxygen consumption for the series made at 20°C (»summer«) and at 5°C (»winter«) exhibit similar variations (Fig. 2). This did not depend on the duration of the light phase, at it was uniform in all series. It would not, however, appear that lack of differences in the light period was of great significance here since, as stated by Gębczyński (1964) on the basis of studies of the European pine vole, at 5°C the duration of the light phase does not affect the activity pattern.

Possession of a nest and grouping effect the activity pattern. The action of the first of these factors is evident in measurements made at 5°C, when there is a great difference between temperatures inside and outside the nest. When the mice emerge from the nest there is increase in their metabolic rate, and in this case resting periods are distinctly separated from the active periods outside the nest. This demarcation far less distinctly if the animals have no nest, since in such cases transition from the resting phase is not connected with the possibility of making use of the thermostatic properties of the nest. It may thus be said that possession of a nest exerts an intensifying effect on the daily rhythm pattern.

The results obtained do not permit establishing any clear regularity in the effect of numbers in a group on the activity pattern. Indistinct resting and activity periods described for voles by Gębczyński (1969) does not occur here. In the case of the field mouse grouping in a nest the pattern is accentuated, probably connected with increase in the degree to which the nest is used by more numerous groups. The effect of grouping of rodents on their daily activity pattern is a complicated phenomenon. Such factors as, e.g., social and sex structures of the group may play some part here (Aschoff, 1957).

2. Effect of the Action of Behavioural Thermoregulation on Metabolic Rate. Energy Budget of the Field Mouse

Making use of the fact that in the case of *Apodemus agrarius* in the temperature range from 5 to 20°C, thermoregulation varies in an almost

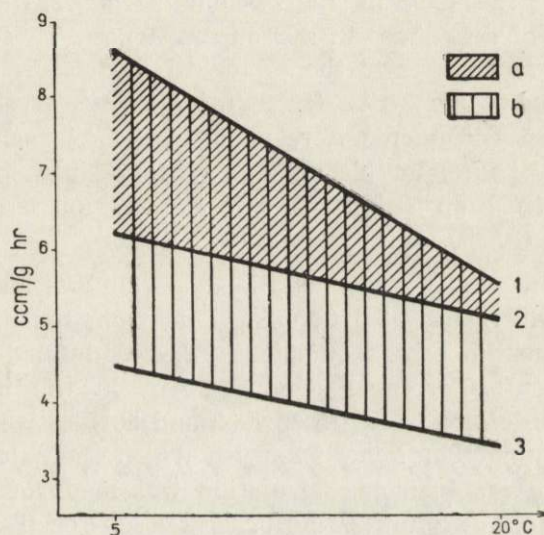


Fig. 3. Oxygen consumption in *Apodemus agrarius* depending on temperature. 1 — resting metabolic rate of single individuals (RMR) calculated after data given by Górecki (1969), 2 — oxygen consumption by single animals in nest (series 5N-1 and 20N-1), 3 — oxygen consumption by groups of animals in nest (series 5N-3 and 20N-3), a — effectiveness of use of nest, b — effectiveness of combined use of nest and effect of huddling in group.

straight line (Górecki, 1969), it was possible to give data on the metabolic rate of field mice examined under different conditions in one diagram (Fig. 3). In this way a graphic interpretation was obtained of the effectiveness of different forms of behavioural thermoregulation in comparison with the resting metabolic rate of single animals (RMR). Data

are given in Fig. 3 on the metabolic rate of field mice at 5 and 20°C as follows: calculated from the thermoregulation curve (1), defined in the present study for single animals in a nest (2), and for groups in nests (3). The area contained between lines (1) and (2) form a measure of the effectiveness of action of the chief thermoregulating mechanism, that is, use of the nest, and the area contained between lines (1) and (3) a measure of the effectiveness of the combined action of use of the nest and the effect of grouping. It can be seen that the action of these two mechanisms increases with decrease in temperature.

Data obtained for *Apodemus agrarius* permit more accurate definition of the energy budget of this rodent. The basic assumption of this budget is the differences in energy supply depending on daily activity. For that part of the day in which the animals are active the metabolic rate at ambient temperature of a single animal without a nest should serve as a basis, and for the part of the 24-hour period spent sleeping — the metabolic rate of an animal in a group in a nest. These premises bring the present budget closer to the ecological model formulated by Trojan & Wojciechowska (1969) for *Microtus arvalis* — but in the present study measurements were made over a 24-hour period, and not just for several hours. In this way it was possible to avoid defining energy expenditure on activity outside the nest on the basis of resting metabolic rate (RMR).

After accepting the above premises calculation was made of the energy budget of a field mouse at 5°C, using data from the present study and also the average time spent outside the nest, defined by Smirnov (1960) as 4.5 hours. For the 19.5 hours spent in the nest the average metabolic rates defined in series 20N—2 and 20N—3 were taken for calculating. Assuming that $RQ = 0.8$, with which the caloric value of one litre of oxygen was 4.8 kcal, calculation was made of energy dispersal during this time, and found to be 0.333 kcal/g. For the 4.5 hours spent outside the nest the average metabolic rate of single mice without a nest at 5°C (5NN—1) was taken as a basis, and this after analogical conversion as before gave energy dispersal for this period as 0.178 kcal. Thus the total daily energy requirements are 0.511 kcal/g. A similar budget, also for winter, based on data from Górecki's study (1969) converted to 5°C without taking into consideration the modifications described above, was 0.640 kcal/g. This is 25% more than the budget calculated in this study.

The new energy budget of the field mouse does not take into consideration the relation between metabolic rate and the animal's body weight, and also omits costs of reproduction. It would, however, appear

that this budget for the winter period is more empirical and closer to the natural conditions under which the animals normally live.

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WPLYW TERMOREGULACJI ETOLOGICZNEJ NA METABOLIZM DOBOWY
MYSZY POLNEJ

Streszczenie

Badano wpływ termoregulacji zespołowej i efektu wykorzystania gniazda na metabolizm dobowy myszy polnej *Apodemus agrarius* (Pallas, 1771). Pomiar dobowego zużycia tlenu prowadzono w 5 i 20°C w 9-litrowych komorach przy pomocy respirometru systemu zamkniętego. Myszy badano pojedynczo i w grupach po dwa i trzy osobniki z gniazdem lub bez niego. Zwierzęta skupione w grupy miały zawsze niższe zużycie tlenu niż zwierzęta pojedyncze (Tabela 1). Obniżenie to było bardziej widoczne w pomiarach prowadzonych u grup myszy posiadających gniazdo i wynosiło u grup po trzy myszy w 20°C — 32%, a w temp. 5°C — 27% w stosunku do zwierząt pojedynczych (Fig. 1). Działanie termoregulacji zespołowej jest więc wzmacniane przez fakt posiadania gniazda. Możliwość wykorzystania gniazda również powoduje spadek metabolizmu myszy polnych. Jest on bardzo wydajny u grup po trzy myszy, osiągając 29% w 20°C i 31% w 5°C w porównaniu do grup pozbawionych gniazda.

Łączny wpływ wykorzystania gniazda i efektu skupiania się pozwala myszom na obniżenie zużycia tlenu o 37% w 20° i aż o 46% w 5°C. Przy wspólnym działa-

niu obu badanych form termoregulacji etologicznej silniejszy wpływ ma zawsze efekt wykorzystania gniazda, dając oszczędność energii większą niż skupianie się. Efektywność obu mechanizmów termoregulacyjnych jest wyższa w temp. 5°C. W tej temperaturze zachodzi też przekształcenie wzorca rytmiki dobowej z jednodzielnego nocnego w 20°C (Fig. 2A) w dwudzielny nocny (Fig. 2C i 2D).

Efektywność działania termoregulacji zespołowej i wykorzystania gniazda nie jest jednakowa w ciągu całej doby (Fig. 1). Zwłaszcza w temp. 20°C zaznacza się silne zróżnicowanie. Trzy myszy w gnieździe obniżają swoje zużycie tlenu w dzień aż o 40%, w nocy tylko o 27% w porównaniu do metabolizmu zwierząt pojedynczych w takich samych warunkach (Fig. 1). Podobne zróżnicowanie wykazuje efektywność wykorzystania izolacyjnych właściwości gniazda.

W oparciu o uzyskane dane skonstruowano dobowy budżet energetyczny myszy polnej. Oparto go na określeniu zapotrzebowania energetycznego osobno dla okresu aktywności (ze zużycia tlenu przez pojedyncze myszy bez gniazda w temp. 5°C), a osobno dla okresu spoczynku zwierząt w gnieździe (ze zużycia tlenu mierzonego w 20°C u grup myszy w gnieździe). Obliczony w ten sposób dobowy budżet energetyczny (*DEB*) myszy polnej dla okresu zimy wyniósł 0,511 kcal/g.