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

VOL. XVI, 16: 221—229.   BIAŁOWIEŻA   August, 1971

Anna F E D Y K

Social Thermoregulation in *Apodemus flavicollis* (Melchior, 1834)*

[With 2 Tables & 3 Figs.]

Oxygen consumption was estimated in relation to ambient temperature in one hour respirometric runs in groups of A. flavicollis consisting of 2, 3, 4 and 5 individuals. For comparison similar determinations were carried out with single individuals. In the range of 5—20°C oxygen consumption computed for unit of body weight was found to be correlated with the numbers of individuals in a group. The lowest energy requirements were shown by individuals in groups consisting of 5 mice. Exceptionally at 25°C, due to increased locomotory activity of the animals, groups consisting of 4 and 5 individuals consumed more oxygen than those of 3. Significant economy of energy by social thermoregulation is visible in groups of four or five individuals.

I. INTRODUCTION

Among different signs of adaptative changes in the behaviour of mammals, as a reaction to low ambient temperatures, social thermoregulation plays an important function. Its importance was, however, underestimated for many years in considerations of the mechanisms of body temperature regulation. Although already Richter (1927) and Pearse & Hall (1928) regarded the phenomenon of mammals huddling as the thermoregulatory action, Benedict (1938) claimed that huddling of mammals has no effect on their metabolism rate. Brody (1945) and other later authors hold an opposite opinion.

Detailed studies on the effect of huddling are relatively recent. Sealander (1952) demonstrated that both insulatory properties of the nest, and huddling of *Peromyscus* prolong the survival time of these animals at low ambient temperatures and with the lack of food.

* This study was carried out under the Small Mammal Project of the International Biological Programme in Poland.

Reduced rate of energy loss in adult individuals in result of huddling was studied by means of food rationing in laboratory mice by Prychodko (1958) and in the bank vole by Gębczyńska & Gębczyński (1970). On the other hand, oxygen consumption in groups consisting of various number of individuals was investigated in different mammals by Ponugaeva (1960), Pearson (1960), Górecki (1968; 1969), Gębczyński (1969), Trojan & Wojciechowska (1968; 1969). This problem in the aspect of various seasons was studied in a few rodent species by Visinescu (1969).

The present study was aimed at investigation of social thermoregulation in *Apodemus flavicollis* — the species living often in groups, *e. g.* when occupies nest boxes for birds.

II. MATERIAL AND METHOD

A flavicollis was trapped in the Białowieża National Park, in the *Tilio-Carpinetum* forest, in the period 26 July — 10 August 1969. Then the animals were placed in cages in such groups as later used for the experiments. Groups of 2, 3, 4 and 5 individuals consisted of males and females, or representatives of only one sex. Females prevailed in larger mixed groups. The animals were kept in the laboratory, where climatic conditions and food supply were identical to those described by Gębczyński (1969).

Oxygen consumption by single individuals and groups of animals was measured during the period of 1.5 h in a modified Morrison respirometer in 9 l chambers, without nest material and food. The experiments were carried out in the range of temperature 5 to 25°C in five degree intervals, between November 1969 and February 1970. Respirometric determinations were always carried out in morning hours after feeding animals. Each group was used many times in the experiments. By the end of May 1970 a new series of animals was trapped, and after 4-weeks acclimatization they were used for the experiments at 5°C, since previously obtained number of determinations was found to be insufficient. Altogether 371 experiments were carried out.

Initially the animals were weighted (the whole group) both before placing in the respirometric chamber and after the experiment. Since, however, in the studied range of temperatures no differences in the weight were observed to occur in this interval of time, later the mice were weighted only before the experiment. The employed animals showed considerable variations in body weight (from 19 to 46 g) despite the fact that they all were adult.

III. RESULTS

The obtained results are shown in Table 1. Oxygen consumption is given in ccm/g hr in relation to temperature and group size.

The oxygen requirement of *A. flavicollis* depends not only on ambient temperature but also on the number of animals in a group. In all studied temperatures, except 25°C, oxygen consumption computed per unit of body weight is lower in groups than in single individuals (see Table 1). The lowest oxygen requirement at a given temperature was noted in the most numerous groups (5 individuals). With decreasing number of animals oxygen consumption gradually rises. In groups consisting of two individuals it is still lower than in single individuals, the differences being statistically significant at 10, 15 and 20°C (at the confidence interval P=0.05 in *t*-Student test). Oxygen consumption by three individuals in comparison with pairs is significantly different only at 10 and 25°C. When a similar comparison is carried out for groups composed of 3 and 4 individuals the differences are significant at all studied temperatures except 25°C. Analogous differences between groups consisting of 4 and 5 individuals are not significant except the data for 5°C.

Table 1

Oxygen consumption in *A. flavicollis* in relation to temperature and group size. Numbers of determinations are given in brackets.

Temp., °C	1 individual		2 individuals		3 individuals		4 individuals		5 individuals	
	Wt., g*	ccm/g hr ± S.D.	Wt., g	ccm/g hr ± S.D.	Wt., g	ccm/g hr ± S.D.	Wt., g	ccm/g hr ± S.D.	Wt., g	ccm/g hr ± S.D.
5	34.47 (30)	6.31 ± 1.89	74.80 (30)	5.47 ± 1.32	105.00 (15)	5.00 ± 0.99	153.50 (15)	4.12 ± 0.64	201.20 (20)	3.52 ± 0.33
10	39.90 (16)	5.85 ± 0.48	76.20 (12)	4.80 ± 0.42	116.25 (12)	4.39 ± 0.42	157.22 (12)	3.71 ± 0.84	205.45 (12)	3.24 ± 0.81
15	37.96 (12)	5.25 ± 0.47	73.00 (16)	4.51 ± 1.12	118.80 (10)	3.90 ± 0.27	142.50 (10)	3.25 ± 0.51	175.30 (16)	2.97 ± 0.36
20	37 10 (16)	4.73 ± 0.76	79.50 (10)	3.81 ± 1.16	114.90 (15)	3.35 ± 0.17	165.10 (15)	2.71 ± 0.41	219.80 (16)	2.67 ± 0.28
25	40.54 (10)	3.76 ± 0.50	78.10 (12)	2.98 ± 0.11	106.40 (12)	2.50 ± 0.20	153.00 (12)	2.61 ± 0.51	200.17 (15)	3.10 ± 1.19

* Average body weight of the individual or group.

When the amount of oxygen (in ccm/g hr) consumed by a single individual at each studied temperature is assumed as 100% (Fig. 1) then two individuals consume from 14.1 to 20.8% less oxygen in the studied range of temperatures. After computation per one degree this amounts on average to 3.56%. In groups consisting of 3, 4 and 5 individuals compared with single mice the corresponding figures of reduced oxygen consumption per 1°C are 5.50, 7.31 and 7.88%, respectively.

In the studied range of ambient temperatures (Fig. 2) relative decrease of oxygen consumption shows with increased temperature a similar character both in single individuals and in groups consisting of two or three individuals. A different situation exists in groups of 4 or 5 in-

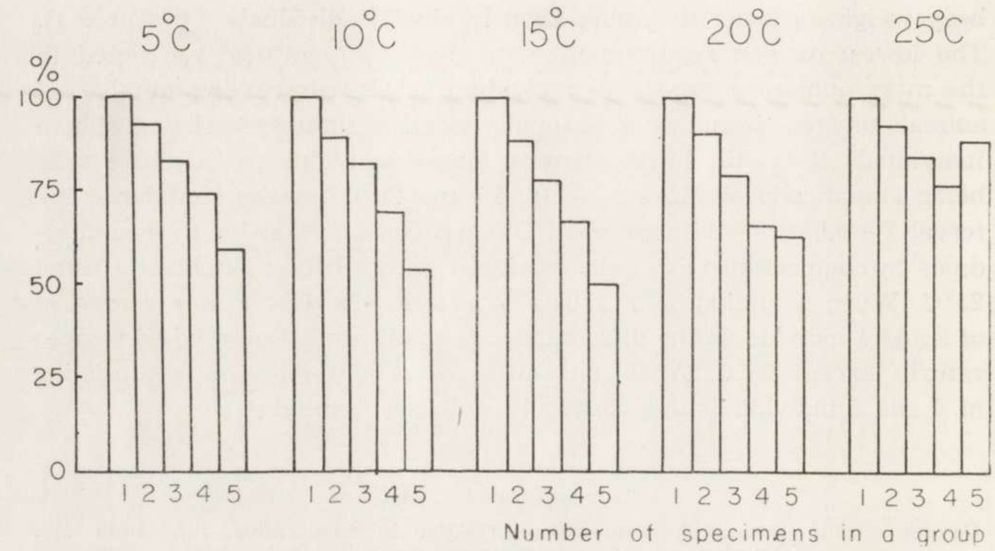

Fig. 1. The effect of huddling of mice on the metabolism rate. The amount of oxygen in ccm/g hr consumed by one individual in a given temperature is assumed as 100%.

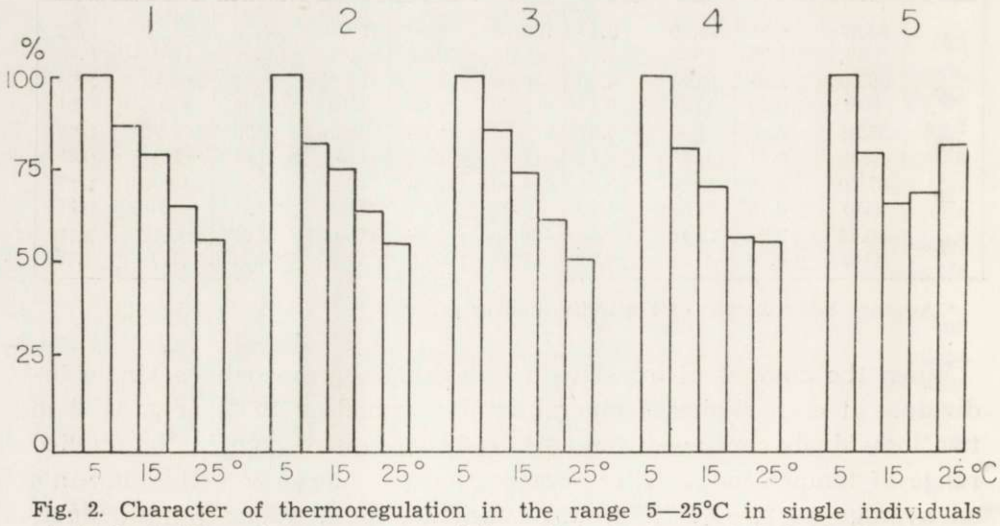

Fig. 2. Character of thermoregulation in the range 5—25°C in single individuals of *A. flavicollis* and in groups consisting of 2, 3, 4 and 5 individuals. Oxygen consumption at 5°C assumed as equal to 100%.

dividuals at higher temperatures. This results probably from increased locomotory activity of these groups, as observed at 25°C.

When, however, the lowest oxygen consumption in each group is assumed as being equal to 100%, then in single individuals oxygen consumption increases by 3.37%/°C, for two individuals by 4.17% and for three by 5.0%. On the other hand, for four individuals it increases only by 2.89% and for five — by 2.12%/°C.

After computing oxygen consumption per metabolic unit of body weigth ($W^{0.75}$) the reduction of metabolism in groups of four or five individuals in comparison with other groups is also well visible (Fig. 3).

IV. DISCUSSION

The existence of social thermoregulation, well documented in other species of mammals, has been now demonstrated in the yellow-necked field mouse. The amount of consumed oxygen computed for unit of body

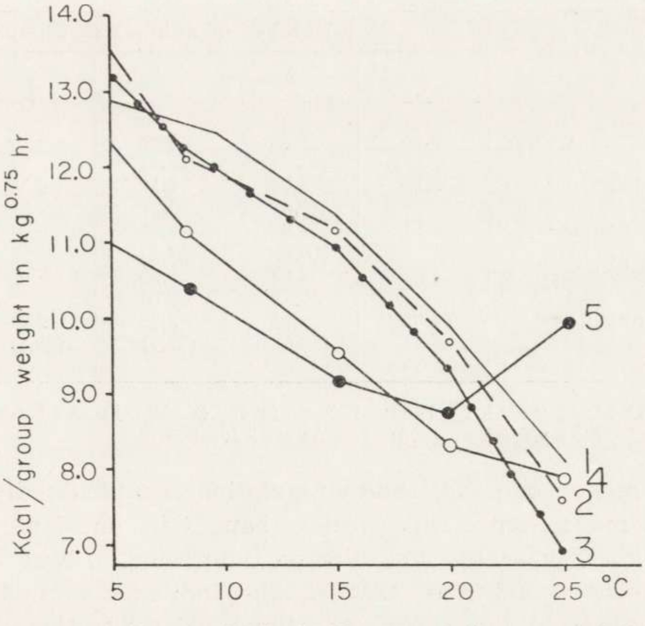

Fig. 3. Oxygen consumption in *A. flavicollis* computed per metabolic unit of body weight. Numbers 1—5 indicate the number of individuals in a group.

weight is considerably lower in mice which had the possibility of huddling. This relationship is stronger expressed in more numerous groups. A similar situation was observed in the laboratory mouse (Prychodko, 1958), harvest mouse (Pearson, 1960), bank vole (Gębczyński, 1969), and other species (Ponugaeva, 1960). In the common vole the effect of huddling was visible only in larger groups consisting of more than four individuals (Trojan & Wojciechowska, 1968).

The efficiency of social thermoregulation depends not only on the group size. Its existence is particularly striking at low temperatures but is reduced at higher ones. At 5°C the mice in the group of five individuals consume 44.3% less oxygen per gram body weight per hour than single individuals. At 15°C this difference amounts to 49.2%, but at 25°C in the two most numerous groups an increased oxygen consumtion is observed. However, when for each group the lowest oxygen consumption is assumed as equal to 100%, then the rise of oxygen consumption increases by 3.37%/°C in single individuals and only by 2.12%/1°C in a group of five.

Table 2

Comparison of reduction of oxygen consumption (ccm/g hr) in different rodent species in relation to group size at 20°C. Percentage reduction of metabolism in comparison with single individuals is given in brackets.

Species	Number of animals in group				
	1	2	3	4	5
Clethrionomys glareolus [1]	5.56	4.32 (22.4)	3.82 (31.3)	—	4.18 (24.9)
Microtus arvalis [2]	5.11	5.06 (1.0)	5.10 (0.2)	4.38 (14.3)	3.88 (24.1)
Microtus oeconomus [3]	3.31	2.97 (10.3)	2.83 (14.5)	—	—
Apodemus agrarius [4]	5.81	4.24 (27.1)	3.55 (39.0)	—	—
Apodemus flavicollis	4.76	3.81 (20.0)	3.35 (29.7)	2.71 (43.1)	2.67 (44.0)

References: [1] Gębczyński, 1968; [2] Trojan & Wojciechowska, 1968; [3] Gębczyńska, 1970; [4] Górecki, 1968.

The phenomenon of social thermoregulation is undoubtedly important for the field mouse, since this species changes its one-family model of life in the breeding season to collective wintering. It was observed in outdoor enclosure conditions, that all the individuals of *A. flavicollis* occupied in winter only one of the nest boxes offered to them (Olszewski, unpubl.). In normal conditions the field mouse is probably not exposed to extreme low ambient temperatures because apart from collective nesting it uses winter nestes lying 15—17 cm below the ground surface. In some cases nest chambers are found at the depth of 104 cm, and galleries reach 150 cm down in the ground (Snigirevskaja, 1952). At such depths the soil temperature is stable and much higher than that at the surface. Moreover, field mice store food for winter. The amount of stored food may be shown by the fact that during two weeks one pair of mice carried to the burrow 37.958 beech seeds (*i. e.* 7.8 kg)

(S v i r i d e n k o, 1951). Provisions discovered in *A. flavicollis* burrow contained: 4 kg of acorns approximately 4 kg of hazel nuts, 150 g of lime seeds, 100 g of maple seeds, 150 g of ash seeds and 25 g of evonymus fruits (N a u m o v, 1948; after N o v i k o v, 1959). Such accumulation of highly caloric food makes these animals independent of the environment to a certain degree. Hence voles or their tracks are often encountered on the snow, while mice — almost never (N o v i k o v, 1959).

Since the adaptation of organism to cold depends on reduction of heat losses, and not on increasing heat production, it may be realized by winter changes of behaviour such as nest building, reduction of locomotory activity and social thermoregulation.

The phenomenon of social thermoregulation is undoubtedly important to most rodents. However, the available data are too fragmentaric (Table 2), and the conditions of experiments too artificial. Still it is possible to conclude that in *A. flavicollis* the efficiency of social thermoregulation depends in the highest degree on the group size. In the group of 2 and 3 individuals (in comparison with single individuals) the reduction of oxygen consumption is almost identical in the field mouse and bank vole, but in the group of 5 mice oxygen consumption is reduced by 19.1% more than in such group of voles.

The thermoregulation, even on the population level, is variable, depends on many factors and is related among others to the thermal history of animals (see H a r t, 1953). Hence at the present stage of our knowledge of this subject the comparison is rather premature.

Acknowledgements: The author is grateful to Dr. M. G ę b c z y ń s k i for suggesting the subject of this study, for help and constructive remarks in the course of experiments, as well as for critical reading of the manuscript. Laboratory assistance of Mr. W. B a j k o and Mrs. J. L i p i ń s k a is also acknowledged.

REFERENCES

1. B e n e d i c t G. F., 1938: Vital energetics. Carnegie Institution of Washington: 1—215, Washington D. C.
2. B r o d y S., 1945: Bioenergetics and growth. Reinhold Publ. Corp.: 1—1079, New York.
3. G ę b c z y ń s k i M., 1969: Social regulation of body temperature in the bank vole. Acta theriol., *14*, 29: 427—440.
4. G ę b c z y ń s k a Z., 1970: Bioenergetics of a Root vole population. Acta theriol., *15*, 3: 33—66.
5. G ę b c z y ń s k a Z. & G ę b c z y ń s k i M., 1970: Insulation properties of nest and social temperature regulation in the bank vole. Ann. Zool. Fennici, 8 104—108.

6. Górecki A., 1968: Metabolic rate and energy budget in the bank vole. Acta theriol., *13*, 20: 341—365.
7. Górecki A., 1969: Metabolism and energy budget in striped field mouse. Acta theriol., *14*. 14: 181—190.
8. Hart J. S., 1953: The relation between thermal history and cold resistance in certain species of rodents. Canad. J. Zool., *31*, 1: 80—98.
9. Naumov N. P., 1948: Očerki sravnitelnoj ekologii myševidnyh gryzunov. Izd. AN SSSR, 1—203. Moskva-Leningrad.
10. Novikov G. A., 1959: Ekologia zverej i ptic lesostepnyh dubrav. Izd. Leningr. Univ.: 1—352. Leningrad.
11. Pearse A. S. & Hall F. G., 1928: Homeothermism. The origin of warm blooded vertebrates. John Wiley and Sons Inc.: 1—119. New York.
12. Paerson O. P., 1960: The oxygen consumption and bioenergetics of the harvest mouse. Physiol. Zöol., *33*. 2: 152—160.
13. Prychodko W., 1958: Effect of aggregation of laboratory mice (*Mus musculus*) on food intake at different temperatures. Ecology, *39*, 3: 499—503.
14. Ponugaeva A. G., 1960: Fizjologičeskie issledovanija instinktov u mlekopitajuščih. Izd. AN SSSR: 1—180: Moskva-Leningrad.
15. Richter C. P., 1927: Animal behaviour and internal drives. Quart. Rev. Biol., *2:* 307—343 (cited after Sealander, 1952).
16. Sealander J. A., Jr 1952: The relationship of nest protection and huddling to survival of *Peromyscus* at low temperatures. Ecology, *33*, 1: 63—71.
17. Snigirevskaja E. M., 1952: Rojuščaja dejatel'nost' i ubežišča želtogorloj myšy. Zool. Ž. *31*, 5: 744—750.
18. Sviridenko P. A., 1951: Značenije gryzunov v probleme lesozvedenija i zaščita ot nih pitomnikov i polezaščitnyh lesnyh polos. Tr. In-ta zool. AN USSR, *6:* 3—45.
19. Trojan P. & Wojciechowska B., 1968: The effect of huddling on the resting metabolism rate of the European common vole *Microtus arvalis* (Pall.). Bull. Acad. Polon. Sci., Cl. II., *16*, 2: 107—109.
20. Trojan P. & Wojciechowska B., 1969: Ecological model and tables of the daily costs of maintenance (*DEB*) of *Microtus arvalis*. Ekol. pol., A, *17*, 17: 314—342.
21. Visinescu, N. 1969: Efectul de grup al termoreglarii la unele mamifere salbatice. St. si cerc. biol., Zool., *21*, 1: 95—101.

Accepted, February 10, 1971.

Mammals Research Institute,
Polish Academy of Sciences,
Białowieża, Poland.

Anna FEDYK

TERMOREGULACJA ZESPOŁOWA U *APODEMUS FLAVICOLLIS* (MELCHIOR, 1834)

Streszczenie

Zmierzono zużycie tlenu u 120 myszy wielkookich leśnych w zespołach o liczebności 2—5 osobników, w zakresie temperatur otoczenia 5—25°C.

Zużycie tlenu u *A. flavicollis* zależy nie tylko od temperatury otoczenia, ale również od liczebności grupy (Tabela 1). W badanym zakresie temperatur z wyjątkiem 25°C zużycie tlenu przypadające na jednostkę ciężaru ciała jest istotnie niższe u osobników w grupach. Najniższe zapotrzebowanie energetyczne zanotowano w grupach składających się z 5 osobników. W miarę zmniejszania liczebności grupy zużycie tlenu stopniowo wzrasta. Tym nie mniej, w zespołach złożonych z dwu osobników jest ono niższe niż u pojedyńczych myszy. Wyjątkowo w temperaturze 25°C grupy 4 i 5-osobnikowe wykazywały wyższe zużycie tlenu niż zespoły trzyosobnikowe, co wiąże się niewątpliwie ze zwiększoną ruchliwością zwierząt w tych zespołach.

Przy porównaniu ilości zaoszczędzonej energii przez poszczególne zespoły i przez pojedyńcze osobniki (Ryc. 1) okazuje się, że dwa osobniki zużywają średnio na 1° o 3,56% tlenu mniej, a grupy trzy-, cztero- i pięcio-osobnikowe odpowiednio o 5,40%, 7,31% i 7,88% mniej.

Jeśli jednak przyjmiemy najniższy dla każdej grupy poziom metabolizmu za 100% to istotna oszczędność energetyczna zaznacza się dopiero w zespołach złożonych z 4 i 5 osobników, co również uwypukla się po przeliczeniu zużycia tlenu na metaboliczną jednostkę ciężaru grupy (Ryc. 3).