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

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Andrzej MYRCHA

Bioenergetics of an Experimental Population and Individual Laboratory Mice

[With 11 Tables & 13 Figs.]

The values of bioenergetic indices were defined for laboratory mice examined singly aged from 1—11 months, during the period of development in the nest and also during gestation and lactation. Measurements were made of the amount of food consumed (*C*), its assimilation (*A*) and amount of faeces (*F*) and urine (*U*) excreted, and also the amount of oxygen consumed by the animals and of the CO_2 they produced. All measurements were made under uniform conditions at a temperature of 22°C — 23°C. The above elements of the full energy balance, together with production value (*P*), were also measured at weekly intervals for a whole mouse population freely developing over a period of 7 months in a metabolic cage. Using the measurements made on individual animals, calculation was made of the instantaneous and cumulative energy balance of this population and compared with analogical balances obtained empirically. It was found that the energy budget of the whole population is far more economical than that of individuals living singly. The calculated values of consumption, assimilation and respiration are almost double the values found experimentally, with the same production value. Coefficients of production efficiency $K_1 = (P{:}C) \times 100$ and $K_2 = (P{:}A) \times 100$, and also the ratio $P{:}R$ of the whole population, are far made favourable than these indices calculated from data obtained for individual animals. It was also found that some elements of the ecological organization of the population significantly affect the level of its metabolism.

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I. INTRODUCTION

Studies on the productivity of different types of ecological systems require a knowledge of a large number of basic bioenergetic values, permitting of tracing the way in which energy flows through these systems and of understanding the laws governing energy management in nature. This is connected with the necessity of ascertaining the role of populations of different species of animals and the energy chains of these ecosystems. It is for this very reason that there has been such marked development of bioenergetic studies in land ecology during the last ten or more years. These studies have led to the elaboration of a whole group of concepts and to formation of equations permitting of calculating the energy balance of any given ecological unit (Petrusewicz, 1967; Petrusewicz & Macfadyen, 1970; Klekowski, 1970):

$$C=P+R+U+F=D+F$$
$$D=P+R+U$$
$$A=P+R$$

where: C — consumption, food requirements, D — digesting energy, the part of food which is digested and assimilated, P — production, energy used for the production of the individual's own body tissues and products of reproduction, R — respiration, costs of maintenance, F — feaces, that part of consumption which is not digested, U — urine, A — assimilation, the sum total of production and respiration.

Determination of the coefficient of food assimilation $[(A:C)\times 100]$ is very helpful in such studies, as is also determination of the coefficients of production efficiency, indicating what part of energy ingested together with food $[K_1=(P:C)\times 100]$ and assimilated $[K_2=(P:A)\times 100]$ was utilized in production processes (Winberg, 1962, 1965; Klekowski, 1970).

Bioenergetic research of wild small mammals, chiefly rodents, has developed particularly intensively. Data have now been accumulated on the caloric value of the bodies of the commonest species, which are simultaneously of greatest importance (Golley, 1961; Górecki, 1965; Myrcha, 1969; Fleharty *et al.*, 1973). These data are used for calculating production value of study populations in energy units in given periods of time. At the same time accurate methods have been worked out which permit of grasping the extent of daily requirements and energy losses. Several models for calculating energy budgets are applied, in which the starting point is formed by measurements of basal metabolic rate — *BMR* (McNab, 1963), resting metabolic rate — *RMR* (Trojan, 1969 a; Trojan & Wojciechowska, 1969) or average daily metabolic rate — *ADMR* (Grodziński & Górecki, 1967; Górecki, 1968, 1969; Grodziński, 1971). This last method of calculating the daily energy budget (*DEB*) may be considered the most accurate, as it permits of eliminating a large number of corrections (activity of animals, specific-dynamic action of food, daily rhythm *etc.*) which are essential when the other methods are used. After taking into account data on extent of consumption and digestibility of different kinds of food obtained by the use of metabolic cages (Golley, 1960; Drożdż, 1966, 1967, 1968; Gębczyńska, 1970), all necessary information is obtained on the energy requirements of the animals examined, and this makes it possible to calculate their complete energy balance.

When calculating these balances changes in the values examined connected with the animals' age, sex and physiological state (gestation and lactation), season of the year and also the effect of variable physical habitat factors (temperature, humidity *etc.*) and certain behavioural factors (group effect, influence of nest) are taken into consideration.

The above data are obtained by laboratory investigations of animals caught in the field. Before the actual measurements were made these animals were given few days to adapt themselves, in order to eliminate any possible errors due to the stress creating effect of such factors as an abrupt change in living conditions or contact with the observer.

The results obtained from the studies made in this way are used to calculate energy flow through whole populations of animals living in differents ecosystems (Golley, 1960; Grodziński *et al.*, 1969; Ryszkowski, 1969; Trojan, 1969 b; Grodziński, 1971; Fleharty & Choate, 1973).

Energy balances of populations drawn up in this way are, however, burdened with certain errors resulting from the failure to take into consideration the effect of intrapopulation factors on the level of bioenergetic values of the individuals forming these populations. The existence of the effect of inter-individual relations and certain elements of population organization found by many authors, in particular density, on the course of a large number of physiological processes in representatives of many species of small mammals would appear to confirm the above assumption (Allee, 1931; Retzlaff, 1938; Christian, 1956, 1961; Louch, 1956; Chitty, 1960; Bronson & Eleftheriou, 1963; Houbhan, 1963; Ader, 1967; Albert, 1967). It is well known that behavioural and hormonal factors, exerting a strong influence on the physiological state of different individuals have been recognized in the case of mammals as one of population regulating mechanisms (Christian, 1959; Christian & Davis, 1964; Christian *et al.* 1965; Welch, 1961).

In the ecological literature available, however, we know of only a few studies drawing attention to the possibility that ecological organization of a population may influence the level of the bioenergetic indices of small mammals. Brown (1963), found that differences occur in the metabolic rate of individuals from experimental populations of *Mus musculus* Linnaeus, 1758, depending on whether there had been 110 or 26 mice in the cage. Buckner (1964), on the other hand, observed a certain rise in the metabolic rate of shrews with greater density of populations of these animals. Differences in the amount of oxygen intake by laboratory rats living in cages containing differents numbers of animals were also observed by Cosnier *et al.*, 1965. Myrcha & Szwykowska (1969), who examined animals from experimental populations of laboratory mice, found that dominating individuals had about 60% higher metabolic rate than was the case with subdominants. In addition the metabolic rate of animals occupying lower positions in the dominance hierarchy, after they had been isolated from the population for 1 week, rose to the level observed in the dominating individuals. Le Boulangé (1974) also found a lower metabolic rate for mice living in populations in comparison with the amount of oxygen consumed by these animals before introducting them and after removing them from the population. These results thus simultaneously suggest that during the few days preparation period used in bioenergetic studies on small mammals, the pressure of the given population organization to which the animals used for the experiment may weaken considerably, and this fact may be reflected in the values obtained for the bioenergetic indices of these animals.

The purpsose of the present study was to examine as accurately as possible all elements of the energy balance and coefficients of production efficiency for a freely developing population of laboratory mice examined as a whole, and to compare these data with values calculated for the same population in accordance with generally accepted methods, on the basis of results obtained for animals examined singly. Preliminary attempts were also made at examining the influence of population density and number of animals on the metabolic rate of individuals forming these populations.

II. MATERIAL AND METHODS

Animals used for the studies were obtained from the breeding station of the Institute of Ecology, Polish Academy of Sciences. The values of bioenergetic indices characterizing single individuals of *Mus musculus* Linnaeus, 1758 were defined by examining animals taken from breeding cages in pairs of adult animals lived with their progeny. Experimental populations were formed from animals taken from the breeding cages and not previously used for other studies. In all examination was made of nearly 1000 mice of both sexes, varying in age and physiological condition.

All bioenergetic measurements were made in the same laboratory room and at the same ambient temperature of 22°C—23°C. Both in the breeding centre and during the experimental period the animals were fed *ad libitum* on standard granulated *MSL* food, a brand of commercial food for mice in Poland, and supplied with drinking water. Pregnant and lactating females were additionally given sprouting wheat grains.

Using the metabolic cages described by Szczygieł & Ziombski (1960), daily food requirements, and amount of faeces and urine excreted, were defined for individual mice aged 1, 4, 7—8 and 9—11 month old, and calculation was made of the coefficients of digestion and assimilation of their food. An introductory period of a few days was allowed, followed by the actual experiment lasting 2 whole days. All animals were weighed with accuracy up to 0.01 g, both before

0.1 g during the course of 24 hours were eliminated from the experiments. At the and after each 24-hour period. Individuals whose body weight varied more than same time the amount of food by weight which each mouse consumed during the 24 hour period, and also the feaces and urine it excreted, were defined. Samples of faeces and urine were taken from each mouse, and also 10 portions of the standard food given to the mice, were dried in a vacuum dryer at a temperature of 40°C, the burnt in a Berthelot system KL-3 calorimeter. Nijkamp's method (1965) was used to determine the caloric value of urine, evaporating a given amount of urine on exactly weighed circles of polythene sheeting, the caloric value of which was deducted from the energy contained in the whole burnt sample.

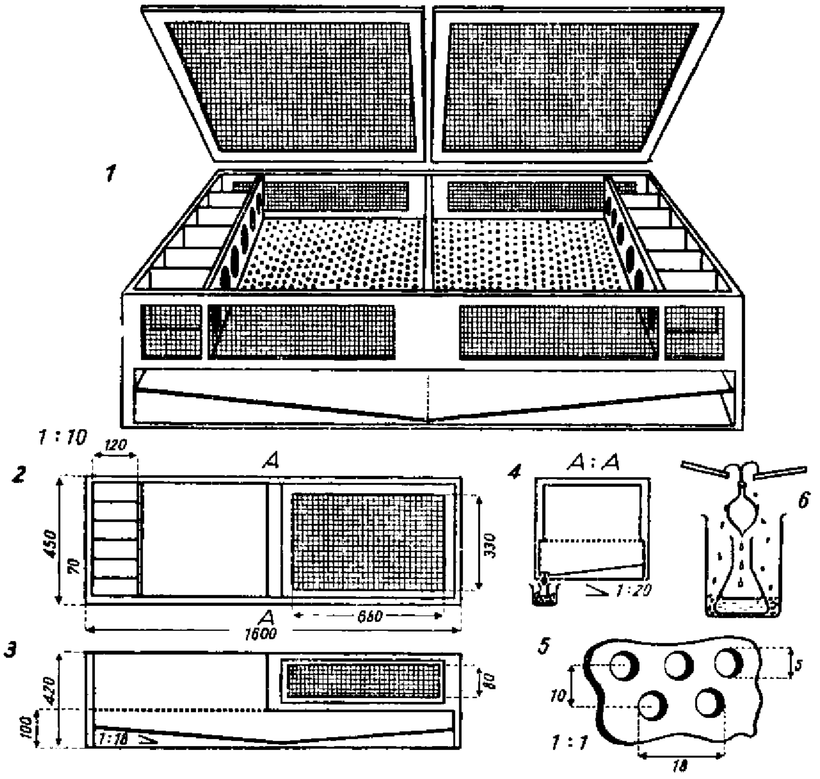

Fig. 1. Population metabolic cage.
1 — general view (wire-netting indicated by chequered field, bottom of cage consists of double floor of plexiglass: the upper floor horizontal with holes and the lower set at an angle and tilted towards the back of the cage, to allow faeces and urine to flow into the separator; 2 — view from above; 3 — side view; 4 — cross-section; 5 — section of upper floor; 6 — device separating faeces from urine.

Changes in the value of elements of the energy balance of each day of gestation and lactation for females of *M. musculus* were calculated on the basis of experiments carried out in a similar way, the results of which were published earlier on (Myrcha *et al.*, 1969).

In order to define changes in elements of the energy balance during development of the experimental population of laboratory mice, a metabolic cage was constructed measuring 160 cm × 40 cm × 14 cm, that is, the measurements of typical cages used in population studies in the Institute of Ecology (Fig. 1). Eight 4-months old mice (5 ♀♀ and 3 ♂♂) were introduced into this cage and population development observed for 29 weeks under constant conditions, simultaneously defining at approximately weekly intervals the amount of food consumed, the amount of faeces and urine excreted and the production value of this population. Each of the mice living in the population was marked at the age of 4 weeks. All animals were weighed weekly, their age defined and for females the day of gestation and lactation. In addition, during the daily inspections made all newborn animals, and also those which had died or been eaten by other mice, were recorded. If cases of cannibalism occurred on the days in which food experiments were carried out, than the energy contained in the bodies of the eaten mice was added to consumption defined on the basis of the amount of standard food consumed. When calculating the production of this population allowance was made for those individuals, born but dying soon afterwards between two neighbouring days on which bioenergetic measurements are made and on neither of which was it possible to grasp the presence of these individuals. The energy value of production was calculated on the basis of previously determined changes in the caloric value of the body through the whole life of laboratory mice (Myrcha & Walkowa, 1968).

The above data permitted of grasping the full instantaneous energy balance at the various moments examined of a population's development, and its coefficients of production efficiency in accordance with the equations commonly used in ecology (Winberg, 1962, 1965; Petrusewicz, 1967; Petrusewicz & Macfadyen, 1970; Klekowski, 1970; Klekowski *et al.*, 1972). Using these data values were also determined of the element of cumulative energy balance (Klekowski *et al.*, 1967, 1972) of an experimental population over the whole period of its development: cumulative consumption

$$\left[C_c = \int_{\tau_0}^{\tau_n} C_i(\tau)\,dt \approx \sum_{\tau_0}^{\tau_n} C_i\right]$$

where C_c — cumulated value of food consumption over the whole development of the study population from π_0 to $\tau_n=189$ days, C_i value of food consumption on different days of the population's development,

cumulative faeces $\left[FU_c = \int_{\tau_0}^{\tau_n} FU_i(\tau)\,dt \approx \sum_{\tau_0}^{\tau_n} FU_i\right]$

cumulative assimilation $\left[A_c = \int_{\tau_0}^{\tau_n} A_i(\tau)\,dt \approx \sum_{\tau_0}^{\tau_n} A_i\right]$

cumulative production $\left[P_c = \int_{\tau_0}^{\tau_n} P_i(\tau)\,dt \approx \sum_{\tau_0}^{\tau_n} P_i\right]$

cumulative respiration $\left[R_c = \int_{\tau_0}^{\tau_n} R_i(\tau)\,dt \approx \sum_{\tau_0}^{\tau_n} R_i\right]$

On the basis of results obtained in food experiments for single animals calculation was made of the instantaneous and cumulative energy balance of a population identical to the experimental population. As age and sex structures were exactly known, and also the physiological state of females, the values of the elements of the energy balance at different moments in the development of this population could be calculated in accordance with the following formula:

$$C_{\mathrm{pop}}=C_a \times B_a+C_b \times B_b+.....,$$

where: C_{pop} — calculated value of consumption of the whole population during a 24-hour period, C_a, C_b,....., — values of consumption of the various groups of individuals forming the population (age, sex, day of gestation or lactation) calculated in kcal/g 24h for animals examined singly, B_a, B_b,....., biomass of the above different group of animals.

The values of consumption and assimilation calculated in this way for the population over a 24-hour period were underestimated by the value of the production of this population, since in experiments carried out on single animals only individuals with unvarying body weight were taken into consideration, and thus by $P=0$. Consequently the value of production obtained at different times during the development of the experimental population of laboratory mice was added to the above calculated elements of the energy balance.

In addition to studies of the food balance examination was also made of metabolic rate of mice living singly, and also of experimental populations of these animals. Two-hour measurements of the amount of O_2 consumed and CO_2 produced were made by means of an open flow respirometer — Kipp and Zonen diapherometer, always under the same temperature conditions (22°C—23°C) and during the same hours (9.00—14.00).

In the case of animals from the breeding cages examination was made of changes in metabolic rate during nest development (1—26 days) in mice of both sexes at the age of 1, 4, 7—8 and 9—11 months, and also in females during gestation and lactation. Measurements of metabolic rate in mice from 1—26 days old were made by recording respiration of whole litters transferred together with the nest to a respiration chamber.

Measurements of the amount of O_2 consumed and CO_2 produced by the experimental population were made on the same days on which food experiments were carried out on it. For this purpose the whole population metabolic cage was covered by a large respiration chamber for the measurement period.

On the basis of the above data, as in the case of the whole energy balance, calculation was made of the amount of energy dispersed in the metabolic processes of all animals forming the population at different moments of its development, comparing them with results obtained experimentally for the whole population.

A several number of experiments were also made in order to attempt to trace the effect of density and numbers of experimental populations of laboratory mice on their metabolic rate.

In the first experiment 3 populations were set up for each of the following groups, composed respectively of 5, 10, 20 and 40 males of approximately uniform body weight, kept in normal population cages measuring 160 cm × 40 cm × 14 cm. Respiration was measured for all the above populations as a whole on the day the were set up, after one week and after two weeks.

In further studies use was made of animals obtained from experiments in which examination was made of the effect of density and numbers of experimental populations on a large number of population parameters such as natality, mortality, viability of the young animals, production of the population, *etc.* (see Adamczyk, unpubl. data). Several populations, differing in density and size of group, were set up in populations cages of the above size, in the following way: 2, 10, 20, 40, 60, 100 and 220 animals per cage. Sex ratio in all populations was 1 : 1. The whole cycle of the population studies made on them by Adamczyk (unpubl. data) lasted 5 months. Throughout the whole time the same density of animals was maintained in the given cage by removing all young individuals which survived up to the 5th week of life from the population. They were allowed to remain only in cases in which it proved necessary to make good losses due to deaths of adult animals. At the end of Adamczyk's experiments measurements were made of the metabolic rate of adult individuals and animals from 4—5 weeks old coming from these populations. The procedure followed in these studies was as follows: single animals chosen at random from each population (omitting pregnant and lactating females) were placed in a small respiration chamber containing food and water. After a short adaptation period of about one hour, measurements of respiration were made for two hours, after which the animal was replaced in its population and the next animal taken. A fault in the respirometer unfortunately made it impossible to carry out in this experiment measurements of the amount of oxygen consumed by adult individuals from the cages containing 2 adult animals. In a further series of experiments examination was made of the effect of the number of animals forming the population on the metabolic rate of adult laboratory mice. In this case, adhering to the same procedure as before, measurement was made of the amount of O_2 consumed and CO_2 produced by animals from a population with sex ratio 1 : 1, in which density was uniform, *i.e.* in which there was the same area of cage bottom per mouse (30 cm^2 and 120 cm^2), although actual numbers of animals differ from 2 to 220 animals. Populations of the same density were kept in cages of identical shape but diferent size, depending on the number of animals. The number of animals in each cage was maintained unchanged in the same way as in the previous experiment (Adamczyk, unpubl. data).

In the studies on the effect of the two elements of population organization of laboratory mice on their metabolic rate endeavour was made to exclude pregnant and lactating females. Any possible errors were made only in the case of females in the initial days of pregnancy.

III. BIOENERGETIC INDICES FOR LABORATORY MICE EXAMINED SINGLY

1. Values of Consumption, Digestion and Assimilation of the Food of Different Age Groups

Consumption, digestion and assimilation of food was examined in nonreproducing laboratory mice of both sexes, belonging to a different age groups (Table 1). The average caloric value of 1 g dry mass of the food given to the animals was 3840.0 cal, whereas that of excreted faeces was 4184.4 cal. The caloric equivalent of 1 ml of urine for the animals examined was on average 225 cal.

Both the value of energy consumed, digested and assimilated, when calculated for 1 g of body weight during the 24 hours, was highest in one-month-old mice and decreased with the animals' age. It would appear

Table 1

Elements of the food balance (in kcal/g 24h) for different age groups of *M. musculus* (temperature 22°C—23°C).

	1 month		4 months		7—8 months		9—11 months	
	M	F	M	F	M	F	M	F
No. of animals	8	17	14	11	10	17	8	8
Body weight before experiment (g)	14.7±1.3	15.0±0.6	26.6±0.6	23.7±1.2	29.3±0.9	27.4±1.3	32.8±4.0	29.6±3.5
Body weight after experiment (g)	14.7±1.0	15.1±0.5	26.6±0.8	23.7±1.2	29.4±0.9	27.5±1.3	32.9±3.9	29.6±2.8
Consumption (C)	1.195±0.135	1.218±0.057	0.857±0.119	0.925±0.070	0.864±0.092	0.907±0.071	0.701±0.168	0.893±0.123
Feaces (*F*)	0.257±0.029	0.263±0.006	0.166±0.023	0.189±0.024	0.144±0.021	0.156±0.025	0.125±0.020	0.135±0.027
Urine (*U*)	0.014±0.015	0.008±0.005	0.006±0.003	0.013±0.007	0.007±0.003	0.007±0.003	0.005±0.003	0.011±0.001
Digested energy (*D*)	0.938±0.099	0.954±0.060	0.691±0.116	0.735±0.070	0.720±0.096	0.749±0.064	0.576±0.150	0.756±0.152
Assimilation (*A*)	0.924±0.091	0.946±0.060	0.684±0.117	0.722±0.066	0.714±0.091	0.742±0.066	0.570±0.155	0.745±0.135
Coefficient of digestibility (%)	78.4±2.0	78.1±1.5	79.6±3.8	79.3±2.9	83.3±2.1	82.5±1.8	81.9±2.6	84.5±2.7
Coefficient of assimilation (%)	77.3±1.8	77.8±1.5	79.5±3.5	78.6±2.9	82.5±2.2	81.1±1.9	81.2±2.6	83.5±2.6

that these changes are due primarily to differences in the body weight of mice, since animals 9—11 months old were more than twice as heavy as one-month-old mice. This assumption is confirmed by the calculated relation between consumption value (expressed in kcal/g 24h), and body weight of the animals examined ($y=1.527-0.025x$), with a high coefficient of correlation ($r=-0.933$).

The greatest differences connected with the animals' age occur in the amount of energy consumed by mice together with their food. The value of consumption for individuals 9—11 months old, calculated per unit of body weight, is 34% smaller than the value of this same index in one-month-old animals, while digestion energy decreases by 31.5%, and assimilation by only 28.5%. This fact is probably connected with a certain increase in the degree to which older mice utilize food, as is shown by the increase in value both of coefficients of digestion and of assimilation with increasing age of the rodents examined.

Generally speaking, higher values of all these indices are found for females that for males, irrespective of the age of the mice. Statistically significant differences between average values of food consumption and assimilation and of coefficients of digestion and assimilation, calculated for the two sexes, were, however, found only in the group of oldest animals, *i.e.* 9—11 months.

The above data coincide with results obtained for *Microtus pensylvanicus* (Golley, 1960) and for 5 other species of rodents (Drożdż, 1968; Gębczyńska, 1970), in which the coefficient of digestion fluctuates, depending on the kind of food, within limits of 70%—90%, and coefficient of assimilation from 65% to 91%. There are unfortunately no data on the changes in these indices with age in wild rodents. The differences observed in this study between the values of the two coefficients in animals aged one month and 9—11 months are the same as the interspecies differences given by Drożdż (1968) between average values determined for different groups of voles and mice.

2. Metabolic Rate

(a) Changes in Metabolic Rate during Nest Development

Indices describing the metabolic rate of laboratory mice at temperature of 22°C—23°C are subject to abrupt changes during the period of these animals' development in the nest (Table 2). The amount of oxygen consumed, when converted to a unit of body weight in a unit of time, at first relatively low, rises considerably during the first 7 days of life, and this in turn is followed by a distinct decrease in the value of this index, lasting until the 11th day of life of these mice. As from this time a repeat increase can be observed in oxygen consumption, lasting until approximately the 22nd day of the animals' life, when a rate of about 8.0 ml O_2/g h is reached and thereafter remains unchanged.

The value of the respiratory quotient (*RQ*) also varies during the period of nest development of laboratory mice (Table 2). Highest *RQ* values are observed in the youngest animals, up to the 4th day of life and after the 20th day of postnatal development. On the 26th day *RQ* comes close to the value 1.0. Between the 5th and 20th day of the animals' life there is a marked decrease in the value of the respiratory coefficient, probably due to the intensive protein metabolism taking place during this period of the organism's development.

Table 2

Changes of metabolic rate during the nest development of laboratory mice.

Age, days,	No. of litters	No. of animals	Body wt. g	*RQ*	ml O_2/g h	kcal/kg$^{0.75}$ 24h
1	3	23	1.21	0.86	1.83	94.0
2	3	22	1.27	0.97	3.45	164.9
3	3	24	1.49	0.89	4.01	208.6
4	3	21	1.72	0.91	5.19	223.5
5	3	24	2.44	0.79	5.07	230.6
6	3	18	2.35	0.84	4.53	205.3
7	5	29	2.79	0.80	5.70	242.2
8	5	31	2.98	0.80	4.87	208.1
9	4	27	3.25	0.80	4.48	197.2
10	5	28	3.93	0.81	4.80	187.5
11	5	28	3.95	0.78	4.32	173.9
12	4	23	4.55	0.76	4.21	164.1
13	2	11	5.21	0.81	5.97	241.8
14	4	21	4.74	0.83	5.96	231.3
15	4	20	5.86	0.82	5.38	210.2
16	3	17	5.69	0.79	6.43	246.4
17	3	15	6.93	0.79	6.92	253.3
18	3	18	6.19	0.87	6.58	252.6
19	4	22	6.78	0.85	7.52	283.4
20	3	14	7.61	0.88	7.43	272.9
21	4	23	6.76	0.92	7.50	290.0
22	4	22	7.63	0.90	8.36	300.1
23	3	17	8.79	0.87	7.82	284.3
24	3	17	9.34	0.84	8.08	297.0
25	3	16	9.60	0.90	7.46	278.8
26	3	16	9.89	0.98	7.93	306.6

The above changes in the value of *RQ* in a certain way modify the course of variations in metabolic rate expressed in kcal/g 24th, but in this case also, as in the amount of oxygen consumed, it is possible to distinguish two periods in the nest development of mice, lasting respectively from the 1st to 11th day and after the 11th day of life (Fig. 2).

The fact that the variations in metabolic rate described above during the nest development of mice are primarily connected with age, and to a lesser degree with differences in the animals' body weight, is demonstrated by variations in metabolic rate expressed in kcal per metabolic unit of body weight ($kg^{0.75}$) over a 24-hour period (Table 2).

Changes in the amount of oxygen intake during postnatal development in laboratory mice at a temperature of 22.5°C were examined by Locker & Weish (1967), who observed the highest metabolic rate in the study animals between the 12th and 28th day of their life, absolute values being close to those obtained in the present study. Allometric equations calculated by these authors show that the amount of oxygen consumed by young mice rises very intensively until the animals reach a weight of about 6 g, and that this is followed by less intensive reduction in the value of this index. The above results also form evidence that changes in metabolic rate during the nest period are connected primarily with the animals' age, and thus with the different degree of their physiological development.

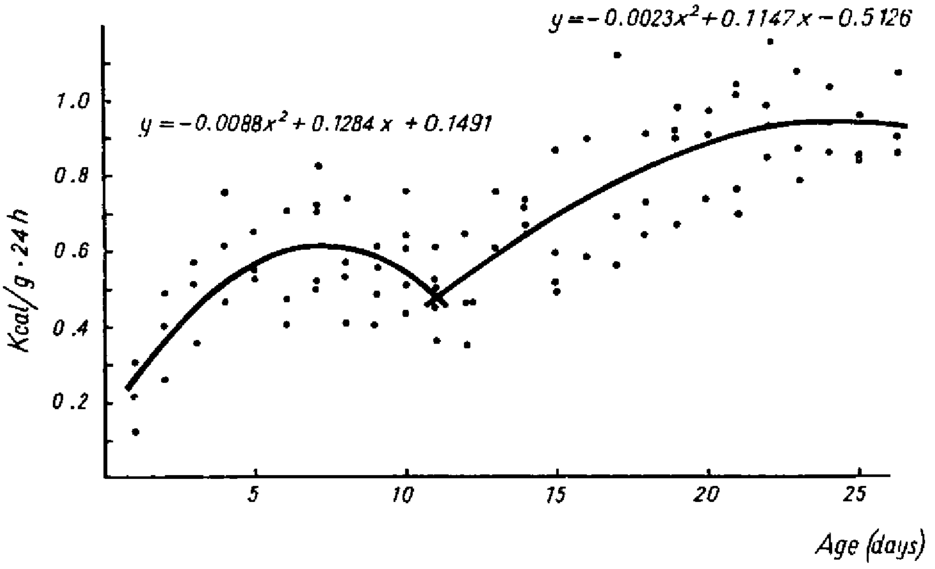

Fig. 2. Variations in metabolic rate during the postnatal development of laboratory mice.

Phases of intensive growth, and then a decrease in the amount of oxygen consumed by the animals (Bašenina, 1962; Taylor, 1960; Kleiber, 1961; Rožaja & Maslennikova, 1968) also occur over the course of changes in metabolic rate during postnatal development of other rodents, whether wild or laboratory. The duration of these phases, however, differs in different species. When Kleiber *et al.* (1956) examined female rats they found that the first peak in metabolic rate occurs at the age of about 3—5 days, and a second peak about the 40th day of life. Taylor's studies (1969) also show that the above changes take place in rats during the first 40 days after their birth, whereas in hamsters they end about the 20th day of life (Rožaja & Maslennikova, 1968).

(b) Metabolic Rate of Different Age Groups

The amount of oxygen consumed, when converted to unit of body weight in a unit of time, is highest in laboratory mice one month old, and decreases with the animals' age (Table 3), while the value of the respiratory quotient is in principle uniform in all the groups examined and is close to 1.0. Only the *RQ* of females over 6 months old is slightly lower in value. Consequently differences in metabolic rate, expressed in kcal/g 24h, are analogical between the various groups to differences in the amount of oxygen consumed.

Table 3

Metabolic rate of different age groups of *M. musculus* (temperature 22°C—23°C).

Age, months	Sex	No. of animals	Body wt. g	*RQ*	ml O_2/g h	kcal/g 24 h	kcal/kg$^{0.75}$ 24 h
1	M	9	13.9 ± 1.5	1.00 ± 0.08	7.21 ± 1.07	0.869 ± 0.115	302
	F	10	14.2 ± 1.0	1.00 ± 0.02	7.05 ± 0.50	0.849 ± 0.052	299
4	M	10	27.8 ± 1.2	0.98 ± 0.02	5.88 ± 0.36	0.705 ± 0.058	289
	F	11	22.8 ± 1.1	0.98 ± 0.03	5.71 ± 0.45	0.690 ± 0.066	269
7— 8	M	14	30.2 ± 1.7	0.93 ± 0.05	5.48 ± 0.98	0.648 ± 0.101	271
	F	14	29.5 ± 1.3	0.88 ± 0.09	5.21 ± 0.42	0.611 ± 0.490	252
9—11	M	12	30.3 ± 1.1	1.00 ± 0.06	5.54 ± 0.68	0.670 ± 0.720	282
	F	15	32.5 ± 1.0	0.88 ± 0.08	4.86 ± 0.47	0.571 ± 0.530	243

The physiological metabolic rate expressed in kcal per metabolic unit of body weight is the same in one-month-old mice as that in mice over 20 days old examined during nest development, but decreases slightly in the oldest mice, although even in individuals 9—11 months old it does not fall below the value of 250 kcal/kg$^{0.75}$ 24h (Table 3). These are higher values than those given by Poczopko (1971) for a large number of species of laboratory and wild rodents examined in a range of physiologically neutral temperatures. Similar physiological values of metabolic rate were obtained by Górecki (1971) for *Micromys minutus* Pallas, 1778, with body weights of 8—12 g.

The values of metabolic rate for adult laboratory mice obtained in this

Table 4

Changes of metabolic rate during pregnancy and lactation in female laboratory mice (temperature 22°C—23°C).

Days	No. of animals	Body wt. (g)	*RQ*	ml O_2/g h	kcal/animal 24h
		Pregnancy			
1	2	26.5	0.89	5.90	18.42
2	3	27.5	0.96	5.61	18.45
3	2	27.1	0.96	6.35	20.08
4	2	27.8	1.01	6.16	20.57
5	3	27.1	0.92	6.44	20.80
6	2	29.9	1.01	6.40	23.10
7	2	30.7	0.95	6.25	22.69
8	2	31.6	0.87	6.55	24.24
9	3	30.3	0.95	6.05	21.90
10	3	33.0	0.91	6.06	23.74
11	2	34.5	0.83	4.91	20.10
12	3	37.7	0.89	5.60	24.88
13	3	38.8	0.91	3.88	17.88
14	3	40.8	0.81	3.86	18.16
15	4	42.6	1.01	4.18	21.28
16	4	42.6	0.94	3.90	19.18
17	4	44.3	1.03	3.70	18.88
18	5	46.1	0.93	3.99	21.60
19	3	48.5	1.03	3.57	20.96
		Lactation			
20	3	28.3	0.95	5.37	18.17
21	3	28.4	1.03	5.74	19.72
22	3	29.1	1.11	5.67	20.03
23	4	30.9	1.07	6.32	23.65
24	1	30.5	1.18	6.63	24.51
25	2	31.7	1.00	7.01	26.93
26	4	29.2	1.02	6.83	24.03
27	5	31.2	0.98	6.66	25.19
28	3	29.0	0.98	7.12	24.80
29	3	30.4	1.04	6.76	24.90
30	2	30.5	0.92	7.63	27.42
31	2	29.6	0.96	7.81	27.77
32	1	30.3	0.95	8.27	29.96
33	2	31.2	0.93	7.60	28.31
34	4	29.0	0.92	7.66	26.46
35	3	31.3	1.02	7.55	28.48
36	4	31.0	1.00	7.54	27.66
37	4	27.9	0.92	7.56	25.10
38	3	29.1	0.99	7.24	25.12
39	4	27.9	0.90	7.58	24.98
40	4	29.4	0.96	6.90	24.29
41	4	28.2	0.96	6.55	21.94
42	5	30.9	0.96	5.99	22.03
43	3	30.1	0.91	5.81	20.65
44	3	30.5	0.98	5.60	20.59

study considerably exceed the value of metabolism in *M. musculus* examined by Morrison (1948). They are, however, very similar to data obtained by Górecki & Krzanowska (1971) for laboratory mice from 5—6 months old of the *KE* and *KP* lines.

The differences presented above in the metabolic rate of different age groups of mice studied, expressed in kcal/g 24h are closely correlated with variations in the animals' body weight. This is shown by the highly statistically significant coefficient of correlation $r = -0.979$ calculated for this relation. The exponent of power in the exponential equation describing the above relation ($M = 4.05\ W^{-0.555}$, where M — metabolic rate in kcal/g 24h, W — body weight in grammes) is very close to those calculated for the relation between the average daily metabolic rate (*ADMR*) and body weight in many species of small wild rodents (Górecki, 1968, 1971; Grodziński, 1971; Grodziński & Górecki, 1967; Hansson & Grodziński, 1970). The value of coefficient b of these intraspecies equations always fluctuated around -0.50.

(c) Changes in Metabolic Rate of Females during Pregnancy and Lactation

The amount of oxygen consumed per unit of body weight changes unusually abruptly during pregnancy and lactation (Table 4). Two distinct periods can be differentiated here. The first of them lasts from the time of fertilization up to parturition and is characterized initially by a slight increase in this index, and as from the 5th day of pregnancy by a steep fall reaching to the level of 50% of the initial value. During the second period, covering the duration of lactation, there is an abrupt jump in oxygen consumption immediately after parturition. This increase then continues until about the 33rd day of the reproduction period (14th day of lactation), after which there is again a reduction in the amount of O_2/g h consumed by the animal.

RQ in both pregnant and lactating females is relatively high, and during the end period of pregnancy and the first stage of lactation is slightly above 1.0 in value (Table 4). Changes in metabolic rate of pregnant and lactating females, expressed in energy units, thus follow a pattern similar to that of variations in oxygen intake (Fig. 3). On an average for the whole period of pregnancy metabolic rate calculated per unit of body weight is about 91%, and during lactation about 121%, of the metabolic rate of sexually inactive females. It is of course obvious that the reduction observed in metabolism indices, converted to unit of body weight, is due during pregnancy primarily to the considerable increase in the body weight of pregnant females. Females mice examined on the last day of pregnancy were about 90% heavier than their weight on the first day (Myrcha *et al.*, 1969, Table 4). Consequently the value of the metabolism of reproducing females expressed in kcal/animal 24th rises abruptly (Table 4). During pregnancy this increase is, however, far slower than during lactation. The highest value, exceeding the state on the first day of pregnancy by 50%, is reached by this index on the 13—16th day of lactation, after which it decreases fairly rapidly, undoubtedly as a result of the young animals starting to feed independently (Myrcha *et al.*, 1969).

Facts forming evidence of the considerable increase in the energy requirements of pregnant and lactating female laboratory mice and rats have been given by a large number of authors (Brody, 1945; Dewar, 1953; Nelson & Evans, 1961; Fell, Smith & Campbell, 1963; Barnett & Little, 1965). In a study published earlier on (Myrcha *et al.*, 1969) it was found that the food requirements of the female mice examined increase by an average of 33.6% during pregnancy and during lactation by as much as 111.3%. It can be seen from the data given in Table 4, however, that the metabolic rate of reproducing females is only, on an average, 8.0% higher during pregnancy and 48.7% during lactation. Brody *et al.*, (1945) found and average increase of 15% in resting metabolic rate in pregnant female rats, and Kleiber & Cole (1945) an increase of 9—16% in the metabolic rate of fasting pregnant female rabbits. In the pregnant female rats examined by Morri-

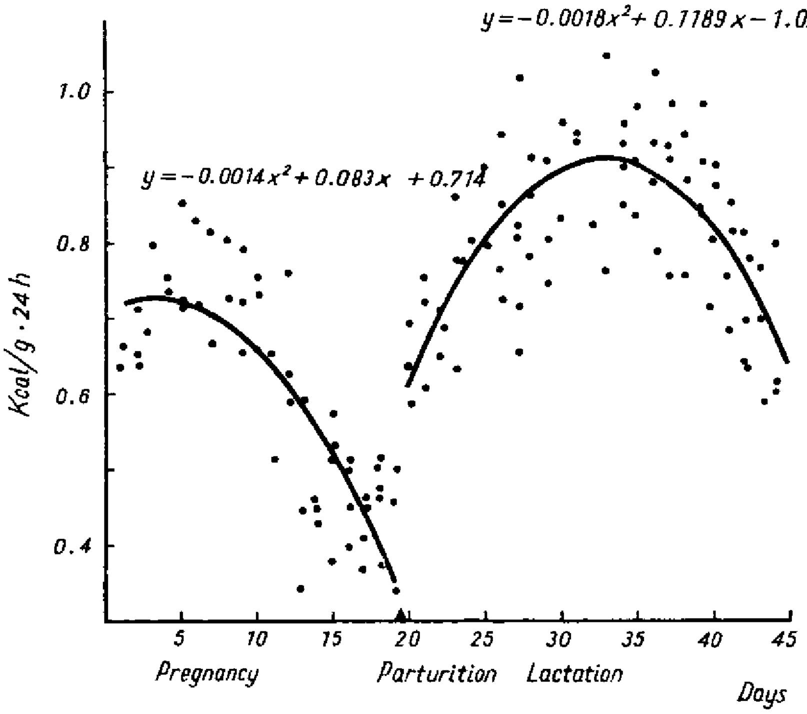

Fig. 3. Variations in metabolic rate of female laboratory mice during pregnancy and lactation.

son (1956) the average increase in resting metabolic rate was also only about 10%. This phenomenon is certainly connected, *inter alia,* with the considerable decrease of even more than 40% in the activity of pregnant females (Slonaker, 1925; Wang, 1925).

These results show that the whole process of reproduction, including both the period of gestation and lactation, is characterized in laboratory mice by very great effectiveness of production. When converting the data on food consumption and assimilation contained in the above study (Myrcha *et al.*, 1969) to unit of body weight, and comparing them with data on metabolic rate, it can be seen that during the peak period of lactation female laboratory mice use as much as about 35% of assimilated energy in the process of production, and only about 65% of energy for metabolic processes.

The bioenergetic indices presented above for pregnant and lactating females of *M. musculus* agree with the results obtained by other authors for wild rodents. Kaczmarski (1966) found that the energy requirements of females of *Clethrionomys glareolus* (Schreber, 1780) increase by an average of 58% during the whole period of pregnancy and lactation. In *Microtus arvalis* (Pallas, 1778) this increase is even higher, the figure according to the data given by Migula (1969) being 82.5%.

3. Energy Balance during the Period of Nest Development

The energy value of production on different days of the development of the mice examined, obtained from the breeding centre, was calculated by multiplying the current value of their body weight read from the plotted growth curve (Fig. 7) by the corresponding caloric value of 1 g of biomass for these animals (Myrcha & Walkowa, 1968), and deducting the value calculated for the preceding day from the result. The data presented above on changes in metabolic rate during the first 26 days of life of these mice (Fig. 2), on the other hand, formed the basis for calculating daily values of respiration during this period. Value of assimilation was calculated by totalling these two values.

The period of development in the nest lasts about 26 days in the case of the laboratory mice used for these studies, which are fed solely on their mothers' milk up to about the 17th day of life, after which they also begin to find their own food. Feeding on milk ceases on about the 26th day of life of the young animals.

The value of production per 24 hours is fairly low during the first two days of life in these mice, being about 0.140 kcal/animal 24h, then increases intensively, to reach a level of 0.730 kcal/animal 24h on the 9th day of postnatal development, after which it decreases on the following day to 0.546 kcal/animal 24h then remains unchanged until the 19th day. During the subsequent period of the animals' stay in the nest there is a renewed increase in daily production until a value of 0.780 kcal/animal 24h is attained on the 21st—23rd day. At the end of nest development the value of this index decreased, and on the 26th day was 0.468 kcal/animal 24h.

The daily value of energy losses during metabolic processes on the first day of life of these mice is 0.325 kcal/animal 24h. Up to the 8th day of development respiration value increases fairly evenly by about 0.215 kcal/animal 24h, after which it is maintained on a uniform level

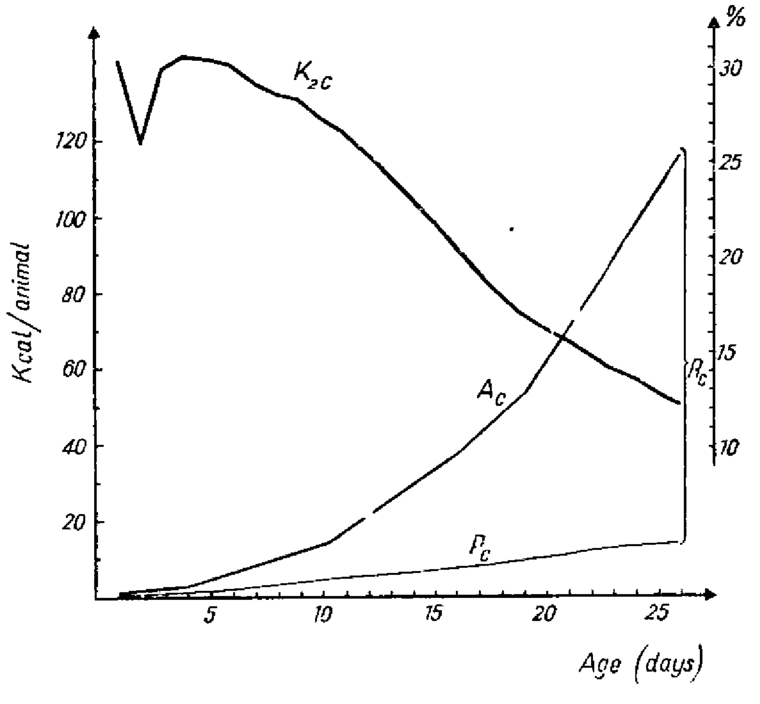

Fig. 4. Cumulative energy balance of single individuals of laboratory mice during nest development (symbols in text).

for the next three days. From this time onwards there is a renewed very intensive increase in this index of about 0.485 kcal/animal 24h, which is maintained up to the 26th day of life in these mice, when the daily value of respiration reaches a level of 9.270 kcal/animal 24h.

The values of the coefficient of production efficiency K_2 changes fairly intensively during postnatal development. Maximum effectiveness of the production process is observed during the first 5 days of life of these mice, when the value of coefficient K_2 is maintained on a level of about 30%. Later there is a gradual and fairly even decrease in value of this coefficient, the value of which is only 4.80% on the 26th day of life.

The elements of the cumulative energy balance for the period of nest development of the laboratory mice examined, calculated for one average individual, are presented in Fig. 4. It can be seen from this diagram that during the first 26 days of life, under laboratory conditions, each animal assimilates an average of 117.2 kcal of energy, 14.3 kcal of which are used in production processes and 102.9 kcal in metabolic processes. The cumulative value of K_{2c} is about 12.2% for this whole period.

The above data show that this period is characterized by very high effectiveness of production in comparison with other times in the life of mice, of course excepting the period of pregnancy and lactation. In the ecological literature to which I had access there is no information on the energy balance of the development period of other species of mammals. Comparison of the results presented in this study with analogical data contained for nesting birds of similar body weight shows, however, that effectiveness of production during the period of nest development of mice is lower than is the case with birds (Diehl & Myrcha, 1973; Myrcha *et al.*, 1972). The value of K_{2c} calculated for the whole nest period averages about 30%. Mice must assimilate an average of 8.2 kcal of energy in order to produce 1 kcal of energy contained in the body tissues, whereas the nestlings of *Lanius collurio* L. assimilate only 3.5 kcal for this purpose (Diehl & Myrcha, 1973). The values of the above indexes calculated for the first 17 days of life of these mice, during which the animals were fed solely on their mother's milk, *i.e.* for a period more closely corresponding to the nest period in birds, are also far lower than the indexes of effectiveness of production for nestling birds. During the 17 days of life of these laboratory mice they use only slightly more than 10% of assimilated energy in production processes, which shows that in order to produce 1 kcal of tissue energy they are obliged to assimilate about 5.2 kcal of food energy.

Using the above elements of the energy balance of single developing mice as a basis, calculation was made of the cumulative energy balance for 26 days development of an average litter of these animals. In these calculations we took the average observed litter size of 7.7 individuals, with an average body weight at the moment of birth of 1.14 g, and also the data given by Adamczyk (unpubl. data) on vialibility of young animals in cages 220 cm^2 in area, that is, similar in size to the breeding cages continuously occupied by adult mice (♂ and ♀) and their progeny up to the age of 4—5 weeks. This author observed that 85% of the newborn animals arrive up to the end of the 1st week of life, 74% up to the end of the 2nd week, while in the 3rd and 4th week of life mortality among young mice under these conditions is 0.

It can be seen from the calculations made that during 26 days of development the average litter of these laboratory mice must assimilate about 685.2 kcal of energy, of which about 86.4 kcal is used in production processes. As much as 598.9 kcal of energy is dispersed in metabolic processes, that is, almost 7 times more than production value. The value of the cumulative coefficient of production efficiency K_{2c} *i.e.* 12.6% is very similar to that calculated for single individuals.

IV. CHANGES IN BIOENERGETIC INDICES DURING THE DEVELOPMENT AND GROWTH OF AN EXPERIMENTAL POPULATION OF LABORATORY MICE

1. Description of the Study Population

The experimental population of laboratory mice examined developed freely over a period of 29 weeks in a metabolic cage 6 400 cm^2 (Fig. 1) in area, into which 5 ♀♀ and 4 ♂♂ aged 4 months were introduced.

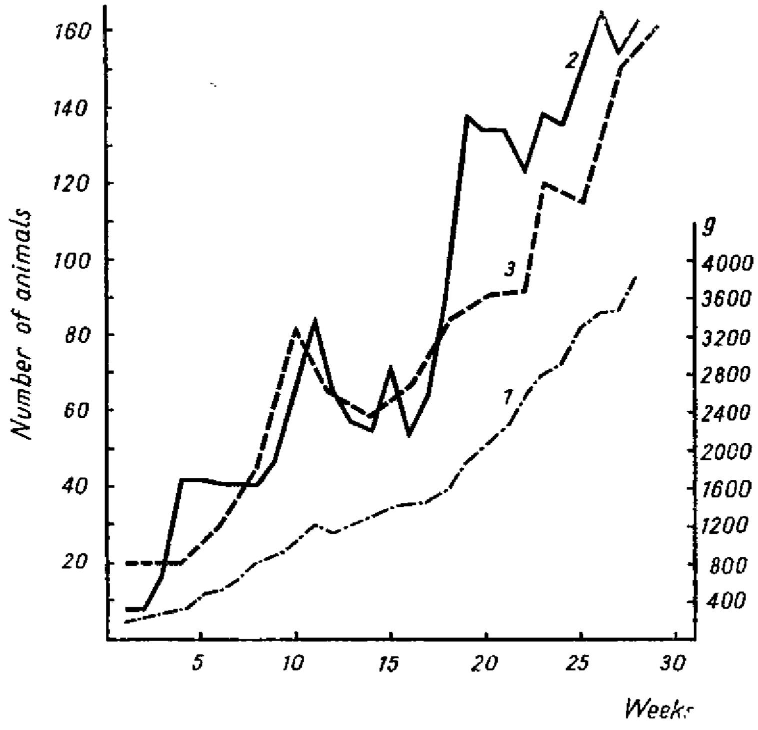

Fig. 5. Variations in the number of animals and their biomass during the development of an experimental population of laboratory mice.
1 — population biomass; 2 — number of animals; 3 — dynamics of experimental population numbers of H_3 laboratory mice examined by Walkowa & Petrusewicz (1967).

The number of animals and their biomass increased intensively up to the 10th week of development of the population (Fig. 5). The second stage of intensive growth of these parameters was observed as from the 16th week of life of the population. Towards the end of the study period the population consisted of over 160 animals and in the 28th week of the experiment its weight exceeded 3.850 g. Changes in the percentage formed by different age and sex groups in the total biomass of the population are illustrated in Fig. 6.

Dynamics of population numbers of these mice, whether living wild or under experimental conditions, forms a fairly variable parameter

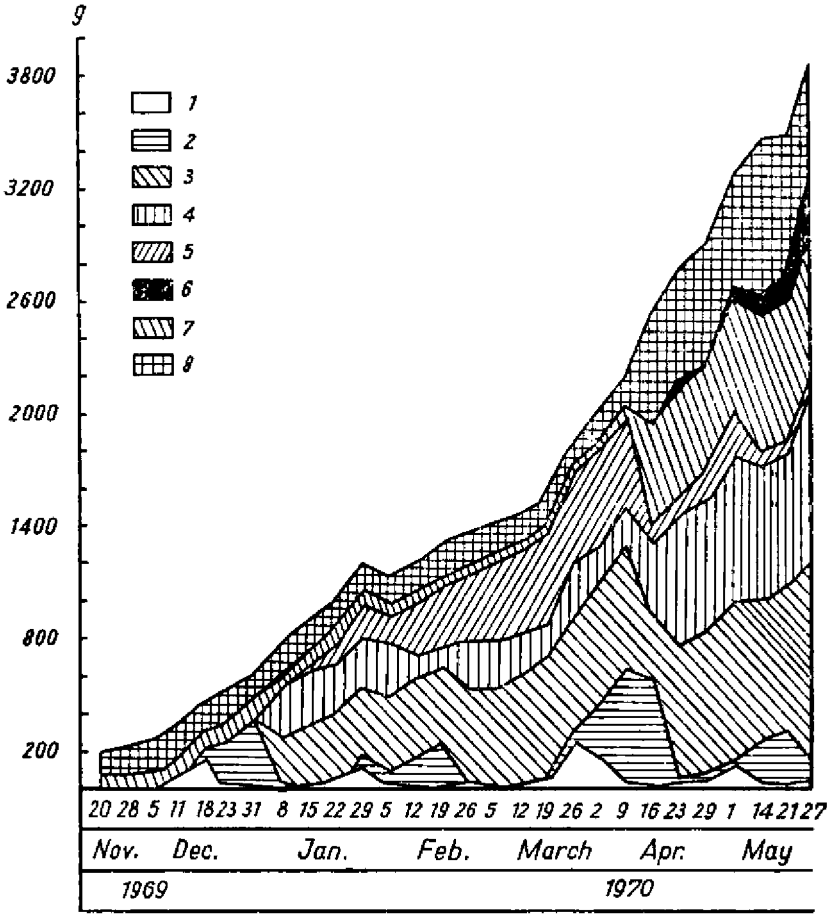

Fig. 6. Variations in the percentage of different age and sex groups in the total biomass of an experimental population of laboratory mice.

1 — juv. 0-2 weeks; 2 — juv. 2 weeks — 1 month; 3 — males 1-4 months; 4 — non-active females 1-4 months; 5 — active females 1-4 months; 6 — non-active females over 4 months old; 7 — males over 4 months old; 8 — active females over 4 months old.

(Strecker, 1954; Southwick, 1955, 1958; Petrusewicz, 1960, 1963; Walkowa & Petrusewicz, 1967; Walkowa 1974). It would seem that the population examined in this study developed according to the normal pattern. Evidence of this is formed *e.g.* by comparing changes in the number of animals during the development of this population with the dynamics of numbers animals of an experimental population of H_3 laboratory mice examined by Walkowa & Petrusewicz (1967) (Fig. 5).

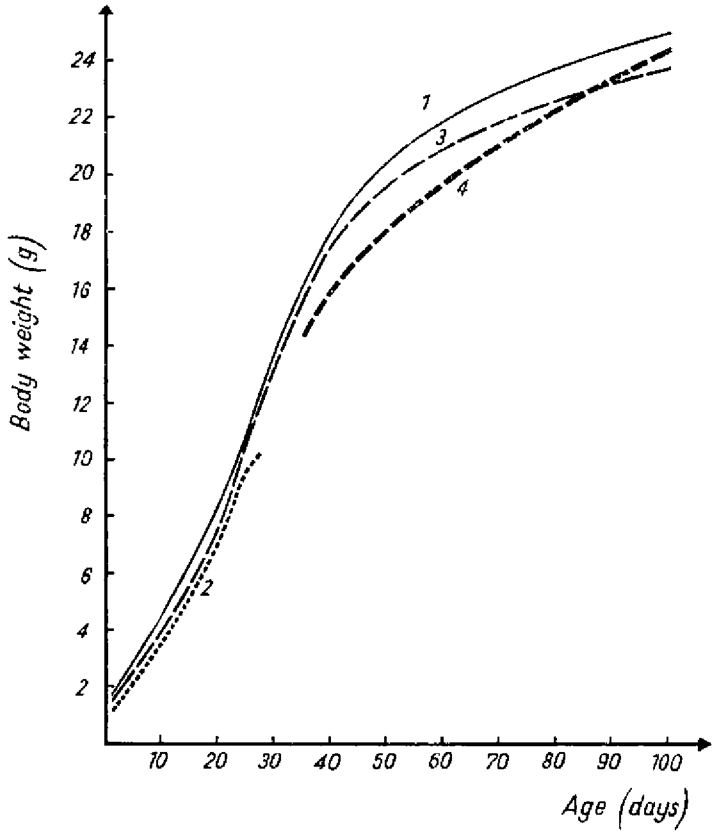

Fig. 7. Growth curves for study laboratory mice.
1 — from present study — population; 2 — from present study — family cages; 3 — from study by Myrcha & Walkowa (1968); 4 — from study by Walkowa (1971).

In addition the growth curve for young individuals born at different times during the development of the study population is typical of the laboratory mice obtained from the breeding centre of the Institute of Ecology. It does not differ from curves calculated for animals living either in reproduction cages (Myrcha & Walkowa, 1968), or in unexploited populations or populations exploited only to a slight degree (Walkowa & Petrusewicz, 1967; Walkowa, 1971) (Fig. 7).

2. Instantaneous Energy Balance

Values of the elements of energy balance determined by experiment at different times during the population's development, converted to a unit of its biomass, are given in Table 5.

Table 5

Values of the elements of instantoneous energy balance of the experimental population of laboratory mice expressed in kcal/g 24h.

Weeks	No. of animals	Biomass of population, g	Consumption (C)	Assimilation (A)	Production (P)	Coefficients of		
						Assimilation, %	Production efficiency, %	
							K_1	K_2
1	8	190.7	0.765	0.628	0.039	81.7	5.07	6.20
2	8	219.8	0.597	0.448	0.029	75.0	4.90	6.54
3	17	264.8	0.574	0.471	0.059	81.5	10.12	12.41
4	42	320.8	0.686	0.546	0.115	79.6	16.81	21.13
5	42	456.3	0.635	0.494	0.037	77.9	5.76	7.39
6	41	507.0	0.662	0.525	0.040	79.3	6.04	7.62
7	41	616.8	0.862	0.558	0.074	78.7	10.47	13.30
8	41	791.6	0.687	0.545	0.053	79.4	7.78	9.80
9	48	908.4	0.612	0.488	0.032	79.8	5.18	6.50
10	65	1021.0	0.569	0.436	0.033	76.6	6.35	8.29
11	84	1200.9	0.593	0.473	0.026	79.1	4.41	5.58
12	65	1131.1	0.798	0.617	0.028	76.6	3.55	4.64
13	57	1202.4	0.735	0.591	0.031	80.4	4.19	5.21
14	55	1312.8	0.708	0.573	0.027	79.7	3.84	4.81
15	71	1376.3	0.603	0.469	0.021	77.8	3.54	4.55
16	54	1424.6	0.647	0.502	0.023	77.6	3.62	4.66
17	65	1474.9	0.599	0.456	0.025	76.8	4.13	5.38
18	91	1596.9	0.553	0.432	0.045	78.1	8.05	10.30
19	138	1871.6	0.527	0.412	0.039	78.7	7.31	9.29
20	134	2044.7	0.594	0.453	0.031	75.9	5.16	6.79
21	134	2224.4	0.641	0.520	0.050	81.2	7.76	9.56
22	123	2545.1	0.702	0.554	0.034	79.0	4.79	6.06
23	138	2795.0	0.582	0.472	0.036	81.1	6.18	7.63
24	135	2932.7	0.572	0.456	0.036	79.6	6.32	7.94
25	150	3287.8	0.516	0.397	0.020	76.9	3.90	5.08
26	165	3468.4	0.606	0.499	0.016	82.3	2.59	3.15
27	154	3495.0	0.574	0.474	0.028	82.5	4.94	5.87
28	163	3858.4	0.551	0.454	0.031	82.4	5.29	6.24

The relatively low values of food consumption and assimilation, in comparison with data obtained for adult animals examined singly and not using energy consumed in food in production processes, are remarkable (cf. Table 1). The coefficient of food assimilation, on the other hand, fluctuating in successive weeks of the experiment within limits of several percent, had an average value of 79.13% and was very similar to the value of this index obtained for 4-months-old mice examined singly.

The population used different amounts of energy for biomass production at different moments during it development. When converted to a unit of population weight the value of its production, at first fairly low, reached the highest level between the 3rd and 8th week of the

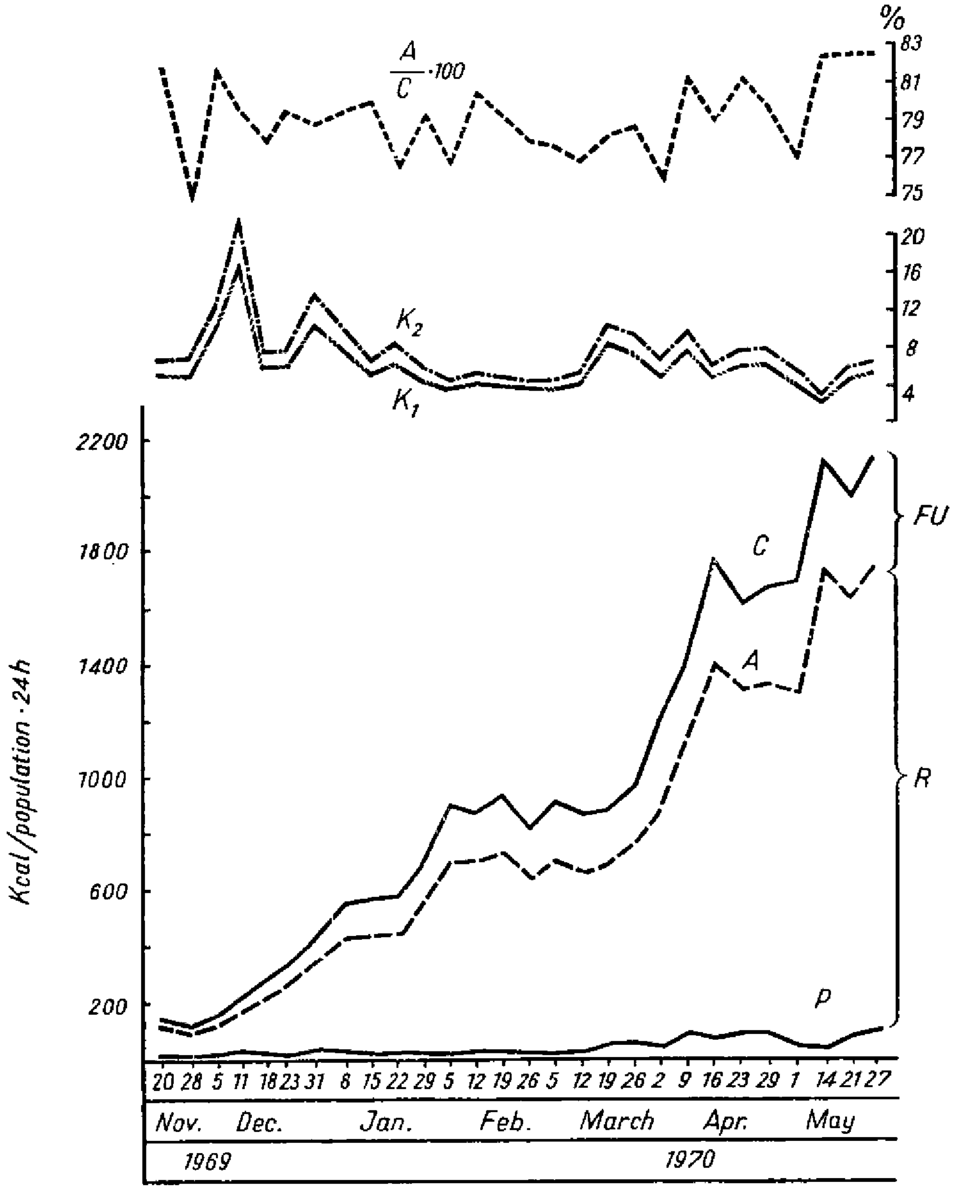

Fig. 8. Instantaneous energy balance of an experimental population of laboratory mice (symbols in text).

experiment. During the remaining period of the population's development production values expressed in kcal/g. 24h are gain far lower, but this index continues to be very variable. The difference between the lowest and highest value of daily production of a unit of biomass of the study population was seven times as much.

The values of coefficients K_1 and K_2 at different observation times are also characterized by considerable variation. The maximum values of these coefficients exceed the lowest values by more than 6 times as much. In general it may be said that the value of the two coefficients of production efficiency increase in periods when the number of young individuals up to the age of 1 month is the greatest in the population.

Average values of all elements of the instantaneous energy balance (in kcal/g 24h) for the population developing over the course of 29 weeks are as follows:

$$C = A + FU \qquad\qquad A = P + R$$
$$0.635 = 0.498 + 0.138 \qquad\qquad 0.498 = 0.038 + 0.460$$
$$100\% = 78.4\% + 21.3\% \qquad\qquad 100\% = 7.6\% + 92.4\%$$

Respiration thus exceeded the average daily value of production by over 12 times $[(P{:}R) \times 100 = 8.2\%]$. The average coefficient K_1 had a value of 6.0%, and K_2 — 7.6%.

The instantaneous energy balance for the whole study population of laboratory mice is given in Fig. 8. As this population develops the values of the various elements of this balance rise, which is of course connected primarily with increase in the population's weight. The rate of increase of population biomass, however, is not exactly the same as the rate of growth of the amount of energy consumed and assimilated by this population biomass increased by over 20 times, whereas the value of its daily consumption increased by only 14.5 times. During the course of development of the study population there were even periods (12—18 week and 22—26 week) in which its biomass increased considerably, while daily value of consumption remained unchanged.

3. Cumulative Energy Balance

Changes in the elements of cumulative energy balance during development of the experimental population of laboratory mice are shown in Fig. 9. The final values of this balance for 189 days of development of the study population (in kcal/population) are as follows:

$$C_c = A_c + (FU)_c \qquad\qquad A_c = P_c + R_c$$
$$175\,241 = 138\,903 + 36\,378 \qquad\qquad 138\,903 = 9\,388 + 129\,515$$
$$100\% = 79.3\% + 20.7\% \qquad\qquad 100\% = 6.8\% + 93.2\%$$

It follows from this that during the production process this population used 5.35% of the value of consumed energy (K_{1c}) and 6.76% of assimilated energy (K_{2c}) over the course of the whole experiment. The cumulated value of respiration for this population is almost 14 times greater than its cumulated value of production.

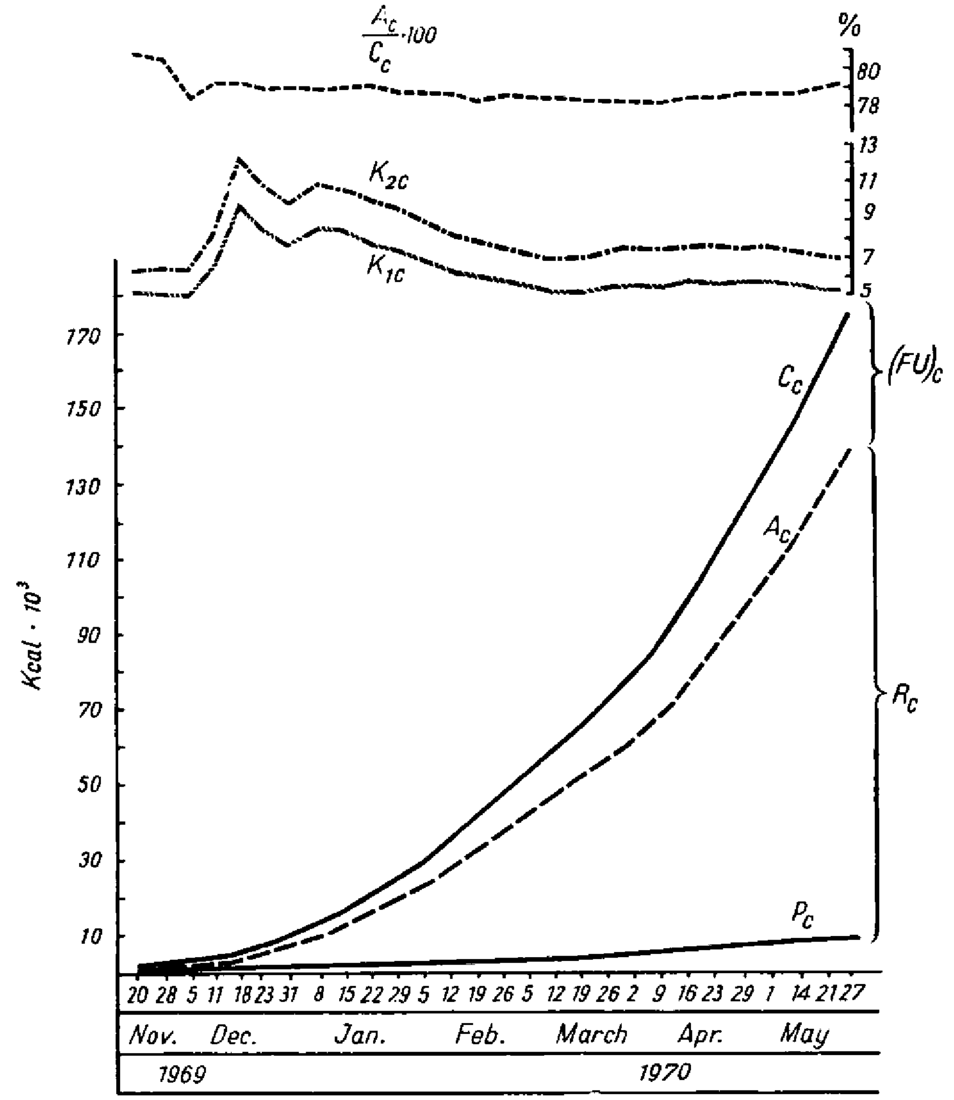

Fig. 9. Cumulative energy balance of an experimental population of laboratory mice.

4. Metabolic Rate of Experimental Population

Changes in the indices characterizing metabolic rate of the study population during its development are shown in Table 6. The amount of oxygen consumed, when converted to unit of population biomass in unit of time, is far lower than the data obtained for individuals of *M. musculus* examined singly (Table 3), while *RQ* values are very similar in both cases. Consequently differences in metabolic rate expressed in energy units are analogical to differences in the amount of oxygen consumed.

Considerable differences, of as much as 100%, in the values of these indices occur, however, at different times during the experiment, but no statistically significant relation was found between metabolic rate calculated per unit of population weight and its biomass or numbers. It can only be said that during the initial period of population development its metabolic rate, expressed in kcal/g 24h, markedly decreases. This decrease lasts until the time when population biomass reaches a value of about 500 g, and it numbers about 40 animals. During the continuation of the experiment the metabolic rate of the population is established in principle on a level of about 0.35 kcal/g 24h, despite intensive changes in its

Table 6

Variations in metabolic rate during the development of an experimental population of laboratory mice.

Weeks	Biomass of population, g	*RQ*	ml O_2/g h	kcal/g 24 h
1	190.7	0.87	4.05	0.499
2	219.8	0.98	3.01	0.363
3	264.8	0.88	2.81	0.329
4	320.8	0.95	2.44	0.292
5	456.3	1.01	2.37	0.287
6	507.0	1.03	2.20	0.267
7	616.8	0.99	2.54	0.307
8	791.6	0.97	2.66	0.320
9	908.4	1.00	3.24	0.393
10	1021.0	0.88	2.32	0.273
11	1200.9	1.01	2.91	0.355
12	1131.1	1.05	3.30	0.407
13	1202.4	1.01	2.82	0.342
14	1312.8	1.01	3.00	0.364
15	1376.3	0.98	3.33	0.401
16	1424.6	0.95	2.89	0.345
17	1474.9	1.02	2.44	0.296
18	1596.5	0.95	3.23	0.386
19	1871.6	0.95	2.84	0.339
20	2044.7	0.91	2.86	0.339
21	2224.4	1.00	3.37	0.408
22	2545.0	0.93	4.80	0.571
23	2795.0	1.00	3.62	0.469
24	2932.7	0.91	2.81	0.340
25	3287.8	0.87	2.88	0.338
26	3468.4	0.79	2.62	0.301
27	3495.0	0.95	3.50	0.418
28	3858.4	0.86	3.10	0.362

biomass and numbers. With increase in numbers to more than 120 animals the metabolic rate increased slightly to a level of about 0.40 kcal/g 24h. An exception to this was the period between the 21st and 23rd week of the experiment, when the values of this index were markedly higher This is probably connected with the relatively large number of young animals (up to 1 month old) and the females feeding them at that time. During this same period a considerable increase is also observed in the value of food consumption and assimilation (Fig. 8).

Table 7

Values of the elements of instantaneous energy balance of the experimental population calculated from results obtained for laboratory mice examined singly.

Weeks	Consumption, kcal g h	Assimilation, kcal/g h	Coefficients of		
			Assimilation, %	Production efficiency, % K_1	K_2
1	0.970	0.769	79.3	3.99	5.04
2	0.938	0.737	78.6	3.13	3.97
3	0.863	0.702	81.4	6.78	8.33
4	1.077	0.874	81.2	10.72	13.21
5	0.985	0.831	84.4	3.71	4.40
6	0.897	0.714	79.5	4.46	5.61
7	1.205	0.954	79.1	6.16	7.78
8	1.139	0.893	78.3	4.69	5.99
9	1.091	0.858	78.6	2.91	3.70
10	1.107	0.871	78.6	3.26	4.15
11	1.026	0.805	78.4	2.55	3.25
12	1.138	0.898	78.9	2.49	3.16
13	1.244	0.966	77.6	2.48	3.19
14	1.109	0.880	79.3	2.45	3.09
15	1.051	0.848	79.9	2.03	2.52
16	1.125	0.897	79.8	2.08	2.61
17	1.178	0.937	79.5	2.08	2.62
18	1.199	0.966	80.6	3.74	4.64
19	0.967	0.770	79.6	3.99	5.01
20	0.962	0.765	79.5	3.19	4.01
21	1.100	0.915	83.1	4.52	5.43
22	1.177	0.949	80.6	2.85	3.54
23	1.179	0.950	80.6	3.05	3.79
24	1.132	0.908	80.2	3.20	3.98
25	1.091	0.873	80.1	1.85	2.31
26	1.086	0.874	80.4	1.45	1.80
27	1.127	0.895	79.5	2.47	3.10
28	1.117	0.898	80.4	2.61	3.25

V. VALUES OF BIOENERGETIC INDICES CALCULATED FOR AN EXPERIMENTAL POPULATION OF LABORATORY MICE

1. Instantaneous Energy Balance

Values of consumption and assimilation of food for the whole population, expressed in kcal/g 24h, calculated on the basis of data obtained for

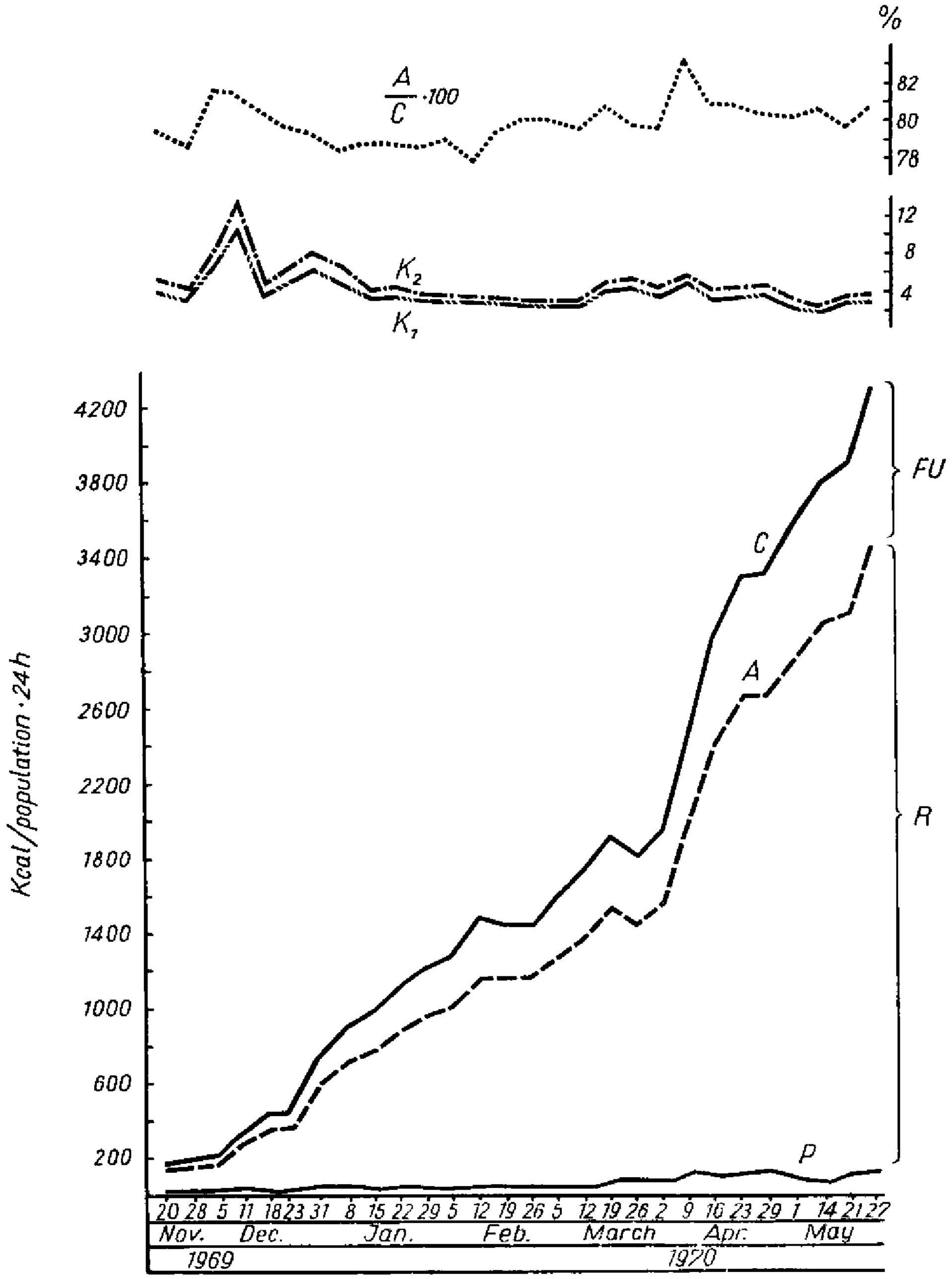

Fig. 10. Calculated instantaneous energy balance of an experimental population of laboratory mice.

animals examined singly, are far higher at different moments of population development than those found by experiment (Table 5 and 7). It follows from these calculations that during the experiment the study population should consume an average of 1.088 kcal/g 24h and excrete 0.223 kcal/g 24h in faeces and urine. Therefore the average calculated coefficient of food assimilation for 28 observation times is 79.9%, and does not differ from that determined by experiment. Accepting the experimentally obtained value of production for the study population in these calculations it may be said that the calculated average value of respiration is 21 times as great [$(P : R) \times 100 = 4.77\%$].

Calculated values of elements of the instantaneous energy balance for the whole study population (in kcal/population 24h) rise parallel to the increase in population biomass (Fig. 10). These values are far higher than those obtained experimentally (Fig. 8), the differences observed increasing with increase in population size. During the initial period of population development the differences between empirical and calculated values of its consumption and assimilation fluctuate within limits of 25% — 50%, but in the final weeks of the experiment they are above the level of 100%. On an average for the 28 measurements made these differences are 74% for amount of consumed energy, and 76% for energy assimilated. As the production value is the same in both cases these differences are primarily due to differences between calculated and empirical values for the population's respiration. In connection with the above the calculated values for coefficients of production efficiency K_1 and K_2 are far lower than those found empirically at all the observation times.

2. Cumulative Energy Balance

Changes in elements of cumulative energy balance as the study population develops are given in Fig. 11. Both the rate of increase in value of cumulative consumption and cumulative assimilation increase with increase in population biomass. It can be seen from this diagram that the cumulative value of consumption for the study population, calculated on the basis of data obtained for single animals, should be 327,437 kcal during the 189 days of its development. From this amount of energy 265,259 kcal should be assimilated by the population, and 62,178 kcal excreted in faeces and urine. As the cumulative value of production of this population is 9,388 kcal, it should use 255,871 kcal of energy in metabolic processes during the study period. It follows from this that the calculated cumulative value of the respiration of this population is more than 27 times greater than the cumulative value of its production [$(P_c : R_c) \times 100 = 3.67\%$].

Of course the calculated cumulative values of the coefficients of pro-

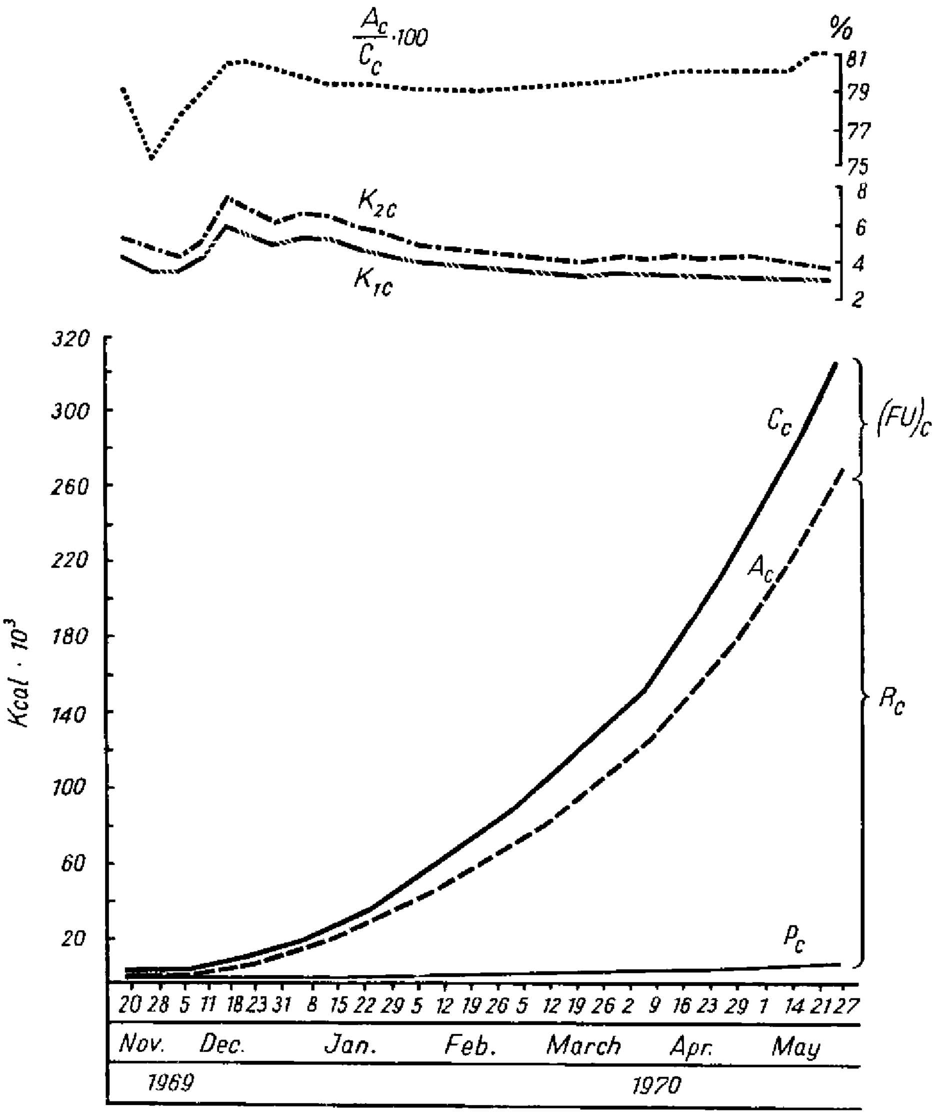

Fig. 11. Calculated cumulative energy balance of an experimental population of laboratory mice.

duction efficiency are almost twice smaller than those determined empirically and are $K_{1c} = 2.87\%$ and $K_{2c} = 3.54\%$.

The calculated values presented above for elements of the cumulative energy balance of the study populations are for higher than the analogical data found by experiment (Fig. 9 and Fig. 11). The calculated value of consumption exceeds the empirical value by 87%, and of assimilation by 91%. The greatest difference, however, since it is almost double, *i.e.* 98%, occurs between the calculated and empirical cumulative respiration value for the population.

3. Metabolic Rate

The metabolic rate of the study population calculated by totalling the appropriate data obtained from measurements made of individual animals, is far higher than the metabolic rate of the whole population measured experimentally (Fig. 12). The value of the calculated metabolic rate of the study population, when converted to unit of its biomass, is 0.726 kcal/g 24h in the first week of the experiment and is 45.5% higher than the empirically determined figure. During the next two weeks the value of this index decreases, then rises regularly and as from the 8th week of the population's development is maintained on a slightly lower level than 0.9 kcal/g 24h. During the last 10 weeks of the experiment the calculated metabolic rate of the study population comes close to 0.8 kcal/g 24h and is about 115% higher than the value found by experiment.

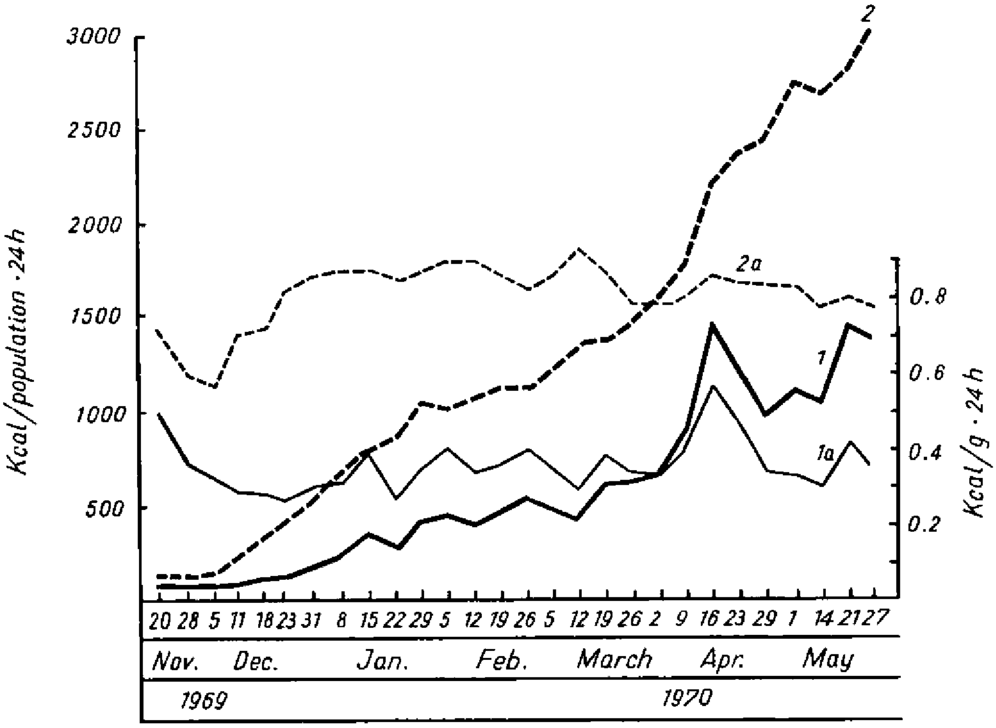

Fig. 12. Empirical (1, 1a) and calculated (2, 2a) data describing changes of metabolic rate during development of an experimental population of laboratory mice.

The calculated amount of energy dispersed in metabolic processes of the whole population rises fairly regularly together with an increase in the biomass of animals forming this population and, like the above index, is also far higher than that determined by experiment (Fig. 12). On an average throughout the duration of the experiment the calculated values for energy dispersed in metabolic processes of the study population are about 133% higher than empirical data.

VI. THE EFFECT OF POPULATION DENSITY AND GROUP SIZE ON THE METABOLIC RATE OF LABORATORY MICE

Examination was simultaneously made in the first experiment of the effect of group size and density of populations of one sex, consisting solely of male laboratory mice, on their metabolic rate (Table 8).

Table 8

Effect of density and group size on the metabolic rate of an experimental population composed solely of male laboratory mice.

Time	No. of animals in cage	Avg. body weight, g	*RQ*	ml O_2 g h	kcal/g 24 h	kcal/kg$^{0.75}$ 24 h
Day of establishment of population	5	25.1	0.95	4.03	0.481	195
	10	26.8	0.92	4.73	0.561	228
	20	25.6	0.98	5.22	0.629	257
	40	25.8	1.00	5.25	0.637	256
After 1 week	5	25.4	1.01	3.03	0.367	150
	10	27.5	0.93	3.21	0.382	157
	20	26.7	0.89	3.52	0.415	170
	40	26.3	0.98	3.61	0.435	179
After 2 weeks	5	27.2	0.91	2.74	0.327	134
	10	28.3	0.96	3.40	0.407	170
	20	27.9	0.96	3.65	0.435	179
	40	27.3	0.84	3.50	0.408	168

On the day the experimental populations were set up the indices characterizing their metabolic rate exhibited the highest values. After the animals had remained a week in the cages the metabolic rate of the study populations decreased on an average by 32%, and after two weeks underwent no further change. Both on the day the populations were set up and after the first and second week of the experiment, however, the organization elements of populations were found to exert a distinct influence on their metabolic rate.

The amount of oxygen consumed by the whole population, when converted to unit of biomass, is lowest in the case of populations composed of 5 males, which are thus simultaneously characterized by the least density. The amount of oxygen consumed by the study populations rises with a rise in density and group size. The difference in the metabolic rate of populations composed of 5 and 10 males was on an average about 15%. Populations composed of 20 and 40 mice, on the other hand, were characterized by a metabolic rate about 25% higher than in populations with lowest density and smallest number of animals.

As the body weight of males from which the above experimental populations were formed was approximately uniform, and differences in the value of the respiratory quotient only slight, the values of the other metabolism indices of these populations changed together with density

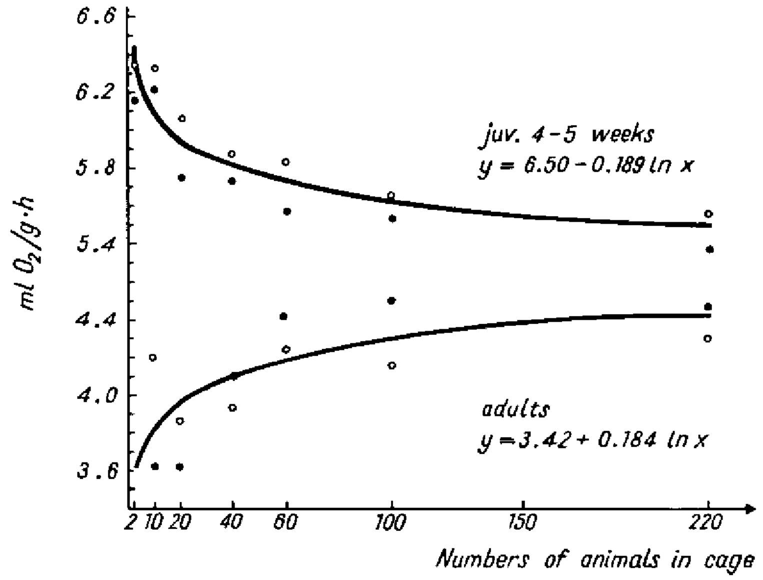

Fig. 13. Effect of density and group size on metabolic rate of laboratory mice.
● — males, ○ — females.

and group size in an analogical way to changes in the amount of oxygen consumed (Table 8).

In the next experiments the gradient of population density and number of animals differed to a far greater degree, i.e. from 2 to 220 mice in a cage of standard size (Adamczyk, unpubl. data).

Population density and group size were found to exert an important influence on the amount of oxygen consumed by both young and adult animals (Fig. 13). The metabolic rate of 4—5 week old mice decreases with an increase in these two elements of population organization, these changes being characterized by the equation $y = 6.50 - 0.189 \ln x$. Oxy-

Table 9

Effect of population density and group size on the metabolic rate of young and adult individuals of *M. musculus* temperature 22°C—23°C).

A — number of animals in cage, N — number of animals.

A	Sex	N	Young animals (4—5 weeks)				N	Adults			
			Body wt. g	*RQ*	ml O_2/g h	kcal/kg$^{0.75}$ 24 h		Body wt. g	*RQ*	ml O_2/g h	kcal/kg$^{0.75}$ 24 h
2	F	9	15.5 ± 2.0	0.86 ± 0.08	6.35 ± 0.76	268 ± 22					
	M	11	16.4 ± 1.4	0.83 ± 0.06	6.17 ± 0.99	261 ± 49					
10	F	8	14.1 ± 1.9	0.82 ± 0.12	6.33 ± 1.49	257 ± 50	14	28.1 ± 3.5	0.97 ± 0.04	4.21 ± 0.61	204 ± 20
	M	10	15.8 ± 1.1	0.83 ± 0.07	6.22 ± 1.34	260 ± 88	14	29.9 ± 2.8	0.94 ± 0.06	3.63 ± 0.36	179 ± 24
20	F	9	16.1 ± 1.2	0.83 ± 0.08	6.06 ± 1.63	254 ± 64	5	33.3 ± 1.8	1.01 ± 0.13	3.87 ± 0.71	212 ± 46
	M	9	15.8 ± 1.5	0.88 ± 0.10	5.76 ± 1.06	242 ± 45	10	30.6 ± 1.9	1.00 ± 0.03	3.62 ± 0.55	183 ± 21
40	F	11	15.4 ± 1.0	0.80 ± 0.03	5.89 ± 0.95	243 ± 30	14	34.7 ± 0.8	0.94 ± 0.03	3.94 ± 0.62	199 ± 25
	M	10	16.2 ± 1.6	0.83 ± 0.07	5.74 ± 0.82	241 ± 37	13	28.2 ± 2.2	0.88 ± 0.10	4.10 ± 0.48	200 ± 13
60	F	13	14.7 ± 0.6	0.82 ± 0.06	5.84 ± 0.23	239 ± 20	14	29.8 ± 1.2	0.95 ± 0.06	4.24 ± 0.23	210 ± 36
	M	5	15.5 ± 1.4	0.73 ± 0.12	5.57 ± 1.63	228 ± 97	15	29.0 ± 1.2	0.92 ± 0.04	4.42 ± 0.51	218 ± 25
100	F	11	14.1 ± 0.8	0.83 ± 0.02	5.66 ± 0.97	232 ± 38	7	31.1 ± 3.4	0.90 ± 0.09	4.16 ± 0.53	207 ± 26
	M	9	14.9 ± 1.6	0.81 ± 0.05	5.53 ± 1.24	228 ± 47	6	29.6 ± 3.3	0.93 ± 0.09	4.51 ± 0.68	222 ± 30
220	F	3	17.3	0.84	5.57	233	5	33.5 ± 2.7	0.89 ± 0.08	4.31 ± 1.04	216 ± 49
	M	3	16.8	0.86	5.37	226	5	29.0 ± 2.5	0.95 ± 0.12	4.48 ± 0.74	221 ± 23

gen consumption by young individuals living in populations composed of 220 animals in a cage is more than 15% lower than the value of this index observed in animals from cages occupied by 2 mice. Simultaneously the average values of metabolic rate for young females were slightly higher in all the populations than the analogical data obtained for males.

The amount of oxygen consumed by adult males and females *M. musculus* increases with an increase in density and number of animals, this increase being most intensive in the gradient of group size from 10 to 40 mice per cage. These changes are characterized by the equation $y = 3.42 + 0.184 \ln x$. The difference in the metabolic rate of mice living in populations composed of 10 and 220 animals is about 12%.

The respiratory quotient for young animals was slightly lower than for adult mice, but in neither case changed to a statistically significant degree with changes in population density and group size (Table 9). Changes in the other indexes describing the metabolic rate of the mice examined take place parallel to changes in the amount of oxygen consumed. No statistically significant differences connected with the sex of the animals were found in the values of any of the above indexes. In exactly the same way as in the case of differences in the amount of oxygen consumed, the character of changes in physiological metabolic rate expressed in kcal/$\text{kg}^{0.75}$ 24h forms evidence that the slight differences in body weight of animals in the groups of mice examined do not exert a significant effect on their metabolic rate. Changes in this values, due to changes in group

Table 10

Effect of group size on the metabolic rate of *M. musculus* with density of 1 mouse/30 cm^2 of cage bottom area.

No. of animals in cage	Sex	No. of animals	Body wt. g	*RQ*	ml O_2/g h	kcal/$\text{kg}^{0.75}$ 24 h
2	M	4	28.0 ± 2.1	0.83 ± 0.12	6.46 ± 1.56	309
	F	4	29.1 ± 2.8	0.86 ± 0.10	6.41 ± 1.34	308
20	M	5	28.1 ± 1.7	0.82 ± 0.07	4.31 ± 1.12	206
	F	5	32.3 ± 3.6	0.84 ± 0.01	4.44 ± 1.73	218
60	M	5	30.9 ± 3.4	0.89 ± 0.08	5.12 ± 2.14	253
	F	5	28.3 ± 2.5	0.79 ± 0.13	5.51 ± 1.46	261
100	M	5	29.7 ± 1.9	0.98 ± 0.07	4.58 ± 1.23	228
	F	5	29.6 ± 2.3	0.87 ± 0.09	5.29 ± 1.70	257
150	M	5	28.7 ± 3.4	0.89 ± 0.08	5.18 ± 2.05	243
	F	5	28.9 ± 3.1	0.92 ± 0.06	4.63 ± 1.84	228
220	M	5	31.4 ± 2.8	0.95 ± 0.07	4.32 ± 1.36	217
	F	5	30.1 ± 3.5	0.88 ± 0.09	4.65 ± 1.11	228

size and density of the experimental study population, are characterized for young animals by the equation: $y = 272.9 - 8.56 \ln x$, and for adult animals by : $y = 174.0 + 8.42 \ln x$.

In succeeding experiments investigation was made only of the effect of group size, that is, the number of individuals forming a population, on their metabolic rate. In this case also use was made of animals originating from populations examined by Adamczyk (unpubl. data), for the purpose of bioenergetic definitions.

In the first experiment there was 30 cm^2 area of cage bottom per mouse, and the size of the groups varied from 2 to 220 animals.

The amount of oxygen consumed by the animals examined in this experiment was the highest in the case of mice from populations with the smallest number of animals, this is, composed only of two individuals (Table 10). These animals had a metabolic rate about 32% higher than the average metabolic rate of the other laboratory mice examined in this experiment. Differences in the metabolic rate of animals from the other populations suggest that the level of this value depends on group size. The smallest amount of oxygen consumption is found for animals originating from populations of 20 individuals. The metabolic rate of mice living in populations composed of 60 animals is over 20% higher than that of the foregoing, while with continuing increase in group size the metabolic rate of the laboratory mice examined again decreased.

Animals living in populations consisting of 220 individuals consumed an average of 4.48 ml O_2/g h. The analogical value calculated for mice examined in the experiment with differing density and group size, taken from cages of similar dimensions in which 220 animals also lived, and thus there was a very similar area of cage bottom (about 29 cm^2) per animal, was 4.42 ml O_2/g h and was statistically uniform.

No statistically significant differences were found in the values of the *RQ* depending on changes in the number of animals forming a population with the above density. The body weight of the animals examined in this experiment was almost uniform and therefore their metabolic rate calculated per metabolic unit of body weight ($kg^{0.75}$) changed with a change in the amount of oxygen consumed.

In the next experiment in which examination was made of the influence of group size on the metabolic rate of laboratory mice, the density of the experimental populations was smaller, that is, the area of cage bottom per animal was greater, *i.e.* 120 cm^2. The number of individuals was not found to exert a statistically significant influence in this experiment on the amount of oxygen consumed by adult laboratory mice, with the exception of the case in which there were only two animals per cage (Table 11). The metabolic rate of mice coming from groups consisting of individuals was about 38% higher than that of animals coming from larger populations.

The line of regression illustrating the relation between the amount of oxygen consumed by the mice examined and group size in the gradient from 20 to 150 animals follows a course almost parallel to the axis of abscissae. This is borne out by the calculated equation of regression $y = 4.88 + 0.00016x$ and the statistically non-significant coefficient of correlation $r = 0.08$. The metabolic rate described by this equation in laboratory mice from populations differing as to the number of their members, in which there was 120 cm^2 area of cage bottom per individual, is very similar to the average metabolic rate calculated for all animals examined in the previous experiment in which there was 30 cm^2 area of cage bottom per mouse, with simultaneous omission of mice coming from the least numerous groups.

Table 11

Effect of group size on the metabolic rate of *M. musculus* with density of 1 mouse/120 cm^2 of cage bottom area.

No. of animals in cage	Sex	No. of animals	Body wt., g	*RQ*	ml O_2/g h	kcal/$kg^{0.75}$ 24 h
2	M	3	29.1	0.86	6.66	325
	F	3	29.4	0.82	7.11	341
20	M	10	27.0 ± 1.1	1.00 ± 0.07	4.58 ± 0.74	224
	F	5	29.8 ± 2.4	0.91 ± 0.11	5.28 ± 1.73	261
60	M	5	28.5 ± 3.1	0.99 ± 0.06	5.34 ± 2.09	263
	F	5	27.8 ± 2.8	0.98 ± 0.04	4.65 ± 1.85	227
100	M	5	29.3 ± 2.5	0.95 ± 0.08	4.48 ± 0.99	227
	F	5	27.1 ± 3.6	0.99 ± 0.05	5.38 ± 0.85	262
150	M	5	26.3 ± 3.0	0.99 ± 0.06	5.20 ± 1.23	254
	F	5	30.7 ± 2.7	0.97 ± 0.09	4.72 ± 1.15	243

As the values of *RQ* for all the groups of mice examined were statistically identical, and differences in body weight slight, relations between the remaining indices of metabolism and group size are similar in character to those in the case of amount of oxygen consumed. The physiological metabolic rate of animals from populations consisting of 2 individuals is also about 40% higher than the values of this index calculated for animals coming from populations consisting of larger numbers of mice. The regression equation calculated here, omitting animals from this least numerous group, takes the following form for the above relation: $y = 235.8 + 0.081x$, while the coefficient of correlation is $r = 0.12$ and is not statistically significant.

VII. DISCUSSION

The results obtained on the energy balance of an experimental population of laboratory mice shows that the energy budget of a population is far more economical than that of individuals living singly. The considerable reduction in loss of energy expended in the metabolic processes of animals living in a population permits of considerable reduction in the amount of energy consumed together with food, while maintaining the same production value. Consequently the factual values of the two coefficients of production efficiency for the experimental population are more than 70% higher than the values for these coefficients calculated on the basis of indices determined for single mice.

The values of these coefficients given in literature, calculated for populations of wild mammals on the basis of laboratory studies of single individuals, are also far lower than those obtained in this study for the experimental population of laboratory mice (Fleharty & Choate, 1973). Golley (1968) calculated his own studies and those of other authors that the value of coefficient $K_2 = (P : A) \times 100$ for natural populations of several species of rodents fluctuated between 1.6% — 3.0%. Grodziński *et al.* (1966) found that the production of a population of rodents living in mountain pastures forms only 1.03% of the amount of energy assimilated by it. Grodziński (1971), who traced energy flow through a population of small mammals in a taiga forest in Alaska calculated that the coefficients of production efficiency K_2 of several species of rodents living there fluctuated from 1.5% to 2.2%. A relatively high value of 3.1% for this coefficient was obtained by Gębczyńska (1970) in her studies on a natural population of *Microtus oeconomus* Pallas, 1776, characterized by very high density.

On the basis of the results obtained in the present study it may be assumed that the above data may be under-estimated, and in reality the natural populations of a large number of small mammals are probably better energy convertors than would appear to be the case from theoretical calculations based on laboratory examination of single individuals.

Increasing the ratio of production to assimilation and consumption for the experimental study population of laboratory mice results in the average empirical value of coefficient $(P : R) \times 100$ of this population, *i.e.* 8.1%, also being far more favourable than that calculated on the basis of data for single animals (4.8%). As shown by calculations made by other authors on the basis of bioenergetical studies of single individuals, in wild populations of small mammals this ratio is also lower than for the experimental population of laboratory mice, *i.e.* the respiration value of these populations is far greater than the value of their production. At the same time the differences between populations of different species living under different ecological conditions are slight. The relation between production values for populations of different species of animals and their respiration, expressed in kcal/m^2/year, were investigated by Engelmann (1966), who found that there are differences between invertebrate and vertebrate animals. McNeill & Lawton (1970) after supplementing Englemann's data (1966) with numerous new facts calculated that this relation for warmblooded animals is characterized by the equation R equals 0.5539 $P^{-0.981}$. The above theoretical calculations were based on data obtained for animals removed from natural populations and examined singly after a certain preparatory period, that is, most likely after the cessation, or at least weakening of the effect of population organization elements on the level of their bioenergetic indices. Bobek's studies (1971) suggest that in a population of *C. glareolus* living in a deciduous forest of the temperate zone, productivity in relation to respiration expenditure, fluctuating from 2.3% to 2.9%, increases when population density decreases. The data given by Gębczyńska (1970) in relation to a population of *M. oeconomus*, on the other hand lead to the reverse conclusion.

The results presented in this study form evidence of the important influence exercised by the ecological organization of a population on the metabolic rate of the laboratory mice forming this population. It would seem that the two population elements examined, defining the prevailing numerical relations, that is, density and number of individuals, may be of considerable significance here. It was found that in all experiments in which population density and group size were simultaneously taken into account, the metabolic rate of adult mice increased with an increase in the number of animals per uniform area of cage bottom. This increase was also observed in population of one sex and in populations with a sex ratio of 1 : 1. In young animals, on the other hand, differences in metabolic rate take the opposite form, *i.e.* maximum oxygen consumption was observed when both population density and numbers of individuals were lowest.

The picture of these changes in young animals is in complete agreement with one of two types of curves illustrating changes in the different individual processes, due to the effect of population density, observed by Allee *et al.* (1949), in which maximum value of this index occurs when density is lowest.

Lowering of metabolic rate in young individuals together with a rise in population density is probably connected with deterioration in living conditions, which affects on the physiological development and condition of the animals. This is also shown by the considerable decrease in the viability of young mice in the most numerous populations (Adamczyk, in litt.). Conversely, in adult animals increase in the number of individuals forming a population may result, through intensification of individual contacts and increase in competition, intensification of the total activity of mice, and consequently increase in their metabolic rate. If the effect of these factors continues for any considerable time it may end by evoking a complex of stress phenomena.

The influence of group size on the amount of oxygen consumed by laboratory mice is probably dependent on population density, *i.e.* on the area of cage bottom per individual. When density was very great, that is, when there was 30 cm^2 of area per mouse, metabolic rate of the animals examined changed with changes in group size. On the other hand, when density was four times less no relation was observed between metabolic rate of individuals and group size. In both cases, however, animal occupying cages in pairs differed from the other groups. The metabolic rate of mice in pairs was 30% to 40% higher than that of animals from more numerous groups. This increase may probably have been caused by intensified activity due to the constant presence and mutual reactions of individuals of different sex and also the maintenance in them of the metabolic rate characteristic of dominants (Myrcha & Szwykowska, 1969), and the stress-creating influence of the cage being too small in size. Comparison of single-sex (males only) populations examined under the same conditions with male animals taken from populations of mixed sex but with the same density and group size, show that the metabolic rate of the latter is on an average more than 10% higher. The results, published in an earlier paper (Myrcha & Szwykowska, 1969), experiments on the influence of dominance structure on the amount of oxygen consumed by male laboratory mice showed that dominant individuals are characterized by more than 60% higher values of this index in comparison with subdominants and simultaneously by equal values of metabolism for individuals living singly.

It is interesting that in the experiment on which both density and group size were differentiated, the metabolic rate of the animals was lower than in the experiments in which only the number of individuals changed. A statistically uniform amount of oxygen consumption was found in the two experiments on animals from populations with group size of 220 individuals, that is, when the density of these populations was also uniform and was approximately 1 mouse/30 cm^2.

The results of these experiments do not, however, permit of concluding which of the two elements of population organization exerts a greater effect on the metabolic rate of mice, neither it is easy to form an opinion on this subject even from the considerable amount of physiological literature available. In the majority of experiments investigating the effect of density or group size on the course taken by many physiological processes in individuals forming laboratory populations of small mammals, the two elements varied simultaneously, since a different number of animals were usually placed in cages of the same size (Christian *et al.*, 1965; Ader, 1967). The majority of the indices examined by different authors, connected with intensivity of metabolism, varied in a similar way to variations in the amount of oxygen consumed by the adult laboratory mice examined in this study in experiments with differing density and group size. Bailey (1966), however, obtained a picture of variations in weight of the adrenals and spleen similar to the above, despite the fact that he kept a different number of male laboratory mice (from 1 to 32) in cages of different sizes, in which the density of the animals was the same.

The experimental population of laboratory mice examined in this study cannot form an accurate model suitable for application in bioenergetic ecological studies on wild populations of small mammals. It does, however, illustrate phenomena which probably do in fact take place in these populations. Laboratory populations are usually overcrowded in relation to the situation formed under natural conditions. In the case of certain species of rodents, however, it is possible to encounter density under natural conditions similar to that occurring in laboratory populations. In years of mass occurrence of *M. arvalis* the density of these animals in fields may even be as much as 10,000 individuals/ha (Bashenina, 1962). It is a well-known fact that this species occurs in colonies, and therefore the actual density in different colonies is probably far higher. The unpublished data given by Adamczewska-Andrzejewska show that even when population density of this species is low (not exceeding 1000 individuals/ha) in a single colony, occupying an area from 1 to several m^2, more than 20 animals may occur. On the other hand it would appear that in the case of laboratory animals it is possible to shift the normal population situations towards greater densities. It is thus likely that in natural populations of wild species these same phenomena may occur even when population densities are far lower.

Intensivity of the effect exerted by different elements of population organization (density, numbers, age and sex structure, social organization, tendency to form groups etc.) on the values of bioenergetic indices may differ in populations of different species, and may also change with the development of these populations. The ways in which these factors affect the level of bioenergetic indices may also differ, for instance social and sex structure of a group may effect the pattern of daily activity (Aschoff, 1957). It is on density, *inter alia*, that intensivity of contacts between individuals depends, which may in the end evoke a complex of physiological processes connected with stress (Chitty, 1960; Christian, 1961). In Shepeleva's studies (1971) the range of fluctuations in the metabolic rate of individuals from developing but still small experimental populations of several species of wild rodents reached as much as 50%, depending on the stage of development of the study population. Differences in the metabolic rate at different times of development of the population of laboratory mice examined in the study were even greater, since they exceeded 100%.

It may therefore be assumed that the energy budgets calculated in ecological studies for wild populations of mammals are burdened with a considerable degree of error, due to examination of single animals, on which the given pressure of population factors has ceased to act. The only manifestation of relations between individuals taken into account in these studies is the so-called group effect, that is, the effect on their metabolic rate exerted by concentration of animals in a group (Górecki, 1968; Gębczyński, 1969; Trojan & Wojciechowska, 1969; Gębczyńska & Gębczyński, 1971; Fedyk, 1971; Tertil, 1972). This phenomenon discovered by Hill (1913) and given this name by Grasse (1946), was at first treated by physiologists solely as one of the thermoregulation adaptations, consisting in appropriate reduction of the surface from which heat is given off in relation to increase in the total mass of the congregating animals. Later studies have, however, shown that this phenomenon is of a more complicated character. In the first place it was found that reduction in the ratio of surface to weight in the rats examined by Hill (1913) was lesser than the reduction in their metabolic rate (Slonim, 1961). Ponugaeva (1952, 1953, 1960) found that the group effect decreased at lower temperatures in *M. arvalis*, that group effect was far greater in animals living in colonies and herds and that this effect disappears during the reproduction period in the case of *Citellus pygmaeus* Pallas, 1779. These facts show that the group effect is not connected under all circumstances with the phenomenon of thermoregulation, but suggest that it is connected with population organization. The result of the experiment in which this author used heat rays to take the place of all other mice but one, kept in separate cages but able to see the other mice, was disappearance of the group effect, which shows quite clearly that in this case it was not connected with thermoregulation adaptations. In *Mesocricetus auratus*, Waterhouse, 1839 and *Hemiechinus auritus* Gmelin, 1770, and also in representatives of *Soricidae* there was even a distinct increase in the metabolic rate of animals living in a group (Ponugaeva, 1960; Gębczyński, 1971).

In bioenergetic ecological studies on small mammals the influence of the group effect on the value of the daily energy budget (*DEB*) is usually taken into account together with the influence of what is known as the nest effect, which is also considered as forming part of the complex of phenomena covered by the term »behavioural thermoregulation« (Trojan & Wojciechowska, 1969; Drożdż *et al.*, 1971; Gębczyńska & Gębczyński, 1971; Tertil, 1972). The above studies show that in the case of small groups of rodents, of 2—3 animals, group effect is generally of less significance than nest effect, particularly at higher ambient temperatures. The influence of the group effect on rodents' metabolism increases considerably in larger groups composed of 5—9 animals (Trojan & Wojciechowska, 1968; Fedyk, 1971).

It would seem that reduction in metabolic rate in representatives of certain species of rodents, observed under laboratory conditions in animals living in small groups for a certain time, may be connected with the formation in these groups of a given social structure. Drożdż *et al.* (1971) observed 16% greater decrease in the metabolic rate of individuals of *Arvicola terrestris* Linnaeus, 1758 living in groups composed of two females and one male, than in groups consisting of two males and one female. As already stated, the effect dominance structure has been shown to exert an important influence on the metabolic rate of males forming small experimental populations of laboratory mice (Myrcha & Szwykowska, 1969). Le Boulangé (1974), on the other hand, found far more intensive decrease in the metabolism of male laboratory mice than in females examined before and after being introduced into the experimental populations. It would therefore appear that the phenomenon termed group effect is far more closely connected with the action of population factors than with the adaptations included in the process of thermoregulation.

The facts presented in this paper form evidence of the necessity for taking into account the influence of a large number of population organization elements in bioenergetic studies on populations. In order to achieve this aim endeavour should be made to elaborate methods permitting of defining the parameters of the energy balance of different individuals directly in their natural habitat, that is, when subject to the pressure of the current population structure. The methods based on use of radioactive elements, and particularly the attempts being made at defining metabolic rate by means of telemetric methods, which are finding increasingly wide application in ecological research, hold out prospects of far more accurate estimation of these indexes. It would be very desirable to undertake studies of this type on a wide scale, on account of the exactitude and correctness of evaluation of the elements composing the energy balance of whole populations which probably utilize energy in a far more economical way than would appear it to be the case from the data obtained for representatives of these populations examined singly.

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Institute of Ecology,
Polish Academy of Sciences,
Dziekanów, 05-150 Łomianki, Poland.

Andrzej MYRCHA

BIOENERGETYKA EKSPERYMENTALNEJ POPULACJI I POJEDYNCZO BADANYCH MYSZY LABORATORYJNYCH

Streszczenie

Określono wartości wskaźników bioenergetycznych dla pojedynczo badanych myszy laboratoryjnych w wieku 1—11 miesięcy, w czasie rozwoju gniazdowego oraz podczas ciąży i laktacji. Mierzono wielkość konsumpcji pokarmu (*C*), jego asymilację (*A*), ilość wydalanego kału (*F*) i moczu (*U*) oraz ilość pobieranego przez zwierzęta tlenu i wydalanego CO_2. Wszystkie pomiary wykonywano w tym samym pomieszczeniu laboratoryjnym i w takiej samej temperaturze otoczenia 22°C—23°C.

Powyższe elementy pełnego bilansu energetycznego, łącznie z wartością produkcji (P), mierzono również w odstępach tygodniowych dla całej, swobodnie rozwijającej się w ciągu 7 miesięcy populacji myszy, żyjącej w dużej klatce metabolicznej (Fig. 1). W oparciu o pomiary przeprowadzone na pojedynczych zwierzętach wyliczono różniczkowy i skumulowany bilans energetyczny tej populacji i porównano je z analogicznymi bilansami otrzymanymi na drodze empirycznej. Wykonano również szereg eksperymentów mających na celu próbę prześledzenia wpływu zagęszczenia i liczebności eksperymentalnych populacji myszy laboratoryjnych na poziom ich metabolizmu. Stwierdzono, że:

1. Wartość konsumpcji i asymilacji pokarmu zmienia się wraz z wiekiem myszy laboratoryjnych, przy czym zmiany te spowodowane są przede wszystkim różnicami w ciężarze ciała zwierząt (Tabela 1).

2. Tempo metabolizmu w rozwoju gniazdowym myszy laboratoryjnych ulega znacznym zmianom. W procesie tym można wyróżnić dwa okresy trwające od 1 do 11 dnia i po 11 dniu ich życia (Tabela 1, Fig. 2). Zmiany te związane są przede wszystkim z wiekiem, a w mniejszym stopniu z różnicami w ciężarze ciała zwierząt.

3. Tempo metabolizmu dojrzałych myszy zależy przede wszystkim od ich ciężaru ciała i jest najwyższe u zwierząt jednomiesięcznych, a obniża się u osobników starszych (Tabela 3). Podczas ciąży wskaźniki metabolizmu przeliczone na jednostkę ciężaru ciała maleją do poziomu 50% wartości charakterystycznych dla samic nie rozradzających się, a w okresie laktacji niezwykle intensywnie rosną (Tabela 4, Fig. 3). Średnio w całym okresie ciąży tempo metabolizmu przeliczone na jednostkę ciężaru ciała ma wartość około 91%, a w okresie laktacji około 121% poziomu metabolizmu samic nieaktywnych płciowo.

4. Okres rozwoju gniazdowego myszy charakteryzuje się dużą wydajnością procesu produkcji tkanek ciała. Skumulowana wartość współczynnika K_2 za cały 26-dniowy okres pobytu zwierząt w gnieździe wynosi około 12,2% (Fig. 4). W okresie tym każde zwierzę asymiluje przeciętnie 117,2 kcal energii, z czego w procesie produkcji wykorzystuje 14,3 kcal, a 102,9 kcal ulega rozproszeniu w procesach metabolicznych.

5. W poszczególnych momentach rozwoju eksperymentalnej, swobodnie rozwijającej się populacji myszy laboratoryjnych wartości konsumpcji i asymilacji pokarmu zmieniały się dość intensywnie, lecz zawsze były znacznie niższe od danych otrzymanych dla pojedynczo badanych zwierząt (Tabela 1 i Tabela 5).

6. Wyliczone na podstawie wyników otrzymanych dla pojedynczo badanych zwierząt wartości elementów różniczkowego bilansu energetycznego całej eksperymentalnej populacji są przeciętnie o około 75%, a wartości elementów skumulowanego bilansu energetycznego o ponad 90% wyższe od stwierdzonych empirycznie (Tabela 5 i Tabela 7, Fig. 9 i Fig. 10).

7. Wartości wskaźników charakteryzujących tempo metabolizmu całej eksperymentalnej populacji zmieniają się w czasie rozwoju jej populacji, lecz zawsze są niższe w porównaniu z danymi otrzymanymi dla pojedynczo badanych myszy (Tabela 3 i Tabela 6). Wyliczone w oparciu o pomiary jednostkowe wartości poziomu metabolizmu badanej populacji przewyższają dane empiryczne średnio o około 133% (Fig. 12).

8. Tempo metabolizmu populacji jednopłciowych, złożonych wyłącznie z samców myszy laboratoryjnych, rośnie wraz ze wzrostem zagęszczenia i wielkości grupy (Tabela 8). Populacje złożone z 20 i 40 myszy charakteryzują się poziomem metabolizmu wyższym o około 25% w porównaniu z populacjami złożonymi z 5 zwierząt.

9. W populacjach obupłciowych, o zagęszczeniu i wielkości grupy zróżnicowanych od 2 do 220 zwierząt w klatce, tempo metabolizmu myszy 4—5 tygodniowych zmniej-

sza się wraz ze wzrostem obu tych elementów organizacji populacji o ponad 15% (Tabela 9, Fig. 13). Poziom metabolizmu dorosłych *M. musculus* badanych w tym eksperymencie zwiększa się natomiast wraz ze wzrostem zagęszczenia i ilości zwierząt o około 12%, przy czym wzrost ten jest najintensywniejszy w gradiencie wielkości grupy od 10 do 40 myszy w klatce.

10. Wpływ wielkości grupy na ilość pobieranego przez myszy laboratoryjne tlenu jest prawdopodobnie uzależniony od zagęszczenia populacji, tzn. od wielkości powierzchni dna klatki przypadającej na jednego osobnika. W wypadku, gdy zagęszczenie populacji było bardzo duże (na jednego osobnika przypadała powierzchnia 30 cm^2) poziom metabolizmu badanych zwierząt zmieniał się z wielkością grupy (Tabela 10). Przy czterokrotnie mniejszym zagęszczeniu nie zaobserwowano natomiast żadnej zależności między tempem metabolizmu osobników a wielkością grupy (Tabela 11).

11. Wyniki wszystkich eksperymentów świadczą o tym, że gospodarka energetyczna populacji jest znacznie bardziej ekonomiczna w porównaniu z pojedynczo żyjącymi osobnikami. Znaczne zmniejszenie strat energii wydatkowanej w procesach metabolicznych zwierząt żyjących w populacji pozwala, przy zachowaniu tej samej wartości produkcji, na poważne zmniejszenie ilości energii pobieranej wraz z pokarmem.