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

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Bioenergetics of Growth in Common Voles

[With 7 Tables & 3 Figs.]

Food consumption and utilization, as well as growth of voles and their respiration were investigated in the animals aged 20 to 50 days. In the control group of animals kept in indentical conditions between 20 and 70 days of life the gross body composition and body caloric value were determined. The voles increased their weight in the experimental period by 6.8 g, but the growth rate (*Y*) slowed down with age (*X*) according to the formula: $X=2.47\ X^{0.51}$. Food intake increased in the experimental period from 10 to 14 kcal per animal/day. The digestibility of food amounted to 92.4% and metabolizable energy (*ME*) to 88.4%. The intake of *ME* in kcal/animal day was equal to: $6.88+ +0.126\,X$ (where X=animal's age in days). The average daily metabolic rate (*ADMR*) of the litters kept in groups in respiratory chambers amounted to: *ADMR* (kcal/animal day)$=1.52\ W^{0.63}$ (where W=body weight in grams). The content of water in the body of voles decreased in the studied period from ca 68 to 60%, and protein content from 51 to 40% of dry weight. The percentage of mineral substances also slightly decreased, while the relative fat content considerably increased from 34.8 to 51.3%. The caloric value of body gain was gradually reduced from 5.7 at the age of 20 days to 5.0 kcal/10 days at the age of 50 days. In the whole experimental period (30 days) one vole consumed on the average 339 kcal *ME*, of which 16.1 kcal was deposited in the body. Hence the total efficiency of growth amounted to 4.74%.

I. INTRODUCTION

The problem of growth rate of animals in the period of postnatal development has focused the attention of investigators since a long time. In this period there occur rapid physiological and morphological changes in the animal organism. From the moment of birth until physiological maturity the growth rate is very fast and the most efficient from the bioenergetic point of view. Hence this period is of considerable importance for the economy of animal production and is interesting for both practical stock-breeders and experimental biologists (Brody, 1945; Blaxter, 1962; Maynard & Loosli, 1962).

The ecologists studying the bioenergetics of ecosystems and energy flow through the populations are also interested in the rate and efficiency of transformation of the energy taken up from the ecosystem by the animals and deposited in their tissues (Davis & Golley, 1963; Phillipson, 1966; Petrusewicz & Mcfadyen, 1970).

The present study was aimed at the investigation of changes in physiological processes occurring during the postnatal development of voles. By means of complex nutritional and respirometric experiments, and by determination of the retention of particular body constituents it was attempted to investigate the processes of bioenergetics of growth and to determine their efficiency, or the ratio of production to consumption and assimilation.

II. MATERIAL AND METHODS

The experiments were carried out on common voles, *Microtus arvalis* (Pallas, 1779), in the age of 20 to 70 days. For the investigations there were used litters consisting of four to five individuals only. The voles aged 20 days were separated from their parents, kept together and fed *ad libitum* with oats, carrot and beets. In the breeding room and during all experiments the temperature of $20 \pm 0.5°C$ and 12 hours daily rhythm of light were preserved.

Two types of experiments were carried out. In the first type the carcasses of animals in the age of 20, 30, 50, 60 and 70 days of life were subjected to chemical analysis for the determination of water, ash, fat and protein content, as well as caloric value. The whole carcasses were dried in a vacuum oven at 60°C to a constant weight in order to calculate water content. The amount of fat was determined by means of ether extraction. The total nitrogen was measured with the micro-Kjeldahl technique, employing the factor of 6.25 to calculate the amount of protein. To determine ash the dried bodies were combusted in a muffle oven at 600°C (cf. Sawicka-Kapusta, 1968; 1970). The caloric value of the vole body was estimated in an adiabatic bomb calorimeter (Górecki, 1965). Altogether 105 individuals were used for the analyses. In each age class the body composition was determined in 17 to 18 individuals.

In the second series of experiments the daily consumption of food, its utilization, as well as the growth of animals and their respiration were studied in a group of voles aged 20 to 50 days. Every 5 days the whole litter was weighed. The average daily metabolism rate (*ADMR*) was measured in the same animals in the age of 20, 30, 40 and 50 days. The respirometric measurements were carried out in 9 litre metabolic chambers similar in size to the cages in which the animals were reared. *ADMR* was measured at 20°C in a Morrison respirometer (Morrison & Grodziński, 1968).

Metabolizable energy (*ME*=assimilation) was determined in metabolic cages (Drożdż, 1968a) in voles being in the same age as those used for respirometric measurements. The experiments were carried out on the total 35 animals. The caloric value of food, feaces and urine were determined in a calorimetric bomb. For the estimation of consumption and respiration jointly 79 animals were used.

For the comparison of the obtained results t-test and coefficient of correlation were employed. In order to illustrate a relationship between the studied parameters the linear and logarithmic regressions were calculated.

III. RESULTS

1. Growth

The body weight of examined voles increased by 6.84 g on the average between 20 and 50 days of life. The relationship between age (X) and body weight (Y) of voles can be described by the regression equation: $Y = 2.476\ X^{0.511}$. Some of the animals increased their weight at a slower rate and hence regression equations were calculated separately for the

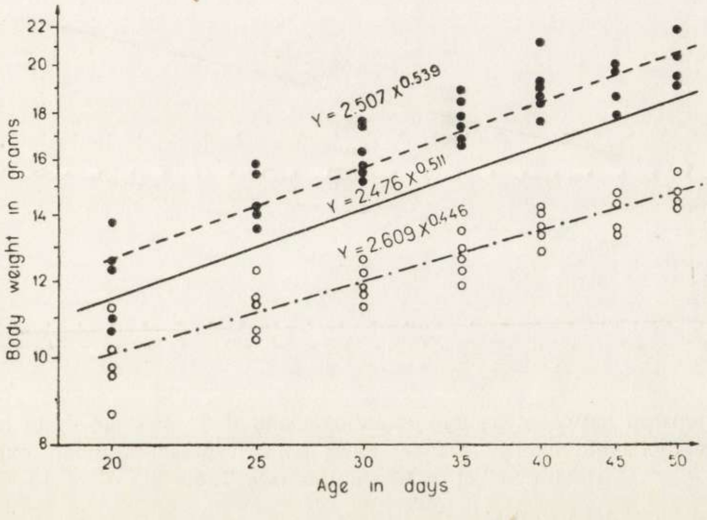

Fig. 1. Growth of voles in the period from 20 to 50 days of life. Solid line represents all animals, open circles represent »smaller animals«, solid circles represent »bigger« animals.

two groups. The difference between the body weight of larger and smaller animals increases with age: in 20 day of life this difference is around 2 g and in 50 day — approximately 6 g. This is also clearly visible when comparing regression coefficients (Fig. 1).

Taking into account 10 day periods the mean increase in weight was the highest between 20 and 30 days of life and equal to 2.65 g, while between 30 and 40 days it was reduced to 2.23 g and in the last decade to 1.97 g.

2. Food Consumption and Utilization

Twenty days old voles consumed daily on the average 1.95 g of oats and approximately 3 g of fresh carrot and beets, which correspond to approximately 10 kcal. During growth the food intake increased reaching at the age of 50 days 2.15 g of oats and 10.3 g of carrot and beets on the average, that is approximately 14 kcal per day (Fig. 2). A small reduction of food intake (by ca 8%) was observed around 42 day of life, this fact being probably related to the sexual maturation of voles.

From the experiments on the digestibility and food utilization it arises that the coefficient of digestibility did not change significantly in the period of vole growth. The losses of energy with feaces amounted on the average to 7.6% of gross energy, and the corresponding figure

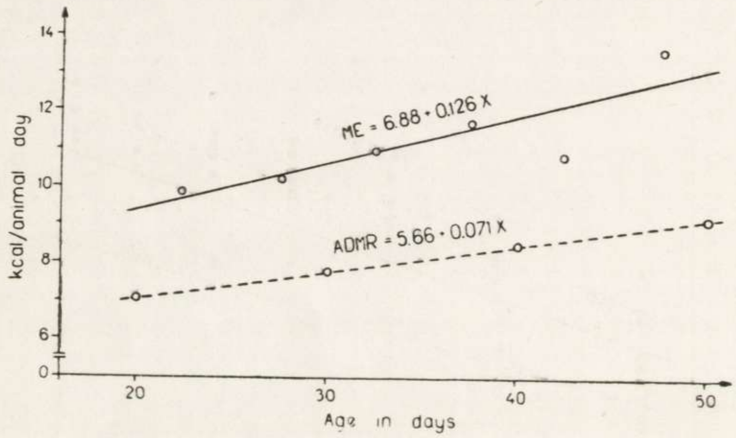

Fig. 2. Relationship between the age of animals and their average daily metabolism rate and metabolizable energy intake. Each point represents mean experimental data for 26 to 44 animals (see Table 2).

for urine was 4% (Table 1). The metabolizable energy (*ME*) of food amounted thus to 88.4%. The relationship between the age of animals (*X*) and *ME* (*Y*) is presented in Fig. 2. Experimental values of *ME* are plotted on the regression line described by the equation: $Y = 6.88 + 0.126\,X$.

3. Daily Costs of Maintenance

The average daily metabolism rate (*ADMR*) determined for the whole litters and computed for the unit of body weight decreased with age from 5.37 (20 days) to 4.48 ccm O_2/g h (at 50 days) (cf. Table 2). Its dependence on the body weight is expressed by the equation: *ADMR* (ccm O_2/g h) = 13.2 $W^{-0.37}$. When this value is calculated for one day and for calories (assuming $RQ = 0.8$), the following relationship is obtained: *ADMR* (kcal/animal day) = 1.52 $W^{0.63}$. Experimentally determined values range from 7.06 to 9.20 kcal/animal day (Table 2).

The relationship between *ADMR* and age of animals was calculated using the linear regression: *ADMR* (kcal/animal day) = $5.66 + 0.071\,X$ (Fig. 2). However, this relationship is different for the animals growing faster ($6.11 + 0.071\,X$) and for those growing at a slower rate ($5.16 + 0.060\,X$).

Table 1

Caloric value of food, faeces und urine. Coefficient of food utilization.

Item	Dry weight, %	Caloric value per g dry wt.	Per cent of gross energy
Food			
Oats	94.25	4.660	
Carrot	14.25	3.987	100.0
Beet	14.08	3.967	
Faeces	—	4.840	7.6
Urine	—	0.101 *	4.0
Metabolizable energy	—	—	88.4

* Caloric value of 1 g liquid.

Table 2

Average daily metabolism rate in voles during growth.

Age, days	Body wt., g	No. of animals	No. of litters	ccm O_2/g h mean ± S.E.	kcal/g day	kcal/animal day	kcal/$kg^{0.75}$ day
20	11.4	43	9	5.37 ± 0.08	0.619	7.06	208.2
30	14.4	44	9	4.64 ± 0.06	0.534	7.83	191.0
40	15.3	31	7	4.66 ± 0.05	0.537	8.50	197.7
50	17.4	26	6	4.48 ± 0.06	0.516	9.20	195.7

Oxygen consumption expressed in kcal for metabolic unit of body weight — $kg^{0.75}$ (K l e i b e r, 1961) is rather similar for all animals independently of age (Table 2) and amounts on the average to 198 kcal/$kg^{0.75}$ day.

4. Gross Body Composition

Between 20 and 70 days of life the body weight of voles is almost doubled and increases from 12.5 to 24.2 g. The coefficient of variation (*C.V.*) in all age classes is rather high and amounts to 18.3%.

The proportion of body constituents in the increase of body weight is not uniform (Fig. 3). The amount of water rises considerably, from 8.5 to 14.4 g, *i.e.* by 85%. The amount of fat increases only from 1.4 to 5.0 g, but in relative figures this corresponds to as much as 357%. The retention of proteins is much smaller, from 2.0 to 3.9 g, and mineral components increase only from 0.4 to 0.7 g.

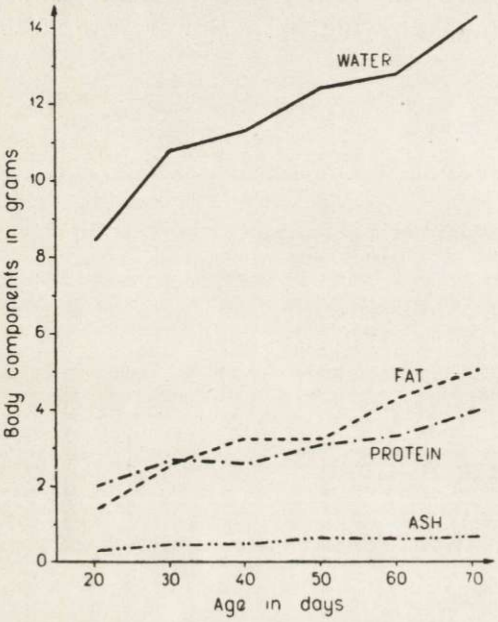

Fig. 3. Changes in the vole body composition during growth expressed in grams of biomass.

Table 3

Correlation between body weight and body composition of voles.

Relation between	Equation	Correlation coefficient *r*
Body weight/water	$y=116.2\,x^{-0.215}$	−0.87
Body weight/fat	$y=8.46\,x^{0.558}$	+0.96
Body weight/protein	$y=90.7\,x^{-0.274}$	−0.78
Body weight/ash	$y=35.3\,x^{-0.499}$	−0.74

The relative body composition of voles, in per cent of dry mass, is correlated with their body weight (Table 3).

The amount of water in the body of voles decreases from 68% in 20 day of life to 60% in 40 day, and later it oscillates around the latter value (Table 4). Similarly, the protein content decreases with age (cf. Table 4), and after 40 days of life it shows a trend of stabilization around 38%. The mean variability (*C.V.*) in the amount of protein within one age class amounts to 17%. On the other hand, the amount of fat increases with age from 35 to 51% showing a small variability ($C.V. = 12.7\%$). The ash content in the tissues of voles after 40 days of life amounts on the average to 7.6% ($C.V. = 19.7\%$).

The energetic values of the dry weight of vole tissues vary within a rather narrow range of 6.26 to 6.77 kcal/g. The changes of this value are independent of age (Table 5) although for the two studied groups are slightly higher and in the remaining four almost identical. The

Table 4

Body composition of voles during growth in per cent of dry weight (mean ± SE).

Body composition	Age in days					
	20	30	40	50	60	70
Biomass g	12.5 ± 0.32	17.2 ± 0.61	19.0 ± 0.88	20.3 ± 0.77	22.1 ± 1.58	24.2 ± 0.87
Water %	68.1 ±0.60	63.1 ± 0.90	60.0 ± 0.99	61.7 ± 0.64	58.8 ± 1.29	59.6 ± 0.42
Fat %	34.8 ± 3.55	42.3 ± 3.36	43.8 ± 1.89	43.0 ± 2.44	47.8 ± 3.89	51.3 ± 1.80
Protein %	51.4 ± 2.31	43.1 ± 1.89	34.4 ± 3.55	38.9 ± 4.75	37.1 ± 2.45	40.3 ± 5.90
Ash %	9.3 ± 0.33	9.1 ± 0.58	7.0 ± 0.43	8.5 ± 0.65	7.3 ± 0.81	7.7 ± 0.60

Table 5

Changes in the vole body composition expressed in grams dry weight calculated from regression equations, and caloric values of vole tissues.

Body constituent in g	Age in days					
	20 *	30	40	50	60	70
Body wt.	11.44	14.08	16.31	18.28	20.07	21.70
Dry wt.	3.73	5.08	6.38	6.98	8.44	9.00
Protein	1.69	2.11	2.58	2.77	3.27	3.40
Fat	1.29	2.10	2.79	3.17	4.01	4.50
Ash	0.37	0.43	0.52	0.55	0.63	0.66
kcal/g dry wt.	6.30	6.29	6.77	6.30	6.69	6.26
kcal/g biomass	2.05	2.26	2.65	2.41	2.81	2.59
kcal/animal	23.5	31.9	43.2	44.0	56.5	56.3

* From Sawicka-Kapusta, 1970.

mean value for the vole in the age between 20 and 70 days of life amounts to 6.50 ± 0.14 kcal/g, and for the ash-free dry weight to 7.15 ± 0.23 kcal/g. The caloric value of biomass increases with age (Table 5). The lowest values were recorded in the two youngest groups of animals, and significantly higher in older groups. The caloric value of the whole animal shows the highest changes, as a function of increasing body weight. But at the same time the caloric value of tissues increases and hence the energy content in the animal body rises by more than 2 times, although the change of body weight did not reach this value.

Since as a rule the amount of fat in the organism varies considerably, and often due to incidental causes, the relative proportion of the remaining body constituents was also calculated in the fat-free biomass (Table 6). This allowed to demonstrate that the relative content of water in the fat-free tissues of voles shows only small variations depending on the age of animals. The highest water content was found in voles aged 20 days, and then it decreases slightly and remains on the level of ca 73% (water content in the fat-free biomass of 70 day old voles is based only on the analysis of 7 individuals). Also the content of proteins shows certain changes almost independent of age. Ash belongs to the most stable constituents and its percentage ranges from 3.3 to 4.0% (Table 6).

Table 6

Composition of vole fat-free fresh weight. The content of water, protein and ash expressed in per cent of fat-free body weight.

Body constituent	Age in days					
	20	30	40	50	60	70
Fat-free biomass, g	11.1	14.5	15.7	17.0	17.7	19.0
Water %	76.6	74.8	72.6	73.6	73.4	75.9
Protein %	18.4	18.9	16.6	17.8	19.1	20.7
Ash %	3.3	4.0	3.4	3.9	3.7	3.9
Ratio protein/water	0.24	0.25	0.23	0.24	0.26	0.27

The relationship between protein and water contents in the fat-free body (index of physiological age — Bailey *et al.*, 1960) increases slightly during the growth of animals: from 0.24 in 20 day old voles to 0.27 in 70 day old, but it shows a rather high variability in particular age classes (Table 6).

IV. DISCUSSION

In the studies on the energy balance of wild rodents the methods used by the nutritionists cannot be employed. The so-called »costs of maintenance« described by them as basal metabolic rate (*BMR*) in standard conditions (Blaxter, 1966) is not acceptable in studies of wild animals. Neither *BMR* nor resting metabolism rate (*RMR*) give the possibility of estimation of the costs of maintenance in wild growing animals. Farm animals, used predominantly by the nutritionists, behave similarly both during rearing and in experimental conditions (Brody, 1945). Hence without a gross error a correction for the activity can be added to the calculated, or less often to directly measured, costs of maintenance during starvation (*BMR*). Also the correction for thermoregulation is not so important for the animals kept in constant conditions (Corbett *et al.*, 1961; Coop & Hill, 1962). The situation is entirely different with wild rodents in which normal activity is high and the reaction to changes of ambient temperature is even higher (Saint Girons, 1966; Górecki, 1968). The only possibility to avoid these difficulties and errors depends on determining *ADMR* as a measure of daily costs of maintenance (Grodziński & Górecki, 1968). It was assumed that the estimation of *ADMR* would provide an answer to the problem of costs of maintenance of the animal which stays in possibly natural conditions (in comparison with other methods of determination of metabolism). In this method the animals stay in a group in the nest temperature with a free access to food and water and possibility of locomotoric activity (Morrison & Grodziński, 1968). It appears, however, that the costs of maintenance measured in such way are slightly lower than those calculated from the difference between consumed *ME* and production (*P*). After the experiment (*i.e.* after staying for 24 hours in the respiratory chamber) the animals either maintained their body weight or even showed a slight loss of weight. Despite the fact that the experimentally determined values of *ADMR* fit very well to the calculated regression line (Fig. 2), they are too low since they do not contain energetic growth costs of animals during one day measurements. For the recalculation of oxygen consumption into calories we assumed the coefficient $RQ=0.8$, as often used in the ecological literature (Pearson, 1947; Gębczyński, 1966; Grodziński & Górecki, 1968). However, in the animals in which processes of catabolism prevail, as it occurred during our determinations of *ADMR*, such assumption may also cause a small error leading to the reduction of costs of maintenance. A similar phenomenon of underestimation of costs of maintenance in guinea pigs kept in respiratory chambers was also observed by Vercoe (1965); he explained this fact as a behavioural reaction of the animal to respiratory chamber. Thus it appears that for the intensively growing animals one day measurement is too short and underestimates the costs of maintenance.

The determination of body composition were carried out up to 70 days of life, and those of consumption and respiration to 50 days. In the first case it was intended to reach the so-called chemical maturity (Bailey *et al.*, 1960), *i.e.* a stable gross body composition. Such maturity was reached by voles only by the end of the studied period, *i.e.* around 50 days of life. In the second case it was attempted to study voles in the period of their most intensive growth. The growth rate and retention of particular body constituents in the studied period are lower than below 20 day of life (Sawicka-Kapusta, 1970), but the voles begin to feed individually only around 18 day of life, and this fact limited the start of feeding experiments. The rate of fat retention was very high, even higher than in natural environment, although it is known that in favourable conditions the voles accumulate fat intensively.

The body composition of voles in individual age classes calculated from regression equations is shown in Table 6. It enables to follow the changes in the body composition and caloric value of voles at different age.

Table 7

Relationships between consumption, assimilation, respiration and production in growing voles.

Item	Age in days						
	20		30		40		50
Body weight in g	11.44		14.08		16.31		18.28
Body gain in g/10 days		2.64		2.23		1.97	
Body gain in kcal/10 days (*P*)		5.68		5.46		4.98	
Consumption in kcal/10 days (*C*)		113.5		127.8		142.1	
Metabolizable energy in kcal/10 days (Assimilation — *A*)		100.4		113.0		125.7	
Assimilation per 1 kcal of deposition		17.6		20.7		25.3	
Assimilation per 1 g of deposition		38.0		50.7		63.8	
ADMR in kcal (10 days *R*)		74.3		81.4		88.6	
P/C		5.0		4.3		3.5	
P/A		5.6		4.8		3.9	
P/R		7.6		6.7		5.6	

The caloric value of growth decreases from ca 5.7 kcal in the first 10 days of life to 5.0 kcal in the last one (Table 7). The percentage of deposited metabolizable energy also decreases with age, or in other words the process of deposition costs more in later periods. The utilization of *ME* for 1 kcal deposited increases from 17.6 to 25.3 kcal in the period of 20—50 days of life, similarly as the amount of *ME* for 1 g of deposited tissues. The efficiency of consumption, or the ratio of production (*P*) to the total consumption, decreases in the consecutive decades from 5.0 to 3.5% (Table 7). It depends on the type of consumed food and on the degree of its utilization. In the studied case the consumed food is very similar to natural food consumed by voles in autumn. In the remaining season this efficiency is even lower (D r o ż d ż, 1968b), because bulky foods dominate in the natural diet of voles.

The ratio of production to assimilation (*P/A*) is always higher than the ratio of production to consumption by the coefficient of food utilization (Table 7) (in this study the coefficient of assimilation amounted to 88.4% — Table 1).

In the period from 20 to 50 days one vole consumed on the average 339.1 kcal of *ME*, and of this 16.1 kcal was deposited (Table 7). Hence the total efficiency of the production amounts to 4.74%. Despite the fact that the voles were examined in the period of very intensive growth their total efficiency of biomass production is several times lower than that obtained in the breeding of farm animals (M a y n a r d & L o o s l i, 1962; K l e i b e r, 1961; B r o d y, 1945).

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BIOENERGETYKA WZROSTU POLNIKA ZWYCZAJNEGO

Streszczenie

U polników w wieku 20—50 dni badano konsumpcję pokarmu, jego wykorzyrzystanie, wzrost zwierząt i ich respirację — średni metabolizm dobowy (*ADMR*). U drugiej, kontrolnej grupy zwierząt trzymanych w identycznych warunkach od 20 do 70 dni życia badano skład ciała (woda, popiół, tłuszcz, białko i wartość kaloryczna tkanek). Wszystkie eksperymenty prowadzono w temperaturze 20°C i przy 12-godzinnym rytmie oświetlenia, trzymając zwierzęta całymi miotami (4—5 zwierząt) i karmiąc je owsem, marchwią i burakami *ad libitum*.

Polniki wzrosły w okresie doświadczenia o 6,84 g, szybkość wzrostu malała z wiekiem. Zależność między wiekiem zwierząt (X), a ich ciężarem ciała (Y) wynosi: $Y=2{,}47\ X^{0.511}$ (Fig. 1).

Pobranie pokarmu wzrosło w badanym okresie od 10 do 14 kcal/polnika w ciągu doby. Strawność paszy wynosiła 92,4%, a energia przemienna (*ME*) 88,4% (Tabela 1). Pobranie *ME* wynosiło w ciągu dnia na jednego polnika: ME (kcal)$=6{,}88+0{,}126\ X$ (X — wiek zwierzęcia w dniach, Fig. 2).

ADMR miotów trzymanych razem w komorach metabolicznych przy $RQ=0{,}82$, wyniósł: *ADMR* (kcal/zwierzę doba)$=1{,}52\ W^{0{,}63}$ (*W* — ciężar ciała w g) (Fig. 2, Tabela 2).

W badanym czasie wzrostu zawartość wody w ciele polników maleje od około 68 do 60%, podobnie jak zawartość białka, która maleje od około 51 do 40% suchej masy. Nieznacznie zmniejsza się też procent substancji mineralnych. Wyraźnie wzrasta procentowa zawartość tłuszczu (od 34,8 do 51,3%, Tabela 4), w związku z tym wartość kaloryczna biomasy jest dość wysoka od 2,0 do 2,8 kcal/g (Tabela 5). Wartość kaloryczna przyrostu maleje od 5,7 w wieku 20 dni, do 5,0 kcal/10 dni u średniego zwierzęcia w wieku 50 dni (Tabela 7).

Ilość *ME* na 1 kcal zdeponowaną wzrasta z wiekiem zwierząt od 17,6 do 25,3 kcal, także ilość pobranej *ME* na 1 g zdeponowanych tkanek ciała wzrasta w tym okresie od 38,0 do 63,8 kcal (Tabela 7).

W całym okresie doświadczenia (30 dni) jeden polnik pobrał średnio 339,1 kcal energii przemiennej, z czego zdeponował tylko 16,1 kcal w postaci tkanek ciała, całkowita wydajność procesu wzrostu wynosi więc 4,74%.