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

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Katarzyna SAWICKA-KAPUSTA

Changes in the Gross Body Composition and Energy Value of the Bank Voles during their Postnatal Development*

[With 9 Tables & 11 Figs.]

Changes in the gross body composition of the bank vole during postnatal development were investigated. The voles were divided into three groups (laboratory, out-door pen, terrain) depending on the environment in which they lived. The content of water, protein, fat and ash, as well as caloric values, were determined in the first two groups in the age from 1 to 70 days, and in the terrain group from 1 to 15 months. The mean body weight of voles reared in the laboratory and out-door pen increased in the studied period from approximately 2 to 18 g. The amount of water, protein, fat and ash in the first two groups was highly correlated with body weight. With the progressing age of voles reared in laboratory or out-door pen the water content decreased from ca 84 to 61%, and protein content from 60 to 40%, while fat content increased from 24 to 49%. The composition of fat-free biomass remained almost identical. In free-living voles the concentration of fat in the dry mass was very low and ranged from 10.4 to 14.0%. The content of protein and water decreased with age in a similar range. In the voles living in terrain the winter depression of body weight in the period from September till February was distinctly marked. This depression was caused by quantitative changes of all examined body constituents. The voles reared in laboratory and in out-door pen are very similar in respect of their body composition despite different conditions of life, while both groups differ significantly from free-living animals.

I. INTRODUCTION

Investigation of changes of principal body constituents in the animals during their postnatal development represents one link in the chain of studies on the biological productivity of animal. The period

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of postnatal development corresponds to intensive growth or prompt accumulation of the net production. The latter constitutes one of the elements in the process of energy flow, and corresponds to this part of assimilated energy which is incorporated into body tissues (Petrusewicz & Macfadyen, 1970). The net production in a population appears in effect of reproduction and growth of individuals. Hence the increase in body weight and chemical composition of this increase are principal factors for the production estimation. On the other hand, apart from numbers the production is the basic value for the whole balance of energy flow. In the investigations of the feeding chain important is not only the value of net production expressed in energy (kcal), but also its composition (water, protein, fat and mineral components), especially to the consumers at higher trophic levels.

The bank vole, *Clethrionomys glareolus* (Schreber, 1780) was selected for the investigations, since this species dominates in the forest ecosystems of Europe, and is the subject of broad ecological studies. Especially the productivity and regulatory mechanisms in the vole populations were investigated (Petrusewicz *et al.*, 1968; Bujalska & Gliwicz, 1968; Bobek, 1969). Several bioenergetic parameters, such as metabolism and thermoregulation of bank voles were measured (Grodziński, 1961; Grodziński & Górecki, 1967; Górecki, 1968), as well as digestibility and assimilation of natural foods (Drożdż, 1968). The obtained data permitted for constructing the energy budget of the bank vole and estimating the energy flow through its population (Grodziński *et al.*, 1970).

The present study was aimed at the investigation of bioenergetics of individual development and finding out differences in the process of formation of net production in bank voles living in different environmental conditions: in laboratory cages, in the out-door pen and in terrain. It was also attempted to ascertain in what degree the data on the body composition of voles obtained in the laboratory are valid for free-living animals.

II. MATERIAL AND METHODS

The changes in gross body constituents (*GBC*) were analysed in *C. glareolus* during its postnatal development. The voles were divided into three experimental groups: (1) reared in the laboratory, (2) living in seminatural conditions in out-door pen, and (3) animals from natural habitats. The animals of the first two groups were captured in the Niepołomicka Forest (50°07'N, 20°23'E) in autumn 1969 into live traps. The voles of the first group were kept in laboratory conditions at 12-hr light rhythm and at 20°C, and were fed *ad libitum* with wheat and oats, tree-seeds (oak, ash, small-leaved lime), vegetables (carrot, beets) and milk.

The second group was reared in an out-door pen, 15 m^2 in area, with two walls made of net. Ten Howard houses (Howard, 1949) were dug in there and in November 1969 twenty adult bank voles (10 ♂♂ and 10 ♀♀) were placed. The animals were supplied with food in excess, identical as in the laboratory group, and with water. In summer the pen was sowed with a mixture of grass, and in winter covered with a thick layer of dry leaves. The date of birth of every litter was noted and the animals in a definite age were taken out of the nests, 15-day-old voles being labelled in order to catch them in a definite age. In late autumn and winter the number of animals was around 20 individuals, but in summer their density amounted in some periods up to 50 animals. The period of reproduction in the pen lasted from the middle April until the end of August.

The voles of the terrain group were caught into snap traps using the »Standard Minimum« method (Grodziński, Pucek & Ryszkowski, 1966). Some trappings were also carried out on a trap line. The whole material of the terrain group was collected from September 1970 till July 1971. In the period from September till December the animals were trapped every month, later — every second month. The youngest animals obtained during trappings were one month old. The age of voles was estimated with the accuracy up to one month by measuring the length of M_1 roots with micrometric calipers (Pucek & Zejda, 1968; Lowe, 1971). For estimating the age until third month of life of voles the shape of the tooth was taken into consideration (Mazák, 1963). The changes in body composition of this group of voles were analysed in age classes and in the year cycle.

The laboratory animals were divided into 7 age classes (1, 3, 6, 10, 20, 30 and 50—70 days), and those reared in the pen into 6 age classes without 30-day-old voles. The free-living animals were separated into 9 age classes (1, 2, 3, 4, 5, 6—7, 8—9, 10, 11—15 months) (Tables 2, 4 and 5). In each class the body weight was determined in 9 to 20 individuals. In the animals reared in the laboratory and out-door pen only those litters were used which included 4 to 5 newborn. The content of water, fat, protein and ash was determined in each vole. Immediately after killing the animals were weighed, their abdomen opened and the content of excised stomach was washed out, then dried on blotting paper. The carcasse were dried at 60°C in a vacuum oven to a constant weight. The dried tissues were minced in a homogenizer with rotating blades, then additionally ground in a porcelain mortar in order to obtain uniform material. The water content was calculated from the difference between fresh and dry body weight.

Fat was estimated in a Soxhlet apparatus by extracting dried tissue samples with diethyl ether (Sawicka-Kapusta, 1968). Nitrogen was determined by Kjeldahl method. The amount of protein in vole body was calculated by multiplying total nitrogen of the dry mass by 6.25. The content of ash was estimated from the samples combusted in a muffle oven at 600°C. The sample size was approximately 0.2 g in the youngest age groups, and up to 1.5 g in older animals. From the above determinations the content of protein, fat and ash was calculated in relation to the dry mass. The composition of fat-free biomass wass also computed.

The caloric value body was estimated by combusting a sample of dry mass in a calorimetric bomb (Górecki, 1965). The animals belonging to the youngest age classes were combusted as a whole, while 1—1.5 g samples were prepared from older ones. From calorimetric determinations the caloric value of dry mass was calculated, as well as caloric value of ash-free dry mass and ash content.

Altogether 302 animals were analysed, including 96 animals reared in the laboratory, 55 in the out-door pen and 151 from the terrain group. Statistical analysis of the material concerned calculation of the mean, standard deviation, standard error and coefficient of variability in %. For the calculation of correlation the rectilinear regression was also employed, and significance of differences was ascertained by Student t-test.

III. RESULTS

1. Changes in Gross Body Composition of Voles Reared in Laboratory Conditions

The mean body weight of voles increased during 70 days of life from 2.1 to 17.4 g (Table 2). The variability of weight for all age classes amounted on the average to 16.5%, and was the smallest in 1- and 30-day-old voles (Table 2). During the first three days of life the weight

Table 1

Regression equations (Y) and correlation coefficients (r) between body weight and its principal expressed in g of biomass in three studied groups of voles.

Item	Laboratory	Out-door pen	Terrain
Body wt. — Water	$Y=0.940X^{0.8636}$ $r=0.994$	$Y=0.910X^{0.8765}$ $r=0.998$	$Y=0.79X^{0.9679}$ $r=0.976$
Body wt. — Protein	$Y=0.093X^{1.1946}$ $r=0.997$	$Y=0.291X^{0.6978}$ $r=0.999$	$Y=0.198X^{1.0055}$ $r=0.909$
Body wt· — Ash	$Y=0.106X^{1.4015}$ $r=0.998$	$Y=0,0129X^{1.3516}$ $r=0.998$	$Y=0.0137X^{1.8226}$ $r=0{\cdot}770$
Body wt. — Fat	$Y=0.0258X^{1.6571}$ $r=0.995$	$Y=0.0328X^{1.609}$ $r=0.993$	$Y=0.0074X^{1.5359}$ $r=0.924$

of voles changed only negligibly, while fast growth was observed between 3 and 6 day of life, when the animals gained 0.55 g/day, and the fastest — between 20 and 30 days, when the mean daily increase amounted to 0.70 g. Afterwards the rate of growth decreased (Table 2). The mean growth rate in this group of voles was 0.34 g/day up to 20 day of life, and 0.22 g/day for the whole studied period.

The amount of water, protein, fat and ash are highly correlated with body weight (Fig. 1). In all cases the correlation coefficients r are very high and amount on the average to 0.96 (Table 1). The relationships between body weight and the content of water, fat, ash and protein presented in the form of regression equations are shown in Table 1.

Table 2

Changes in protein, fat and ash in voles reared in laboratory, expressed in per cent of dry mass. Water content in per cent of biomass.

Age, days	N	Body constituent, average, ± *SE*, *C. V.* in %				
		Body weight, g	Water, %	Fat, %	Protein, %	Ash, %
1	11	2.13±0.07 11.3	84.5±0.34 1.3	24.8±3.81 40.7	63.0±3.77 15.9	10.2±0.49 10.8
3	11	2.54±0.15 19.3	81.6±0.34 1.4	29.9±3.24 26.6	59.3±3.27 13.5	9.5±0.37 8.6
6	13	4.20±0.28 26.8	78.2±0.74 3.4	31.5±3.46 29.1	57.4±3.49 16.1	9.0±0.29 8.7
10	18	5.80±0.19 13.8	74.6±0.21 1.2	34.9±1.97 17.0	56.2±1.99 10.6	8.1±0.23 9.5
20	20	8.58±0.39 20.5	73.0±0.49 3.0	31.6±2.88 32.4	57.1±3.19 20.3	9.8±0.32 10.9
30	9	15.61±0.42 8.1	66.1±0.59 2.7	44.5±2.72 16.2	44.1±2.57 15.4	8.8±0.34 9.5
50—70	14	17.43±0.73 15.6	60.9±1.28 7.8	48.9±2.40 14.7	39.2±2.21 16.9	8.8±0.81 24.3

Table 4

Changes in protein, fat and ash in voles reared in the pen, expressed in per cent of dry mass. Water content in per cent of biomass.

Age, days	N	Body constituent, average ± *SE*, *C. V.* in %				
		Body weight, g	Water, %	Fat, %	Protein, %	Ash, %
1	9	2.20±0.11 13.6	83.2±0.28 0.9	28.5±4.39 30.8	59.8±4.49 15.0	10.8±0.61 12.6
3	9	2.30±0.08 9.6	82.5±0.24 0.8	27.6±8.36 60.5	60.8±6.75 6.7	9.7±0.67 15.4
6	10	4.93±0.36 25.1	75.2±0.67 3.1	41.1±3.09 19.9	48.3±2.82 2.8	8.6±0.44 13.6
10	9	5.33±0.17 10.9	72.5±0.55 2.5	42.3±3.74 23.4	48.4±2.46 2.5	8.3±0.42 11.2
20	9	7.86±0.13 4.7	70.9±0.42 1.7	39.7±2.52 15.6	49.6±2.24 2.2	9.1±0.42 11.4
50—70	9	18.40±0.85 13.1	63.7±1.51 6.7	43.5±4.01 24.4	44.6±3.07 3.1	10.5±0.89 19.1

The content of water in the vole body decreased with age and body weight increase. The highest water content was in the youngest animals — 84.5%, and later this value graduallly decreased to reach 61% in the age of 70 days (Table 2). The relative water content in the individuals of a given age class was very similar and showed only slight variability (Table 2).

Protein content in the dry body mass decreased rather conspicuosly during postnatal development. In 1-day-old animals the content of protein amounted to 63%, in 6 to 20-day-old it was fairly constant around 58%, and in 70-day-old the level of protein decreased to approximately 40% (Table 2).

On the other hand, the amount of fat increased with age. Percentage contents of fat and protein were always related: increase of one parameter was associated with the fall of the second one. The mean fat content determined for the whole material ranged from 25 to 49%

Table 3

Energy values of the body of voles reared in the laboratory and in out-door pen in different age classes (each value represents mean of 4—5 animals).

		Age in days						
		1	3	6	10	20	30	50—70
Laboratory	cal/g dry weight	5.562	6.380	6.180	6.063	5.881	6.309	6.601
	cal/g ash-free dry weight	6.246	7.038	6.780	6.663	6.512	6.959	7.187
Outdoor	cal/g dry weight	6.410	6.209	6.446	6.351	6.279	—	6.717
	cal/g ash-free dry weight	7.191	6.972	7.030	6.956	6.943	—	7.369

(Table 2). Fat concentration in the vole body is more changeable than any other body constituents. The coefficients of variability are high and range in different age classes from 14.7 till 40.0% (Table 2).

The relative content of ash in dry mass of tissues of the examined animals was rather constant and comprised within 10.2% in one-day-old voles to 8.8% in 70-day-old ones. In the voles of remaining age classes the ash content was around 9.0%. The content of mineral constituents in voles of the same age showed only small variability (C. V. equal to 9.7% on the average) (Table 2).

The energy values of the body of voles reared in the laboratory were within the range of 5562 to 6600 cal/g of dry mass. The caloric values of ash-free dry weight were slightly higher — by 600 cal for all age classes on the average (Table 3). The lowest energy values were shown by 1-day-old animals, and the highest — by the oldest ones. In the age between 3 and 30 days the values were similar and oscillated around 6160 cal/g.

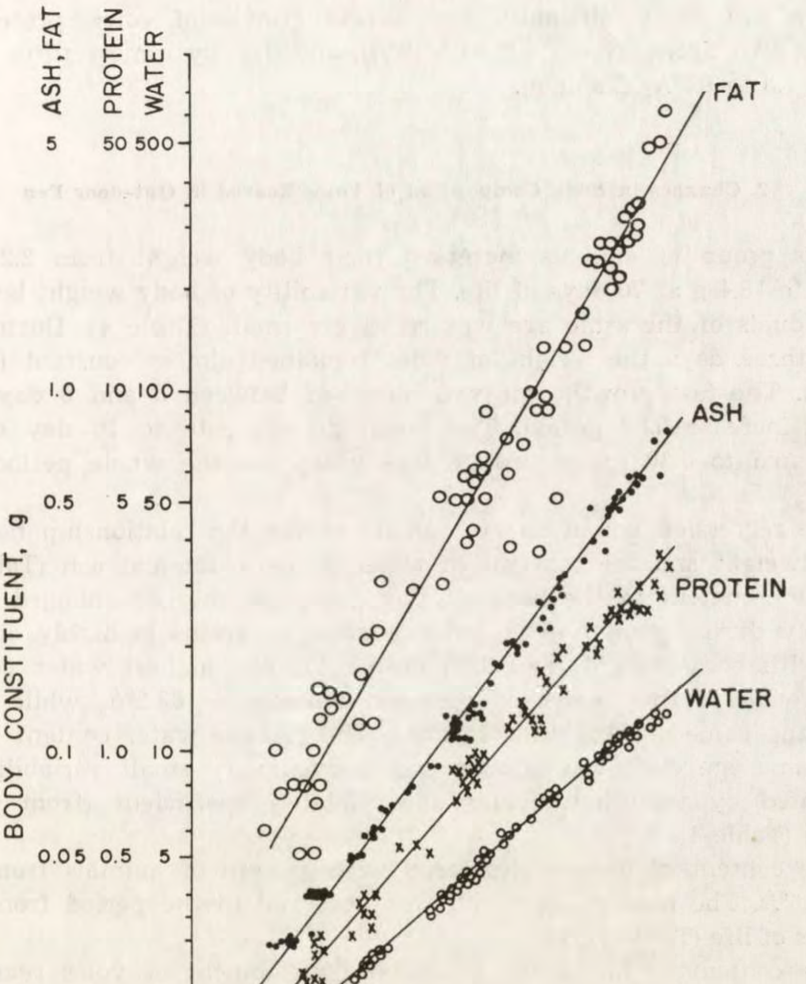

Fig. 1. Amounts of water, protein, ash and fat in the body of voles reared in the laboratory, as the function of their body weight.

The composition of defatted vole tissues also changed in the postnatal development. In the fat-free biomass (*FFB*) not only quantitative proportions of particular body constituents were altered but even the direction of changes was reverse (Table 6). The relative content of water in *FFB* decreased with age from 87.8 to 75.3%. The content of protein and ash significantly rose during growth of voles: protein by almost two times (from 10.2 to 18.9%), and ash by almost three times (from 1.5 to 4.3%) (Table 6).

2. Changes in Body Composition of Voles Reared in Out-door Pen

This group of animals increased their body weight from 2.2 g at birth to 18.4 g at 70 days of life. The variability of body weight between individuals of the same age was relatively small (Table 4). During the first three days the weight of voles remained almost constant (2.2 to 2.3 g). The fast growth rate was observed between 3 and 6 days (the mean increase 0.88 g/day). The mean growth rate to 20 day of life amounted to 0.30 g/day, and to 0.24 g/day for the whole period (Table 4).

The regression equations are calculated for the relationship between body weight and the contents of water, protein, fat and ash (Table 1).

Water content in the body of this group of animals changed considerably during growth. The water content in grams is highly correlated with body weight ($r=0.998$) (Table 1). The highest water content was found in the tissues of youngest animals — 83.2%, while at 70 days the value of 64% was observed. The relative water content within the same age class was similar and showed very small variability, as indicated by very low values of variability coefficient (from 0.8 to 6.7%) (Table 4).

The content of protein decreased with growth of animals from 59.8 to 44.6%. The most marked fall was observed in the period from 3 to 6 days of life (Table 4).

The content of fat in the postnatal development of voles reared in the out-door pen changed in reverse direction in comparison with protein. The percentage of fat in the vole body increased from 28.5 in 1-day-old animals to 43.5 in 70-day-old ones. The most intense increase of fat content in the dry mass occurred between 3 and 6 day of life. Similarly as in voles reared in the laboratory the variability in fat content was very high — the mean C. V.=29.1% (Table 4).

Ash was the most stable component of the vole body. Its content ranged within narrow limits from 8.3 to 10.8% (Table 4).

The caloric values of dry tissue weight were comprised between 6209 and 6718 cal/g, while the energy values of ash-free dry mass were slightly higher and on the average amounted to 7077 cal/g, without significant age-dependent variability (Table 3).

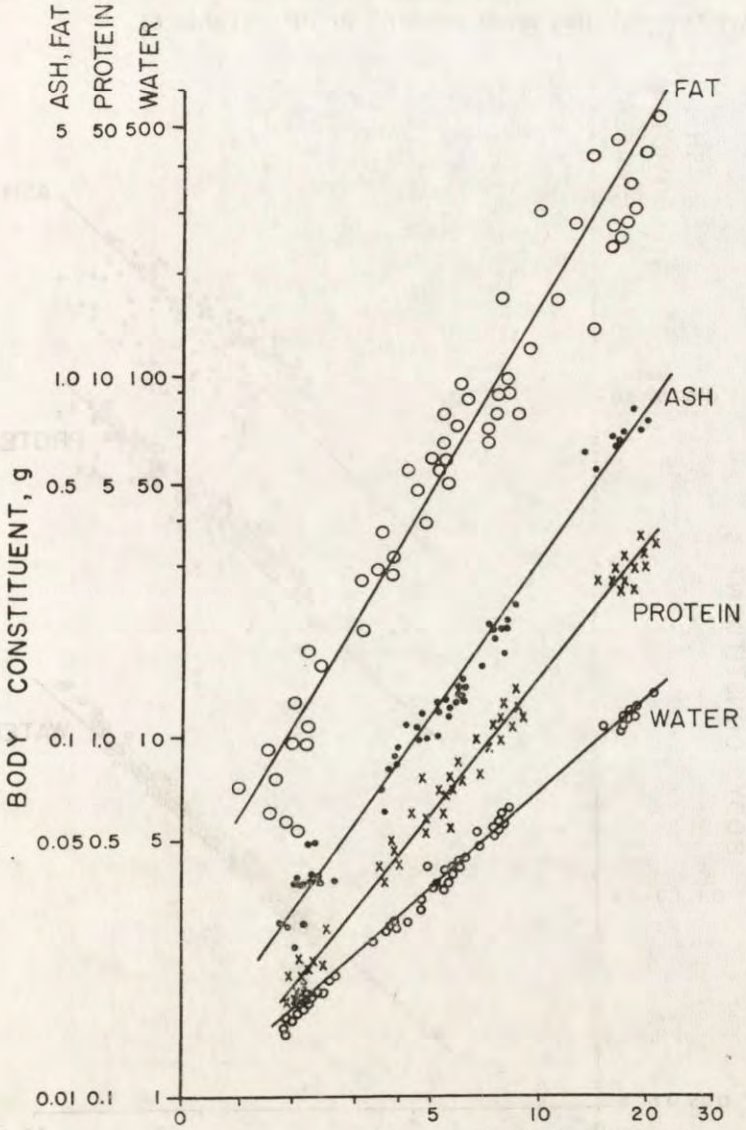

Fig. 2. Relationship between the amount of water, protein, ash and fat in the body of voles reared in the pen and their body weight.

After removal of fat the relationships between remaining body constituents were altered. The defatted biomass showed a rise of protein content with age, from 10.5% in the newborn to 19.0% in 70 day-old animals. Also the content of mineral constituents increased over two times from 1.9 to 4.4%. Similarly as in voles reared in the laboratory the water content decreased from 87 to 76% (Table 6).

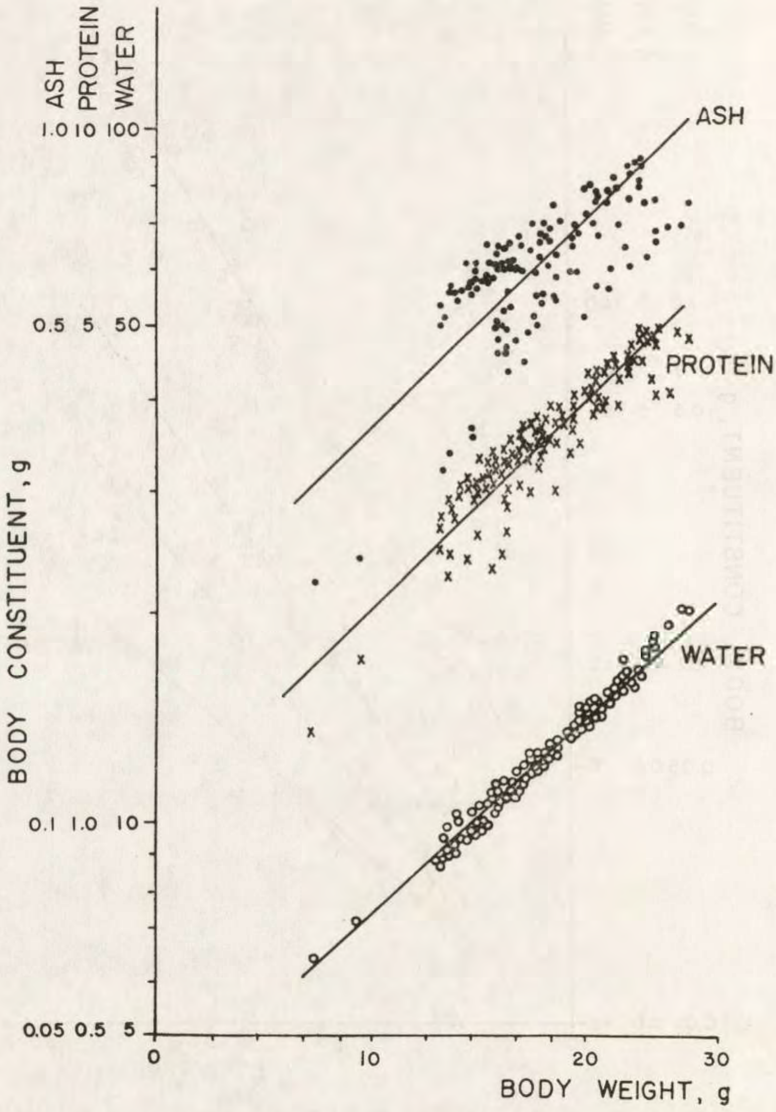

Fig. 3. Relationship between the amount of water, protein and ash in the body of voles from the terrain and their body weight.

Table 5

Changes in protein, fat and ash in voles from the terrain, expressed in per cent of dry mass. Water content in per cent of biomass.

Age, days	N	Body constituent, average, ± *SE*, *C. V.* in %				
		Body weight, g	Water, %	Fat, %	Protein, %	Ash, %
1	10	14.0±1.22 26.1	75.1±2.08 8.3	12.7±1.79 42.2	74.2±1.78 7.2	11.1±0.06 1.6
2	16	17.9±0.74 16.6	74.2±0.27 1.4	11.1±0.95 28.4	75.4±1.01 4.4	11.6±0.15 5.0
3	11	19.1±1.07 18.6	73.9±0.69 3.1	12.5±1.05 26.6	72.4±1.03 4.5	12.0±0.33 9.1
4	14	19.3±1.28 26.3	72.8±0.57 2.9	14.0±1.46 33.1	71.7±1.40 6.2	12.6±0.32 9.5
5	28	15.8±0.48 16.0	70.5±1.57 12.0	12.1±0.54 22.1	72.4±0.51 3.4	13.6±0.14 5.3
6—7	17	15.5±0.53 14.0	70.9±0.25 1.4	10.4±0.50 18.7	74.0±0.57 3.0	13.8±0.17 5.0
8—9	14	17.3±0.82 17.0	70.6±0.36 1.8	12.0±0.68 19.0	72.3±0.59 2.0	13.6±0.14 3.0
10	10	20.8±1.08 16.0	71.3±0.45 2.0	13.3±0.87 18.0	71.4±0.86 3.0	13.1±0.27 6.0
11—15	16	21.3±0.59 11.0	71.2±0.41 2.3	14.0±0.83 20.6	71.2±0.89 4.3	12.8±0.17 5.1

3. Body Composition of Voles Trapped in Natural Habitats

The examined free-living voles were considerably older than the other two groups. The youngest animals trapped in terrain were in the age of one month. For this reason the voles of this group can be compared with the other groups only within age classes of 30 and 70 days. Other age classes were investigated to find out whether the free-living animals reach the high degree of fatness characteristic for voles reared in laboratory and in out-door pen. The mean body weight of free-living voles increased from 14 g in 1-month-old to 21 g in 15-months old. The fastest growth rate was observed in young animals: between one and two month body weight gain was 4 g on the average. Between

Table 6

Percentage composition of fat-free biomass of voles from the laboratory and out-door pen (number of examined individuals in particular age classes given in brackets).

Body composition	Age in days						
	1	3	6	10	20	30	50—70
Laboratory	(11)	(11)	(13)	(18)	(20)	(9)	(14)
Fat-free body weight, %	2.05	2.40	3.91	5.29	7.85	13.26	14.09
Water, %	87.8	86.2	83.9	81.8	79.7	77.8	75.3
Protein, %	10.2	11.7	13.6	15.7	16.9	17.6	18.9
Ash, %	1.5	1.7	2.1	2.3	2.9	3.5	4.3
Out-door pen	(9)	(9)	(10)	(9)	(9)	—	(9)
Fat-free body weight, %	2.10	2.19	4.43	4.71	6.95	—	15.52
Water, %	87.1	86.8	83.7	81.9	80.1	—	75.9
Protein, %	10.5	11.0	13.3	15.1	16.4	—	19.0
Ash, %	1.9	1.8	2.3	2.5	3.0	—	4.4

4 and 9 month of life a decrease of body weight was observed in 7 month-old voles. This was caused by winter depression, since all voles aged 4 to 7 months were trapped in winter (Table 5).

The amounts of water, protein and fat are highly correlated with body weight ($r=0.9$). A slightly lower correlation coefficient was found for ash content (Table 1).

The concentration of water in vole body decreased with age. The highest level of water was found in one-month-old animals — 75.1%. In subsequent months water content decreased to 70.5% in 5-months--old voles and remained on this level to the end of the period of investigations (Table 5).

The content of protein in voles aged 1 to 15 months ranged from 71.2 to 75.4% showing a trend of decrease (Table 5). The lowest content of protein was found in the oldest animals in the age of 10 or 15 months — around 71% (Table 5).

The relative content of fat in the tissues of free-living voles was low in comparison with the two other groups and remained within rather narrow limits from 10.4 to 14.0%. The highest fat content was found in 4 and 15-month-old voles (14.0%), the lowest — in 6—7 month old animals (10.4%) (Table 5).

The content of mineral constituents in free-living voles was rather constant and ranged from 11.1 to 13.8% in different age classes. The lowest values were found in 1 and 2-month-old voles (11.3%). In further age classes the content of ash was similar — around 13.2% on the average (Table 5).

The composition of fat-free biomass of this group showed smaller changes than the composition of the whole body as expressed in per cent of dry mass. The water content decreased in this case from 77.5

Table 7

Percentage composition of fat-free biomass of voles from the terrain (number of examined individuals in particular age classes given in brackets).

Body composition	Age in months (N)								
	1(10)	2 (16)	33(11)	4(14)	5(28)	6—7(17)	8—9(14)	10(10)	11—15(16)
Fat-free body wt., g	13.56	17.39	18.52	18.56	15.20	15.05	16.71	20.00	20.44
Water, %	77.5	76.4	76.4	75.7	73.1	73.1	73.2	74.1	74.2
Protein, %	19.1	20.0	19.6	20.3	22.2	22.3	22.0	21.3	21.3
Ash, %	2.6	3.1	3.2	3.6	4.1	4.1	4.1	3.9	3.8

to 73.1%. A distinct fall was observed till 5 month of life. In further age classes the level of water was stable around 73.5% (Table 7). The concentration of protein rose from 19.1% in one-month-old voles to 22.2% in 5-month old ones. Later it remained fairly constant around 21.8%. The ash content in the defatted biomass increased from 2.6 to 4.1% during 5 months of life and then it remained constant (Table 7).

4. Seasonal Changes of Body Constituents in Free-living Voles

It was observed that both biomass and principal body constituents underwent certain fluctuations during the year. The mean body weight of all voles from the terrain was comprised within 14.4 and 21.7 g. The lowest body weight was observed in February and the highest in May (Fig. 4). The winter depression of body weight, between September and February, was well marked (Fig. 4). The increase of body weight occurred in March leading to the level of approximately 22 g in May. After comparison of body weights in the period October—February with weights of voles in the remaining months, it appeared that the differences are statistically highly significant ($t=5.08$, $P<0.001$). The coefficients of variability of body weight are rather low and amount on the average for all months to 12.2%, but in May and July are exceptionally high (36.6 and 24.8%) due to the presence of a large number of young animals in the analysed sample.

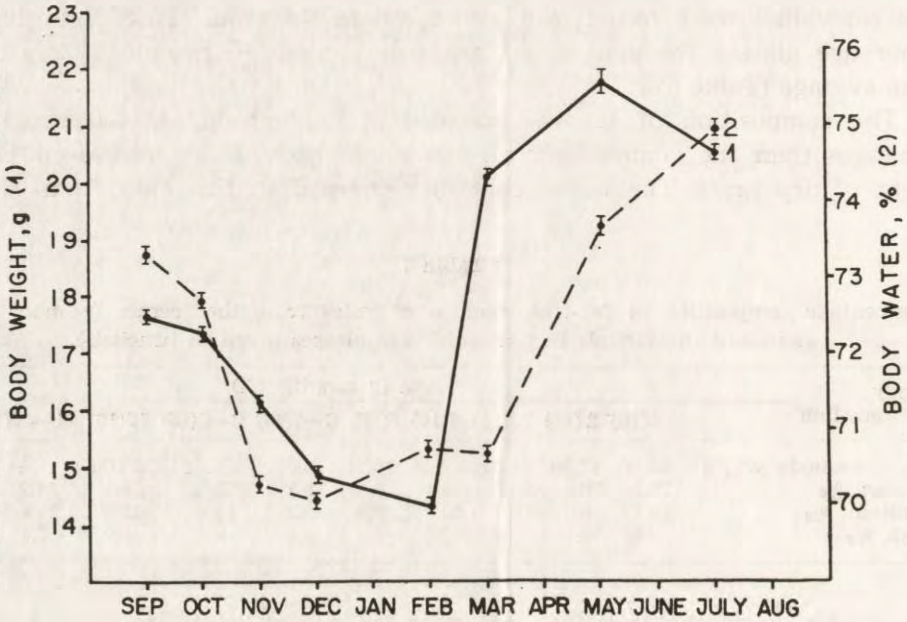

Fig. 4. Seasonal changes of body weight (1) and water content (2) in free-living voles. Each point represents the mean ± standard error.

Seasonal changes of water content were distinctly marked in the year cycle. The water content decreased from 73.3% in September to 70.7% in March. The lowest amount of water was found in winter, between November and March, when a fairly constant level of 70.4% on the average was observed (Fig. 4). After March the amount of water abruptly increased to reach the maximum in July — 75%. The values of water content in the vole body in the period from November till March differ very significantly from the remaining months ($t=6.27$, $P<0.001$). Within each month the coefficients of variability of water content are very low and do not exceed 3%.

Despite the fact that changes in the fat content were small the curve of body fatness of voles showed a distinct peak in March (14.6%). The lowest amounts of fat were found in November and December (around 11%), and then a rise to the maximum occurred. In summer again a decrease was observed to the value of 11.7% (Fig. 5). The maximum body fatness in March appears to be related to the preparation of animals to reproduction. The differences between the maximum amount of fat in March and minimum in November are statistically highly significant ($t=3.913$, $P<0.001$). When comparing body fatness of voles in March in relation to February and May the differences are on the borderline of significance ($P=0.05$).

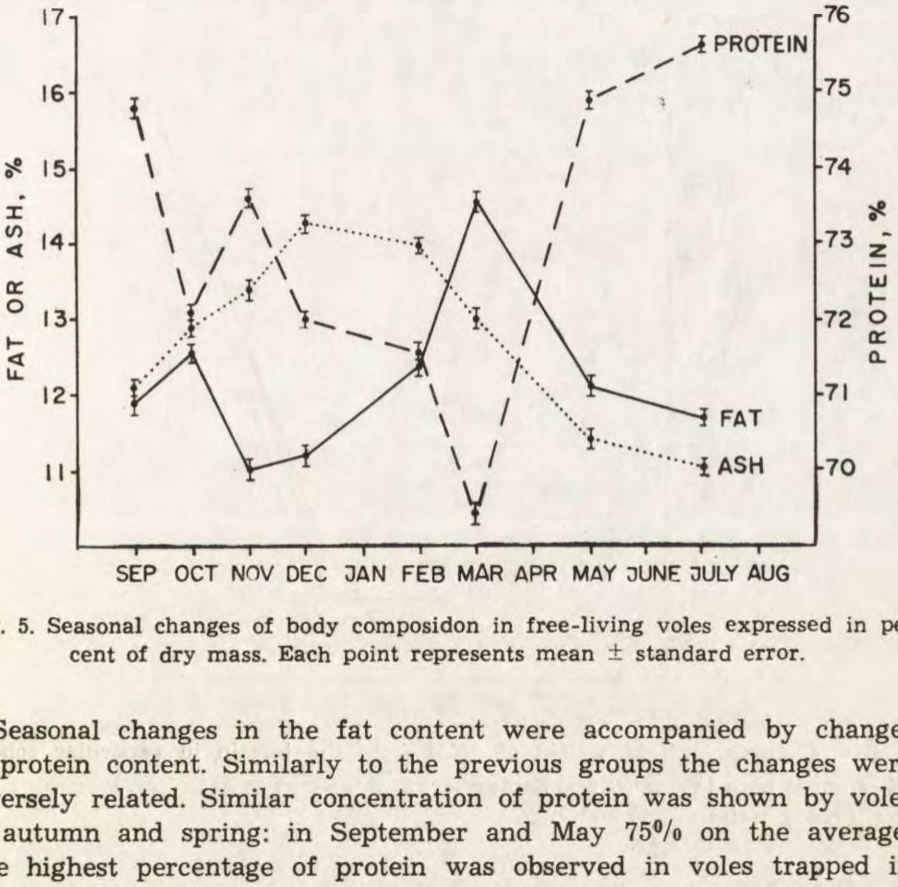

Fig. 5. Seasonal changes of body composidon in free-living voles expressed in per cent of dry mass. Each point represents mean ± standard error.

Seasonal changes in the fat content were accompanied by changes in protein content. Similarly to the previous groups the changes were inversely related. Similar concentration of protein was shown by voles in autumn and spring: in September and May 75% on the average. The highest percentage of protein was observed in voles trapped in July — 75.6%. Since September the protein content in vole body decreased to the minimum in March — around 69% (Fig. 5). The differences in the protein content between March, when the minimum occurred, and May, July, September and November are highly significant

($P<0.001$), and less significant in comparison with the remaining months ($P<0.05$ and $P<0.01$).

The level of mineral constituents depended also on the season. The highest concentration of ash was found in December (14.3%), when the sample contained only adult animals, and the lowest in July (11.0%) when a large number of young animals was present (Fig. 5).

5. Changes of Body Composition of Voles in Cohorts

The discussed changes of principial body constituents in the free-living voles in two aspects of age-dependent and season-dependent

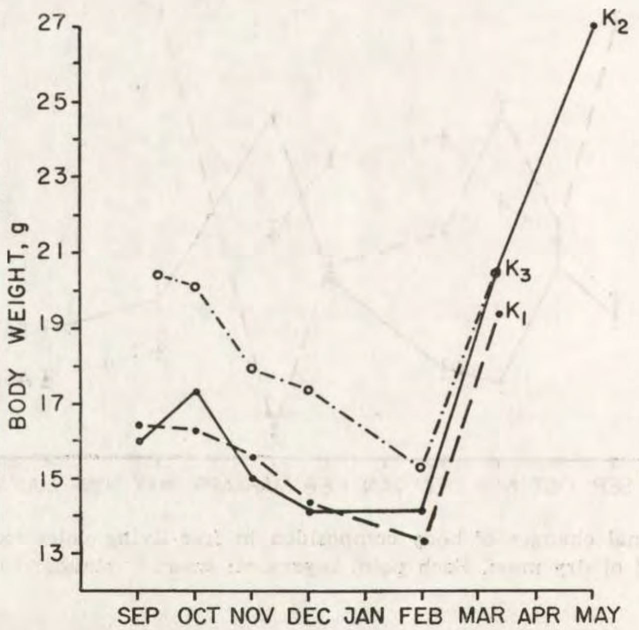

Fig. 6. Changes in body weight of voles from the terrain in particular cohorts.
K_1 animals born in August and September,
K_2 animals born in June and July,
K_3 animals born in May.

variability demonstrated a strong effect of both these factors on body composition. The consideration of changes in *GBC* of animals living in natural conditions should include the effect of both factors. For this reason the free-living voles were divided into three cohorts depending on their age:

1. Animals born in August and September — K_1
2. Animals born in June and July — K_2
3. Animals born in May — K_3.

Since in all voles the decrease of body weight was observed from September the changes of principal body constituents were also analysed from September (Figs 6—9). The cohorts K_1 and K_2 showed similar body weight in September, around 16 g, while the voles belonging to the third cohort K_3 were heavier and their biomass amounted to 20.4 g. The body weight decreased very markedly till February. In K_1 cohort this decrease amounted to 3 g, in K_2 to 2.8 g and in K_3 to as much as 5 g. From February till March a rise of body weight by approximately 6 g was observed in all cohorts (Fig. 6). After March the data are available for only the second cohort in which body weight increased

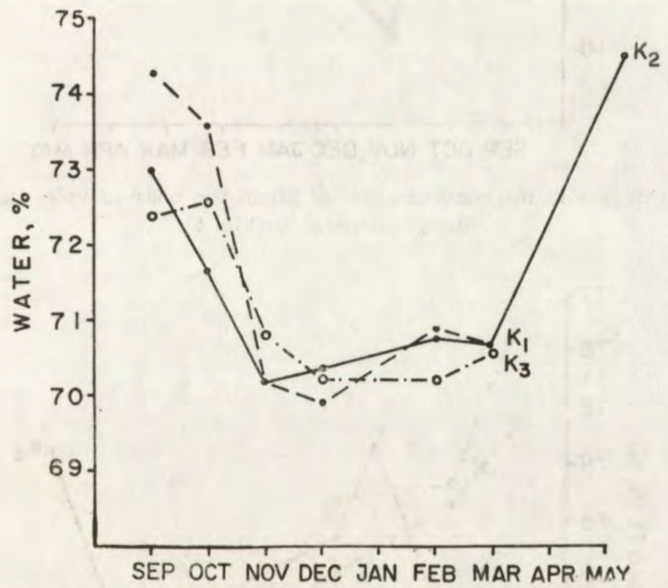

Fig. 7. Percentage content of water in the body of voles in cohorts (designations as in Fig. 6).

further up to 27.0 g. The depression of body weight was accompanied by decrease of water level in tissues of voles between September and March. The percentage of water in all cohorts reached in March 70.7%, although in September particular cohorts showed different values (Fig. 7). The fat content in the period from September to December remained at the level of 11.5% with larger variations in K_2 cohort. Since

December the rise of fat content was visible in all groups, with the maximum observed in March (K_1 — 13.6%, K_2 — 16.2%, K_3 — 14.3%) -- (Fig. 8). The content of protein in the individuals of all groups de-

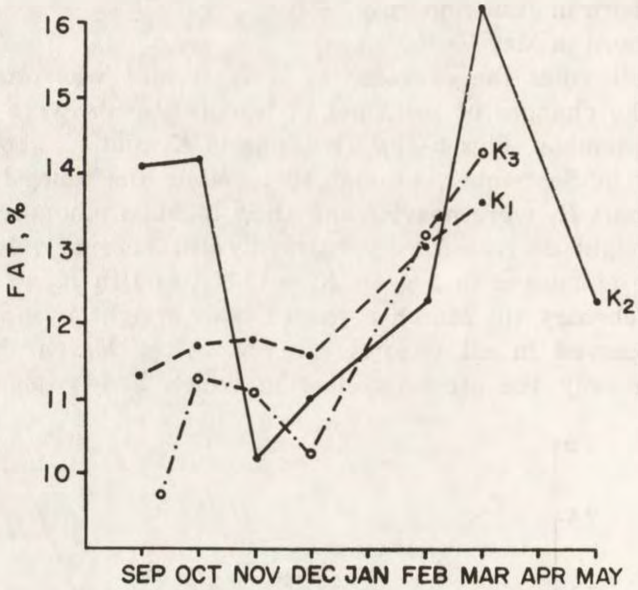

Fig. 8. Changes in the concentration of fat in the body of voles in cohorts (designations as in Fig. 6).

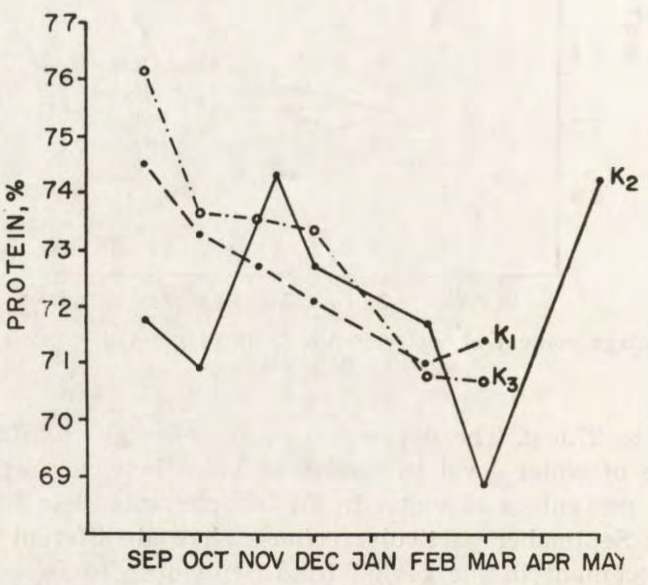

Fig. 9. Protein content in particular cohorts (designations as in Fig. 6).

creased from September till March by a few per cent. In the second cohort, for which the data are available until May, a rise of protein content is observed (up to 74.3%) (Fig. 9).

IV. DISCUSSION

1. Age-dependent Changes in the Vole Body Composition

General regularities of changes in body composition of animals were at first described by A r m s b y, M o u l t o n & M u r r a y for cattle (after B l a x t e r, 1966). Fat exerts the highest effect on the percentage content of other body constituents. The fat content considerably increases during postnatal development, while at the same time relative content of water and protein decreases, and of ash shows small changes. In relation to fat-free biomass the relative content of water decreases, and protein and ash increases in the postnatal development. This general trend of changes in body constituents in grownig animals was also observed in small mammals (B a i l e y *et al.*, 1960; M y r c h a & W a l k o w a, 1968; B r i s b i n, 1970).

The range of body weights and curves of growth of bank voles living in the laboratory and in out-door pen are within the limits reported for this species by other authors (S v i r i d e n k o, 1959; P e t r o v, 1961; M a z á k, 1962; D r o ż d ż, 1965). The growth rate of these two groups of bank voles found in the present study is similar to that reported by P e a r s o n (1962) and S v i r i d e n k o (1959). Both the gross body composition of bank vole expressed in percentage of dry weight, and retention of particular constituents in grams, are in agreement with the trend of changes and with absolute values reported for the laboratory mouse and common vole. Similarly the index of physiological age, *i.e.* the ratio of protein to water observed in bank vole in the range from 0.120 to 0.303 is very close to that found in the cited above rodent species (B a i l e y *et al.*, 1960; S a w i c k a - K a p u s t a, 1970; D r o ż d ż *et al.*, 1972). The composition of fat-free biomass reaches constant values in the bank vole similarly as in laboratory mouse and vole of 50—70 days old (B a i l e y *et al.*, 1960; D r o ż d ż *et al.*, 1972). In two months old voles from the terrain the composition of fat-free biomass is similar to that found in voles of the same age reared in laboratory and out-door pen, and remains constant in older animals (Tables 6 and 7). Slightly different composition of fat-free biomass in the period from 5 to 9 months of life is related to winter depression of body weight and accompanying changes (Table 7).

2. Seasonal Changes of Vole Body Composition

Seasonal changes of body composition and fatness were already investigated in birds (Odum, 1960; Helms *et al.*, 1967; West & Meng, 1968), bats (Baker *et al.*, 1968; Ewing *et al.*, 1970), rodents (Heraux, 1961; Didow & Hayward, 1969; Aleksiuk, 1971; Sealander, 1972).

Fat is the most variable constituent of *GBC*. Seasonal fluctuations in the amount of fat cause changes in the level of remaining body constituents. With the rise of fat index water index decreases in squirrels (Jameson & Mead, 1964), and also in *Peromyscus* (Sealander, 1951; Hayward, 1965).

Seasonal changes of body weight, characterized by winter reduction or inhibition of growth, were observed in different groups of mammals: in *Microtus* (Schwarz *et al.*, 1964; Pokrovski, 1966), *Peromyscus* (Hayward, 1965), shrews (Dehnel, 1949; Borowski & Dehnel, 1952; Myrcha, 1969), as well as in musk-rats (Aleksiuk & Frachlinger, 1971). The winter depression of body weight was observed also in *Clethrionomys glareolus* (Wasilewski, 1952; Marinina, 1966; Tanton, 1964; Zejda, 1971; Bobek in litt.). The free-living voles examined in the present study confirm this phenomenon showing statistically very highly significant fall of body weight between September and February (Table 5, Fig. 4). Since the winter depression of body weight is accompanied by increased content of fat and decreased content of water, it may appear that water is responsible for the reduced weight. For a free-living vole of the mean body weight 20.42 g it was calculated that winter depression of body weight amounting to 5.07 g includes the decrease of water content by 4.0 g, protein by 1.06 g and ash by 0.06 g. At the same time fat increases by barely 0.05 g. For a vole of the same body weight it was calculated that increase of weight between February and March includes simultaneous rise of all body constituents.

It is clear that winter depression of body weight is the result of significant changes in all body constituents. The most important are protein and water while the remaining components (fat and ash) occurring in smaller amounts exert a smaller effect on the total body weight of voles.

3. Gross Body Composition of Voles Reared in Laboratory and in Out-door Pen

From the data on body composition of both groups of voles it appears that despite different conditions of their postnatal development they show several similarities. The curves of growth from 1 to 70 days are almost identical for both groups. The body weights differ only slightly — by 5.4% on 70 day (Tables 2 and 4). The course of changes of all principal body constituents is very similar in both groups (Tables 2 and 4). The direction of changes in the concentration of protein and fat in the dry mass of voles reared in laboratory and in out-door pen is the same, although absolute values are slightly different. The voles reared in the pen have always slightly more fat than laboratory voles (Table 4). Si-

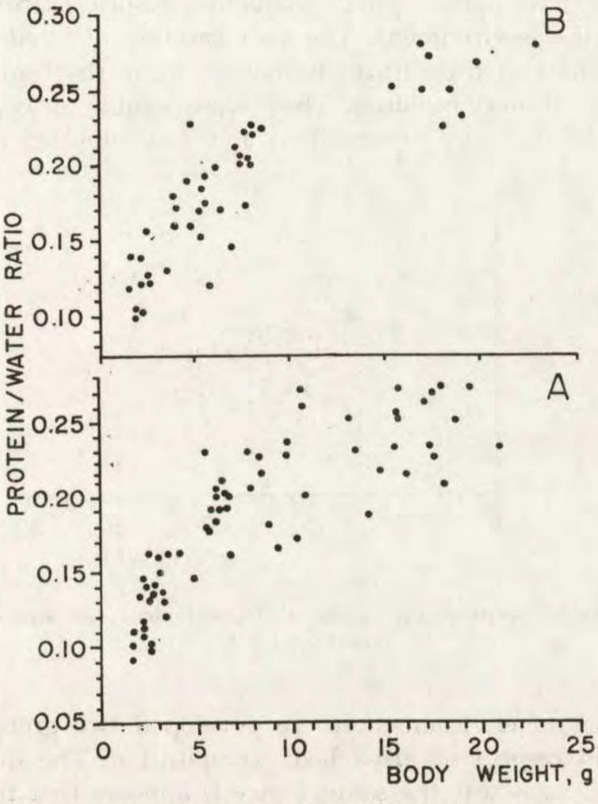

Fig. 10. Relatioship between the index of physiological age and body weight of voles from the laboratory (A) and out-door pen (B).

milarly as with changes of body weight and water content in vole body also in case of fat distinct changes occur in the age of 3 to 6 days. In this time an abrupt increase of fat and decrease of protein content are observed. In voles reared in the laboratory the changes of both investigated components are more uniform (Tables 2 and 4). As shown in Table 8 the body weight and composition of voles reared in the laboratory and in pen are in principle identical when expressed in grams of biomass. Concentration of water, protein and ash in fat-free biomass in both groups differ by less than 1 % (Table 6). For the two compared groups of voles the index of physiological age is comprised within 0.11 to 0.25 — hence it is almost identical (Fig. 10).

From the comparison of changes of body constituents during postnatal development of voles it is clearly visible that both groups — living in the laboratory and in the pen, do not show any significant differences in the process of formation of net production despite extremely different conditions of the environment. The two habitats differed drastically in respect of climate (temperature, humidity, light rhythm), home range and possibility of nest building. They were similar only in respect of food which had the same composition and was supplied *ad libitum*. In

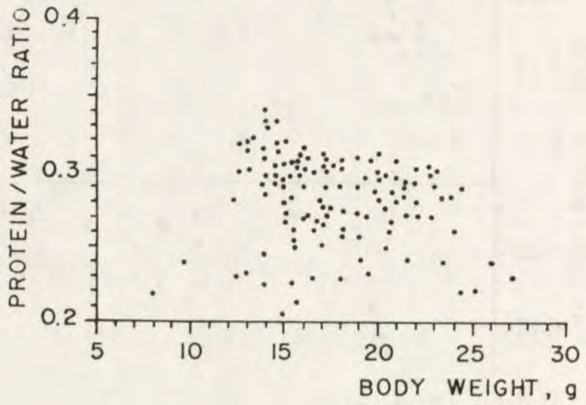

Fig. 11. Relationship between the index of physiological age and body weight of free-living voles.

these two types of environment there developed two groups of animals very similar in respect of gross body composition. The quality of food in the pen and cages was the same, hence it appears that the availability of food given in excess was the main factor modifying vole body composition.

4. Comparison of Body Composition of Voles Reared in Laboratory and in Out-door Pen with the Terrain Group

It is more difficult to compare the two above discussed groups with free-living voles. The voles trapped in terrain are considerably older than those reared in laboratory and in out-door pen, and the estimation of age was possible with the accuracy of one month (M a z á k, 1963;

Pucek & Zejda, 1968; Lowe, 1971). Only one and two months old voles can be compared with two last classes (30 and 70 days old) reared in laboratory, and with 70-day-old ones reared in the pen. Despite the fact that voles reared in the pen were the first generation of free-living animals, their body composition was almost identical with that of voles reared in laboratory. They differed considerably from voles trapped directly in the forest. The voles from the terrain contain less fat but more protein, and slightly more ash and water (Tables 2, 4 and

Table 8

Increase of principal body constituents of voles from the laboratory or out-door pen during 70 days of life, expressed in g of biomass (number of examined individuals given in brackets).

Body composition	Age in days						
	1	3	6	10	20	30	50—70
Breeding room	(11)	(11)	(13)	(18)	(20)	(9)	(14)
Body weight	2.13	2.54	4.20	5.80	8.58	15.61	17.43
Water	1.80	2.07	3.28	4.33	6.26	10.32	10.61
Fat	0.08	0.14	0.29	0.51	0.73	2.35	3.34
Protein	0.21	0.28	0.53	0.83	1.32	2.33	2.67
Ash	0.03	0.04	0.08	0.12	0.23	0.47	0.60
Out-door pen	(9)	(9)	(10)	(9)	(9)	—	(9)
Body weight	2.20	2.30	4.93	5.33	7.86	—	18.40
Water	1.83	1.90	3.71	3.86	5.57	—	11.78
Fat	0.10	0.11	0.50	0.62	0.91	—	2.88
Protein	0.22	0.24	0.59	0.71	0.14	—	2.95
Ash	0.04	0.04	0.10	0.12	0.21	—	0.69

5). The difference in the body composition of 30-day-old voles from the laboratory and from the forest is great. Even the oldest 15-months-old animals from the terrain do not reach the level of fat observed in 30-day-old voles from the laboratory or from the pen. The content of fat in their body constitutes approximately 1/3 of fatness of voles from the laboratory or from the pen.

The body weight of voles reared in the laboratory or in the terrain is in principle similar: 15.6 g of 30-days-old from the laboratory and 14.0 g from the forest, while the animals reared for 70 days or trapped when 2-months-old are almost identical (Tables 8 and 9). At the same time they show considerable differences in the composition of biomass. The amount of fat deviates most significantly: 30-days-old voles reared in the laboratory contain 1.9 g more fat in relation to the individuals from the terrain, and at 70 days the difference amounts to 2.8 g. Also large differences occur in respect of water content; for example 70-days--old vole from the terrain contains 2.7 g more water and 0.8 g more protein in comparison with the animal reared in the laboratory. The level of ash is lower by 0.14 g on the average in the voles from the terrain (Tables 8 and 9). The percentage composition of fat-free biomass is similar in all groups within the comparable age classes (Tables 6 and 7). All the components of defatted biomass increase during the whole period of investigations of voles reared in the laboratory and in the pen. At the age of 50—70 days the composition of fat-free body reaches a stable level. In two months old voles from the terrain the composition of fat-free biomass is constant and in older age classes show only small changes.

Table 9

Increase of principal body constituents of voles from the terrain during 15 months of life expressed in g of biomass (number of examined individuals given in brackets).

Body composition	Age in months (N)								
	1(10)	2(16)	3(11)	4(14)	5(28)	6—7(17)	8—9(14)	10(10)	11—15(16
Body weight	14.0	17.9	19.15	19.30	15.76	15.52	17.32	20.8	21.3
Water	10.51	13.28	14.15	14.05	11.11	11.0	12.23	14.83	15.17
Fat	0.44	0.51	0.63	0.74	0.56	0.47	0.61	0.80	0.86
Protein	2.59	3.48	3.62	3.76	3.37	3.35	3.68	4.26	4.36
Ash	0.35	0.54	0.60	0.66	0.63	0.62	0.69	0.78	0.78

The caloric value of the animal body depends mainly on the amount of fat, hence the values found for the voles reared in the laboratory and out-door pen are conspicuously higher (by approximately 700 cal/g) than those of terrain voles (Table 3).

For ecological studies differences and similarities of the examined groups of voles are important. Majority of bioenergetic investigations are carried out on the animals deriving from the laboratory stock. The animals from the terrain are easily available only after reaching the age of one month (P e t r u s e w i c z *et al.*, 1968; B o b e k, 1971). The age structure of the sample can be estimated only after trapping. For the estimation of net production of free-living population the data obtained on the animals reared in the laboratory or out-door pen are useless, because both growth, caloric values of the body and its composition are different. The animals born in the laboratory or in out-door pen cannot be used for bioenergetic studies on body caloric values, metabolism rate, and majority of feeding experiments. Of course this does not exclude the use of these animals in the investigation of certain physiological parameters showing low variability and independent of conditions of life.

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Department of Animal Ecology,
Jagiellonian University,
Krupnicza 50, 30—060 Kraków, Poland.

Katarzyna SAWICKA-KAPUSTA

ZMIANY SKŁADU CIAŁA I JEGO KALORYCZNOŚCI U NORNICY RUDEJ W OKRESIE ROZWOJU POSTNATALNEGO

Streszczenie

1. W okresie najintensywniejszego wzrostu czyli w okresie rozwoju postnatalnego u nornic rudych hodowanych w hodowli i wolierze oraz nornic z terenu badano zmiany składu chemicznego ciała. U dwu pierwszych grup w wieku 1, 3, 6, 10, 20, 30, 50—70 dni, a w grupie terenowej, która była o wiele starsza w wieku 1, 2, 3, 4, 5, 6—7, 8—9, 10, 11—15 miesięcy. Łącznie przeanalizowano 302 zwierzęta w tym 96 w grupie hodowlanej, 55 w wolierowej oraz 151 w terenowej.

2. Ciężar ciała nornic hodowlanych wzrastał od 2,1 do 17,4 g (Tabela 2). Ilość wody, białka, tłuszczu i popiołu jest wysoko skorelowana z ciężarem ciała (Tabela 1, Ryc. 1). Procentowa zawartość wody i białka zmniejszała się a wzrastała koncentracja tłuszczu od około 25 do 49% (Tabela 2). Wartości energetyczne wynoszą średnio od 5560 do 6600 cal/g (Tabela 3).

3. Ciężar ciała nornic wolierowych wzrastał w bardzo podobnym zakresie. Zawartość białka zmniejszała się w miarę wzrostu nornic od około 59 do 44% a wody od około 83 do 64%. Koncentracja tłuszczu była podobna jak u nornic hodowlanych (Tabela 4).

4. Nornice terenowe zazębiają się z dwoma poprzednimi grupami tylko w obrębie zwierząt 30—70-dniowych. Koncentracja wody malała z wiekiem. Procent białka był zawarty w granicach od 71 do 75% wykazując ogólną tendencję spadkową. Procentowa zawartość tłuszczu była bardzo niska (10,4—14,0% (Tabela 5).

5. Wyraźnie zaznaczała się zimowa depresja ciężaru ciała u nornic terenowych, która trwała od września do lutego. Towarzyszyły jej zmiany wszystkich składników ciała. Uwodnienie tkanek zmniejszało się od września do marca, najmniej wody miały nornice w listopadzie (70,3%), najwięcej w lipcu (75%) Ryc. 4. Krzywa otłuszczenia wykazywała szczyt w marcu (14,6%), zmiany zawartości białka były odwrotne do zmian tłuszczu (Ryc. 5).

6. Rozpatrywanie zmian składu ciała nornic w kohortach uwzględnia wpływ zmienności wiekowej i sezonowej na skład ciała. Zmienność wszystkich składników ciała w trzech kohortach jest podobna (Ryc. 6—9).

7. U wszystkich grup nornic skład odtłuszczonej biomasy ustala się około 2 miesiąca życia, podobnie wskaźnik wieku fizjologicznego (Tabele 6, 7; Ryc. 10, 11).

8. Nornice hodowlane i wolierowe nie wykazują różnic w procesie powstawania produkcji netto pomimo skrajnie różnych warunków środowiska w którym wzrastały. Środowiska te różniły się drastycznie pod względem klimatycznym (temperatura, wilgotność, rytm oświetlenia), areału osobniczego i możliwości gniazdowania. Wydaje się więc, że dostępność dla nornic pokarmu podawanego w nadmiarze była głównym czynnikiem modyfikującym ich skład ciała.

9. Nornice hodowlane i wolierowe zupełnie różnią się od nornic terenowych. Różnice te dotyczą wszystkich składników ciała, a szczególnie tłuszczu którego jest znacznie mniej u nornic terenowych. Zwierząt urodzonych w hodowli i wolierze nie można stosować do badań bioenergetycznych nad kalorycznością ciała, tempa metabolizmu oraz do większości badań żywieniowych.