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Variability of Fat and Water Content in Two Rodent Species*

[With 5 Tables & 3 Figs.]

Examination was made of fat content in dry mass of carcasses (without head, skin or alimentary tract) of two species of rodent *C. glareolus* (N = 773) and *A. flavicollis* (N = 523). The animals were caught in a *Tilio-Carpinetum* deciduous forest in the Białowieża National Park over two periods — 1963—1964 and 1967—1968. The carcasses prepared for ether extraction formed over 50% of the body mass of *C. glareolus* and about 60% of the body mass of *A. flavicollis*. Very great individual differences were found in the degree of fat content in these animals, ranging from about 1 to 19%. The arithmetical averages for percentages of fat varied within limits from 4.8 to 11.6% for different seasonal and age groups of *C. glareolus* and from 2.8 to 13.7% of *A. flavicollis*. The coefficients of variation varied from 14—53% for *C. glareolus* and 25—84% for *A. flavicollis*. Fat content is generally greater in adult than young rodents, and in males higher than in females, although such differences were not always statistically significant. Differences in fat content within the same season are greater in different years than in different seasons of a given year. The rhythm of seasonal changes is similar in the two species and takes a different course in different years. Variations in water content in rodents' carcasses are far smaller (C.V. = 1—5%) and exhibit distinct seasonal rhythm, with a maximum in spring and summer and minimum in winter. The caloric value of fat is a fairly stable value. Coefficients of variation fluctuate from 2.8—6.4% in *C. glareolus* and from 4.1 to 13.1% in *A. flavicollis*, and the arithmetical averages for seasonal groups do not exhibit variations in any particular direction.

I. INTRODUCTION

A considerable amount of data are to be found in literature on the subject of the gross body composition of rodents, but scanty information on the fat content in these animals during their lifetime. H s i a - W u - p i n g & S u n - C h u n g - l u (1963) studied *Clethrionomys rutilus* and estimated the degree of fat content in individuals of different sex and age and

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also differences between successive years. Hayward (1965) compared fat and water content in several geographical races of *Peromyscus* in summer and winter. Variations in the fat content of *Peromyscus* over the yearly cycle have also been discussed by Connell (after Golley, 1962). Sawicka-Kapusta (1968) has shown that there are significant seasonal differences in the fat content of *A. flavicollis*. Not all the studies made, however, have taken into consideration such parameters as age, sex, individual variations, seasonal or long-term variations.

It would therefore appear that there is a need for further studies in order to grasp the different aspects of variations in the degree of fat content found in these animals, since this parameter is important both from the point of view of assessing the caloric value of animal tissues in bioenergetic calculations and also possibly evaluating the animals' condition.

It is to be expected that the degree of fat content found in rodents will vary in successive years, and in fact some authors have already drawn attention to this (Hsia-Wu-ping & Sun-Chung-lu, 1963, Sawicka-Kapusta, 1968).

In order to obtain a knowledge of the range and regularity of such variations chiefly individual, age and seasonal, over both the yearly cycle and in successive years, a study was made of the fat content in two rodent species common to the forests of Central Europe: *Clethrionomys glareolus* (Schreber, 1780) and *Apodemus flavicollis* (Melchior, 1834). Variations in percentage of water content and of the caloric value of fat have also been considered in these studies.

II. MATERIAL AND METHODS

The animals were caught in the Białowieża National Park in *Tilio-Carpinetum* (Traczyk, 1962) biotopes in 1963 and 1964, and also 1967 and 1968. Four seasons were taken into consideration in the material: spring (April, May), summer (July, August), autumn (October and part of November) and winter (January, February and sometimes the last ten days of December). It was not, however, always possible to collect a suitable number of animals in the various seasons, hence the gaps in material which made it difficult to carry out comparisons between the various years. As the material used for these studies was collected for other experiments, only the animals' carcasses were examined.

Snap traps were used to catch the rodents, which were taken to the laboratory, weighed, skinned and decapitated and the alimentary tract removed. Carcasses prepared in this way were weighed again and stored in plastic bags in a refrigerator (approx. -10°C). When a suitable number of carcasses had been collected they were subjected individually to extraction. The carcasses were cut into small pieces and dried in a vacuum drier at 60°C , with CaCl_2 as water absorber, until at constant weight was reached. The percentage of water content was calculated from the difference in weight before and after drying. The dried carcasses were extracted with

ethyl ether in a Soxhlet apparatus at 40°C. Part of the material was extracted directly in flasks, part in extraction tubes. The amounts of fat obtained in both cases did not differ significantly. Excess ether from above the extract was evaporated and the residue dried for 12 hours at 37°C and then weighed.

Caloric value of the fat was determined by burning samples of about 1 g in an adiabatic bomb calorimeter KL-3.

The whole material was divided into groups according to the animals' sex and age. The latter was determined for *C. glareolus* by measuring the length of M_1 tooth roots (Pucek & Zejda, 1968). To begin with ten two-month age classes were distinguished, but in order to facilitate handling the material some of the classes were combined and only young individuals (up to 6 months of age) and adults (more than 6 months old) were segregated as groups.

In the case of *A. flavicollis* age was determined on the basis of wear of the cusps of molar (Adamczewska-Andrzejewska, 1967). Here also only two groups were finally distinguished: young (up to 5 months old) and adults (over 5 months old).

Although the total number of animals available seems fairly large — 1296, consisting of 773 individuals of *C. glareolus* and 523 of *A. flavicollis* yet after segregation according to season in different years and age groups, there were sometimes only a few animals at our disposal. There is a greater number of males (506 *C. glareolus* and 358 *A. flavicollis*) than females (respectively 267 and 165), as we rejected pregnant and nursing individuals. In addition only males were caught in the first phase of the experiments.

Calculated percentages were used for comparisons. Differences between males and females were analysed, taking into consideration both their age and capture period, that is, season and year. The average values calculated described the confidence limits based on variable t .

When elaborating numerical data the analysis of variance was used, applying double classification for non-orthogonal data by Yates' method of unweighed averages. The t Student test was used in certain calculations.

III. BODY AND CARCASS WEIGHT

It can be seen from Table 1 that relatively great variation in body weight is observed in different groups, this applying to both young and adult animals of both sexes. The coefficient of variation comes within limits of 7.0—24.6% for *C. glareolus*, and is slightly higher for *A. flavicollis*, for which it may be as much as 28%.

Males are almost always heavier than females. The average body weight of male *C. glareolus* is about 15 g for young individuals and 20 g for adults, and for females very similarly — respectively 14.7 and 19.4 g.

The corresponding weights for *A. flavicollis* are 30.4 and 41.4 g for males, while the females are lighter, being 23.6 g for young animals and 36.3 g for adults.

The fat content in rodents was defined on the basis of the carcass, which in different groups formed on an average from 44.6 to 56.8% of the body mass of young animals and 46.6—65.4% of adult *C. glareolus* and

Variability of body and
Number of individuals (N), averages and standard deviations ($\bar{x}\pm\text{SD}$), and

Years	N	Body weight		Carcass weight		
		$\bar{x}\pm\text{SD}$	C.V.	$\bar{x}\pm\text{SD}$	C.V.	% body wt.
YOUNG MALES						
Spring						
1968	19	15.7±2.21	14.10	8.5±1.60	18.84	54.14
Summer						
1963	21	18.5±3.59	19.41	9.0±1.50	16.59	48.65
1964	13	13.5±2.04	15.09	6.4±0.94	14.67	47.41
1968	62	14.3±2.43	17.07	7.7±1.78	23.08	53.85
Autumn						
1963	22	17.2±1.70	9.91	8.8±0.76	8.60	51.16
1964	23	14.9±2.04	13.64	6.8±0.73	10.81	45.64
1967	46	13.1±3.22	24.56	6.6±1.82	27.73	50.38
1968	29	14.4±1.01	7.01	7.1±0.61	8.64	49.30
Winter						
1963/64	32	16.5±2.89	17.50	7.4±1.83	24.73	44.85
1964/65	15	15.2±1.57	10.36	6.9±0.78	11.31	45.39
1967/68	19	16.9±3.16	18.65	9.6±2.16	22.50	56.80
Total	301	15.1±2.89	19.12	7.6±1.82	24.01	50.16
YOUNG FEMALES						
Spring						
1968	19	18.0±4.27	23.80	9.3±2.55	27.33	51.66
Summer						
1964	11	19.2±3.53	18.41	9.9±2.17	21.97	51.56
1968	45	13.7±1.94	14.08	7.2±1.51	20.92	52.55
Autumn						
1967	34	14.2±1.99	14.00	7.2±1.26	17.54	50.70
1968	26	13.6±1.15	8.51	6.8±0.61	8.97	50.00
Winter						
1963/64	19	15.7±3.15	20.04	7.0±1.91	27.53	44.58
1967/68	32	13.4±1.58	11.82	6.6±0.95	14.37	49.25
Total	186	14.7±2.95	20.08	7.4±1.79	24.18	50.34

respectively 54.2—63.5% and 56.8—66.5% for *A. flavicollis* (Table 1, 2). In general it may be said that the carcasses formed slightly over 50% of the total body mass of *C. glareolus*, and about 60% for *A. flavicollis*, and were more than twice heavier in the latter than in the former.

Variations in body weight expressed by the coefficient of variation (C.V.) is fairly varied within the groups representing the same seasons

carcass weight in *C. glareolus*.
 coefficient of variations (C.V.) are given for different seasonal and age groups.

Table 1

Years	N	Body weight		Carcass weight		
		$\bar{x} \pm SD$	C.V.	$\bar{x} \pm SD$	C.V.	%body wt.
ADULT MALES						
Spring						
1964	27	22.4±2.46	11.00	12.5±2.21	11.85	55.80
1968	40	22.9±2.24	9.78	14.1±1.25	8.86	61.57
Summer						
1963	7	23.1±1.14	4.96	12.9±0.66	5.15	55.84
1964	36	21.5±1.75	8.14	11.8±1.15	9.72	54.88
1968	4	20.8±1.37	6.58	12.9±1.35	7.57	62.02
Autumn						
1963	7	19.2±3.24	16.91	10.0±1.53	15.28	52.08
1964	7	19.3±1.59	8.22	9.6±1.03	10.68	49.74
1967	8	17.2±1.51	8.78	8.2±0.96	11.72	47.67
1968	4	18.9±1.88	9.96	10.3±1.06	10.32	54.50
Winter						
1963/64	17	19.1±2.91	15.21	9.1±1.95	21.40	47.64
1964/65	14	14.6±1.98	13.54	6.8±1.10	16.19	46.58
1967/68	39	17.8±2.30	12.95	9.8±1.54	15.77	55.06
Total	210	20.2±3.30	16.33	1.2±2.47	22.05	55.55
ADULT FEMALES						
Spring						
1968	6	24.6±2.04	8.29	16.1±1.22	7.62	65.45
Summer						
1964	20	25.5±3.14	12.30	13.7±2.24	16.36	53.72
1968	1	22.0		13.5		
Autumn						
1967	13	18.4±4.12	22.43	9.2±1.51	16.39	50.00
1968	1	18.0		10.2		
Winter						
1963/64	17	18.1±2.03	11.24	8.6±0.93	10.81	47.51
1967/68	28	15.1±1.79	11.84	7.8±1.32	17.06	51.66
Total	86	19.4±4.96	25.28	9.9±3.11	31.38	51.03

in different years, for instance in autumn C.V. varies within limits of 7.01—24.56% for *C. glareolus* and 7.36—28.02% for *A. flavicollis* (Table 1, 2). Coefficients of variation are generally higher in the group of young animals than in adults, in both species of rodent. The carcass mass also exhibits lower variation than body mass (cf. Table 1, 2).

Variability of body and carcass weight

Years	N	Body weight		Carcass weight		
		$\bar{x} \pm SD$	C.V.	$\bar{x} \pm SD$	C.V.	% body wt.
YOUNG MALES						
Spring						
1968	3	20.13		11.67		57.97
Summer						
1963	22	29.14±4.56	15.64	17.60±3.43	19.48	60.40
1964	24	29.72±7.24	24.36	17.25±5.75	33.33	58.04
1968	49	26.25±6.97	26.55	15.72±5.31	33.77	59.88
Autumn						
1963	26	34.88±9.12	26.14	20.69±5.91	28.56	59.31
1964	21	37.02±5.81	15.69	23.41±3.60	16.06	60.53
1967	33	23.62±6.62	28.02	14.18±4.77	33.63	60.03
1968	18	37.30±6.68	17.90	23.69±4.68	19.75	63.51
Winter						
1963/64	30	33.74±6.95	20.59	20.54±5.49	26.72	60.87
1964/65	21	36.05±8.25	22.88	20.68±5.15	24.90	57.36
1967/68	36	26.44±5.40	20.42	16.72±2.98	17.82	63.24
Total	283	30.38±8.12	26.72	18.31±5.47	29.87	60.26
YOUNG FEMALES						
Spring						
1968	2	25.90		15.65		60.42
Summer						
1964	12	28.82±3.58	12.42	16.57±2.62	15.81	58.59
1968	34	26.15±5.11	22.08	13.63±3.55	26.04	58.90
Autumn						
1964	5	30.34±2.55	8.40	18.06±1.69	9.35	59.52
1967	31	20.72±4.95	23.88	11.89±2.95	24.81	57.38
1968	23	26.81±3.74	13.95	16.33±2.51	15.37	60.91
Winter						
1963/64	9	22.78±2.43	10.66	12.34±1.53	12.39	54.17
1967/68	20	20.20±2.85	14.10	11.72±1.86	15.87	58.01
Total	136	23.56±5.25	22.28	13.77±3.44	24.98	58.44

IV. FAT CONTENT

The basis for comparisons of fat content in animals was formed by percentages calculated in relation to dry mass. Preliminary analysis of the material showed that differences in fat content in the two sexes are significant, as are also, although not always, differences between young and adult animals. On this account it was decided to treat the groups distinguished separately.

in *A. flavicollis*. Explanations as in Table 1.

Table 2

Years	N	Body weight		Carcass weight		
		$\bar{x} \pm SD$	C.V.	$\bar{x} \pm SD$	C.V.	% body wt.
ADULT MALES						
1964	29	42.40±5.88	13.86	25.80±4.16	16.12	60.85
1968	2	36.08		23.65		65.54
Summer						
1963	1	37.80		23.90		63.22
1964	24	45.42±5.68	12.50	27.98±3.45	12.33	61.60
1968	1	48.70		32.40		66.52
Autumn						
1964	8	45.61±3.36	7.36	28.00±2.55	9.10	61.39
1967	5	39.13±3.50	8.94	25.83±2.51	9.71	66.01
1968	2	40.75		26.00		63.80
Winter						
1963/64	1	44.70		25.50		57.04
1964/65	4	38.35		21.80		56.84
1967/68	17	33.28±6.38	19.17	21.27±5.00	23.50	63.91
Total	94	41.32±6.89	16.67	25.55±4.48	17.53	61.83
ADULT FEMALES						
Spring						
1968	3	34.50		20.77		60.20
Summer						
1964	19	40.41±5.61	13.88	24.39±4.67	19.14	60.35
1968	1	33.20		20.20		60.84
Autumn						
1964	1	29.70		17.20		57.91
1967	9	32.72±3.28	10.02	20.41±2.58	12.64	62.37
1968	4	34.36		21.21		61.72
Winter						
1967/68	4	30.32		18.95		62.50
Total	41	36.27±5.91	16.29	22.13±4.17	18.84	61.01

1. *Clethrionomys glareolus*

Fat content in the vole carcasses varied within very wide limits, from 1.5 to 19.0%, and average values for different seasonal groups vary from 4.8 to 11.6%. The very high individual variation is expressed in the wide ranges observed and the high confidence limits (Fig. 1).

The calculated coefficient of variation C.V. varies from 13.6—49.8% in young males, and from 22.8—50.8% in adults. In the case of females this coefficient is similar, varying from 24.7—53.1% in young animals, and from 24.5—49.9% in adults (Table 3). It can be seen from table 3 that the

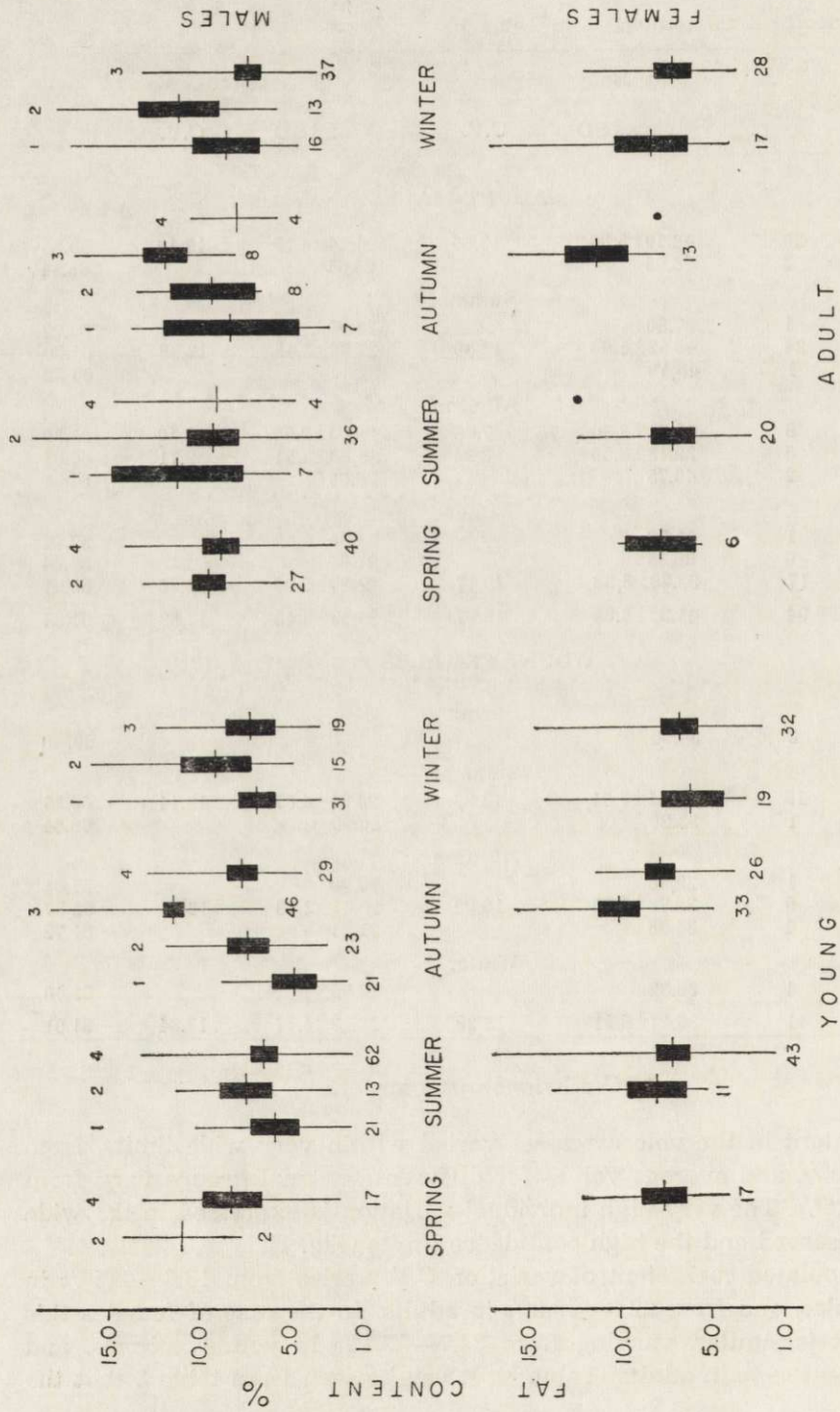


Fig. 1. Changes in fat content expressed as per cent of dry weight of the lean body in *Clethrionomys glareolus*. Vertical lines indicate extreme values, rectangles — 95 per cent confidence limits, and horizontal lines — the averages. Dots represent single specimens. Numbers below vertical lines indicate the sample sizes, and above them — year of sampling, as follows: 1 — 1963, 2 — 1964, 3 — 1967, 4 — 1968, and for winter months: 1 — 1963/64, 2 — 1964/65, 3 — 1967/68.

fat content in adult animals is in general higher, although differences are not always statistically significant.

Material is set out in Table 3 in such a way as to facilitate comparison of fat percentage in different seasons of different years, with due regard to the animals' age. There was no significant difference in the fat content of young adult females in any of the seasons and years studied. The absence of differences in this connection within the same season of different years made it possible to treat females as a uniform group in the various seasons. It will thus be seen that fat content is highest in these animals in autumn, when the percentage of fat is about 9.3%, and lowest in winter — 6.9%. In spring and summer fat content is maintained on the same level, with averages of 7.6 and 7.3%.

It may, however, be observed that the percentage of fat content in male carcasses takes a slightly different form. The percentage of fat was different in two different springs, but the small number of young animals with high fat content in the spring of 1964 did not contribute to significance of differences. Neither young adult voles differed significantly in respect of fat content in the two spring seasons. The average for young and adult individuals taken together gives a fat content of 8.8% for a carcass.

In summer the differences between successive years are not significant in either young or adult animals, but if the whole summer material is compared within the two age groups it will be found that the adults have a higher fat content (9.30%) than the young animals (6.40%), and that these differences are statistically significant ($F=14.36$, with $F_{0.05}=3.92$).

When comparing four different autumn seasons it can be seen that the fat content is different in each autumn, and that differences are statistically significant ($F=12.69$, with $F_{0.05}=2.08$). Age differences are also significant, but not on so high a level ($F=4.81$, with $F_{0.05}=3.92$).

Fat content in voles in winter in three different years is significantly different ($F=3.75$, with $F_{0.05}=3.07$), but there are no significant differences in the fat content of young and adult animals in different winters. This made it possible to calculate average values, which varied from 7.03 to 9.90%.

We can thus see that in males in some seasons (summer, autumn) there are differences in fat content in young and adult animals, and therefore the average for the season cannot be calculated without taking the animals' age into consideration.

The results obtained suggest that in general males have more fat than females, although the differences are not always statistically significant. Comparison of individuals of the two sexes is, however, only possible in relation to the segregated age groups within a given season.

Variability in fat content

Averages for youngs and adults or for particular seasonal groups are listed when

Years	YOUNG			ADULT			Avg. young +adult
	N	$\bar{x} \pm SD$	C.V.	N	$\bar{x} \pm SD$	C.V.	
<i>Clethrionomys glareolus</i>							
MALES							
Spring							
1964	2	10.92		27	9.30 \pm 2.37	25.48	8.76
1968	17	8.29 \pm 3.14	37.88	40	8.60 \pm 3.22	37.44	
Summer							
1963	21	5.77 \pm 2.81	48.70	7	11.00 \pm 3.97	36.09	
1964	13	7.35 \pm 2.46	33.47	36	9.12 \pm 4.13	45.28	
1968	62	6.42 \pm 2.77	43.15	4	8.40		
Avg.	96	6.40 \pm 3.06	47.81	47	9.30 \pm 4.18	44.95	
Autumn							
1963	21	4.84 \pm 2.41	49.79	7	8.13 \pm 4.13	50.80	
1964	23	7.30 \pm 2.33	31.92	8	8.95 \pm 2.78	31.06	7.72
1967	46	11.35 \pm 1.54	13.57	8	11.61 \pm 2.65	22.82	11.32
1968	29	7.56 \pm 2.24	29.63	4	7.61		7.57
Winter							
1963/64	31	6.83 \pm 2.84	41.58	16	8.17 \pm 3.32	40.64	7.28
1964/65	15	9.10 \pm 3.42	37.58	13	10.82 \pm 3.75	34.66	9.90
1967/68	19	7.07 \pm 2.68	37.91	37	7.01 \pm 2.43	34.66	7.03
FEMALES							
Spring							
1968	17	7.61 \pm 2.40	31.54	6	7.70 \pm 1.89	24.54	7.63
Summer							
1964	11	7.97 \pm 2.40	30.11	20	7.02 \pm 2.68	38.18	7.32
1968	42	7.08 \pm 3.02	42.66	—			
Autumn							
1967	33	10.06 \pm 2.95	29.32	13	10.93 \pm 2.72	24.88	9.29
1968	26	7.80 \pm 1.93	24.74	—			
Winter							
1963/64	19	6.12 \pm 3.25	53.10	17	7.96 \pm 3.97	49.87	6.86
1967/68	32	6.72 \pm 2.78	41.36	28	6.84 \pm 2.52	36.84	

It is also clear from the above comparisons that differences in fat content in voles within the same season, e.g. autumn (Table 3) may be greater in different years than in successive seasons of one year.

Differences found between years make it impossible to grasp any distinct seasonal trend. If, however, we arrange the material in chronological order, while retaining the order of seasons, it can be seen that there are certain seasonal trends (Fig. 2). Material was available from

Table 3
 in *C. glareolus* and *A. flavicollis*.
 analysis of variance showed no statistically significant differences between them.

Years	YOUNG			ADULT		
	N	$\bar{x} \pm SD$	C.V.	N	$\bar{x} \pm SD$	C.V.
<i>Apodemus flavicollis</i>						
MALES						
Spring						
1964	1	2.77		29	6.12±2.68	43.79
1968	3	8.10		2	8.36	
Summer						
1963	21	10.15±6.05	59.60	1	5.79	
1964	24	7.81±3.37	43.14	24	7.07±4.37	61.81
1968	48	7.11±2.76	38.81	1	13.71	
Autumn						
1963	26	3.74±1.97	52.67	—		
1964	21	4.20±1.49	35.30	8	4.24±1.98	46.69
1967	33	10.31±4.34	42.09	5	9.04±2.50	27.65
1968	18	5.11±2.46	48.14	2	6.22	
Winter						
1963/64	30	6.25±4.17	66.72	1	10.35	
1964/65	21	6.88±5.76	83.72	4	8.90	
1967/68	35	8.04±5.10	63.40	16	9.32±5.88	63.09
FEMALES						
Spring						
1968	2	7.12		3	6.97	
Summer						
1964	11	12.11±3.08	25.43	19	6.20±2.02	32.58
1968	33	7.59±2.68	35.30	1	3.76	
Autumn						
1964	5	4.64±2.43	52.37	1	4.26	
1967	30	12.29±4.75	38.64	8	9.57±2.58	26.95
1968	23	7.31±2.17	29.68	4	5.84	
Winter						
1963/64	9	8.67±2.92	33.67	—		
1967/68	20	7.88±5.05	64.08	4	7.80	

two cycles, summer 1963 to winter 1964, and from the autumn 1967 to the autumn of 1968 inclusive. Variations take place almost synchronously, in both young and adult animals and in males and females, for instance from summer to autumn in 1963 we observe a slight decrease in percentage of fat content, but in winter an increase, particularly in young individuals (cf. Fig. 2). The relatively high level of fat content in vole carcasses is maintained in the spring of the following year, and also

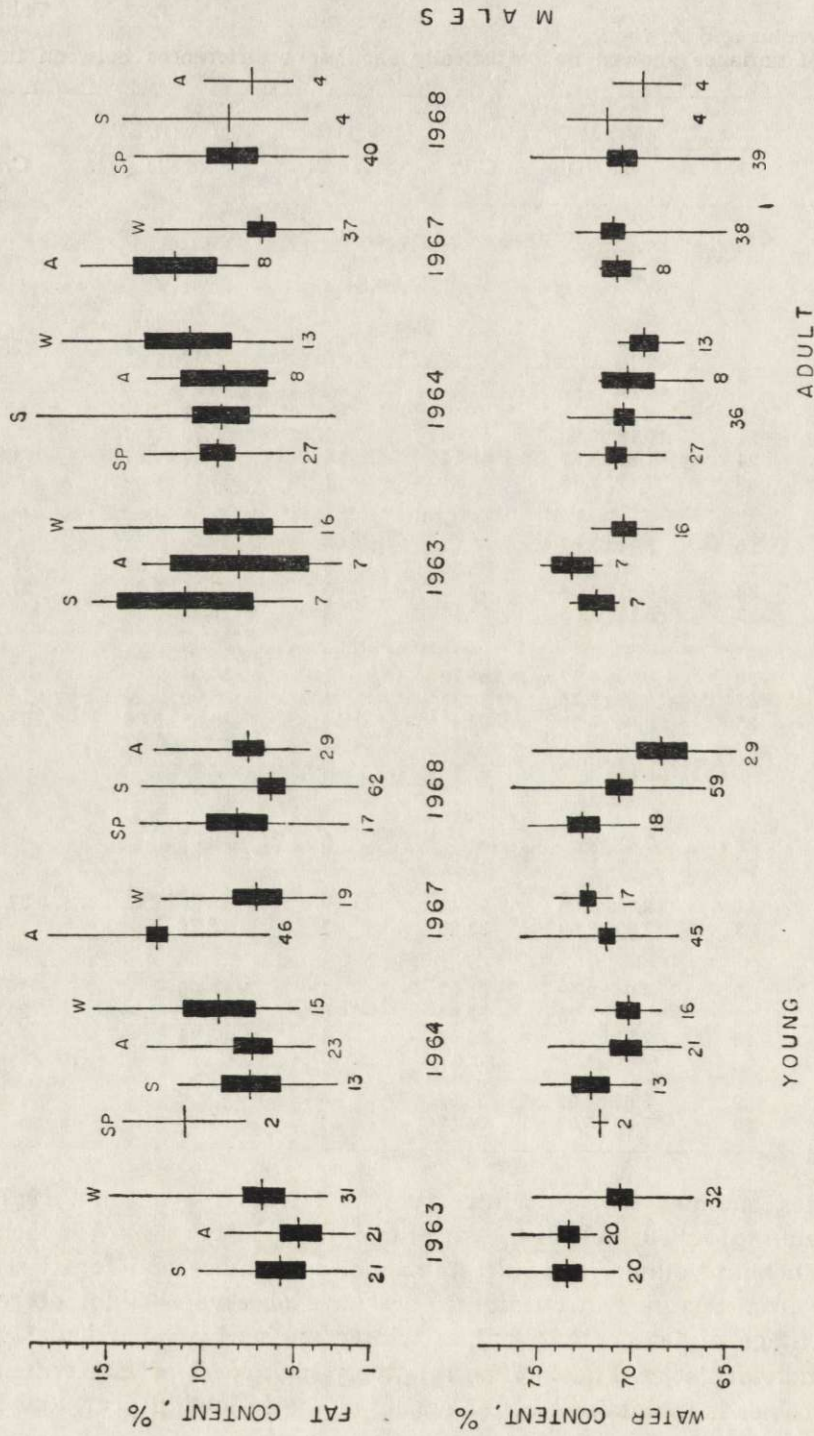


Fig. 2. Seasonal changes in fat and water contents in *Ciethronomys glareolus*. Sp — Spring, S — Summer, A — Autumn, W — Winter. Other explanations as in Fig. 1.

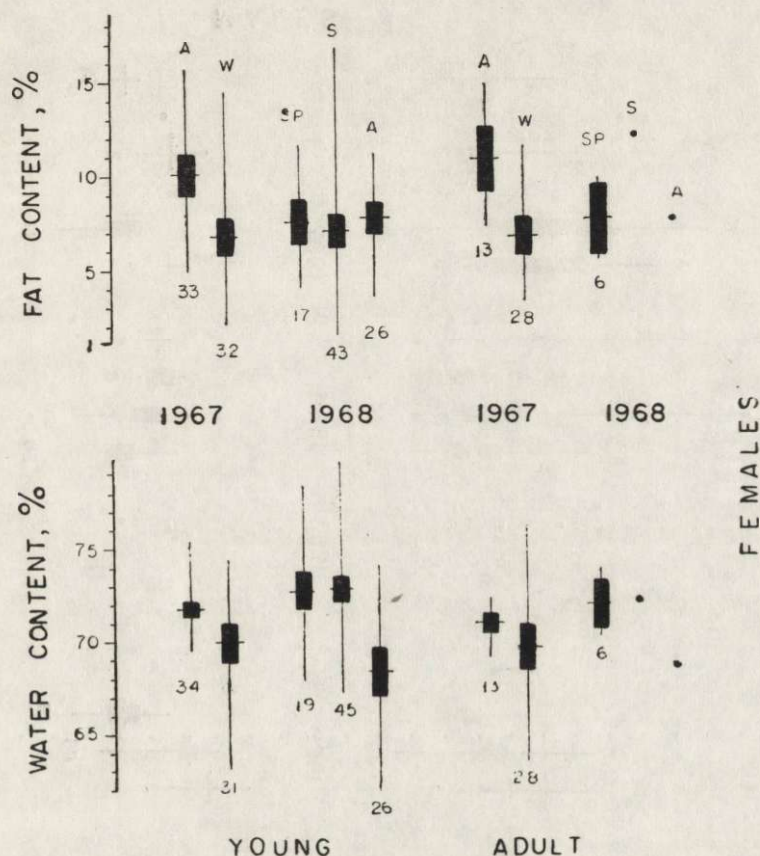


Fig. 2. Continued.

during summer and autumn. During the winter of 1964/1965 a further increase in fat content is found, when the maximum average values for this two-year period are reached (over 9% in young and about 11% in adult animals).

During the period 1967/1968 5 seasonal samples were available, and here the decrease in fat content in vole carcasses from the autumn to winter of 1967 is particularly distinct. The following year, on the other hand, the lowest values are observed in summer and an increase in fat content in autumn (Fig. 2).

It can be seen from the above that differing trends in seasonal changes are observed during the two study periods.

2. *Apodemus flavicollis*

As in the case of *C. glareolus*, there are considerable individual variations in the percentage of fat content in the carcasses of *Apodemus fla-*

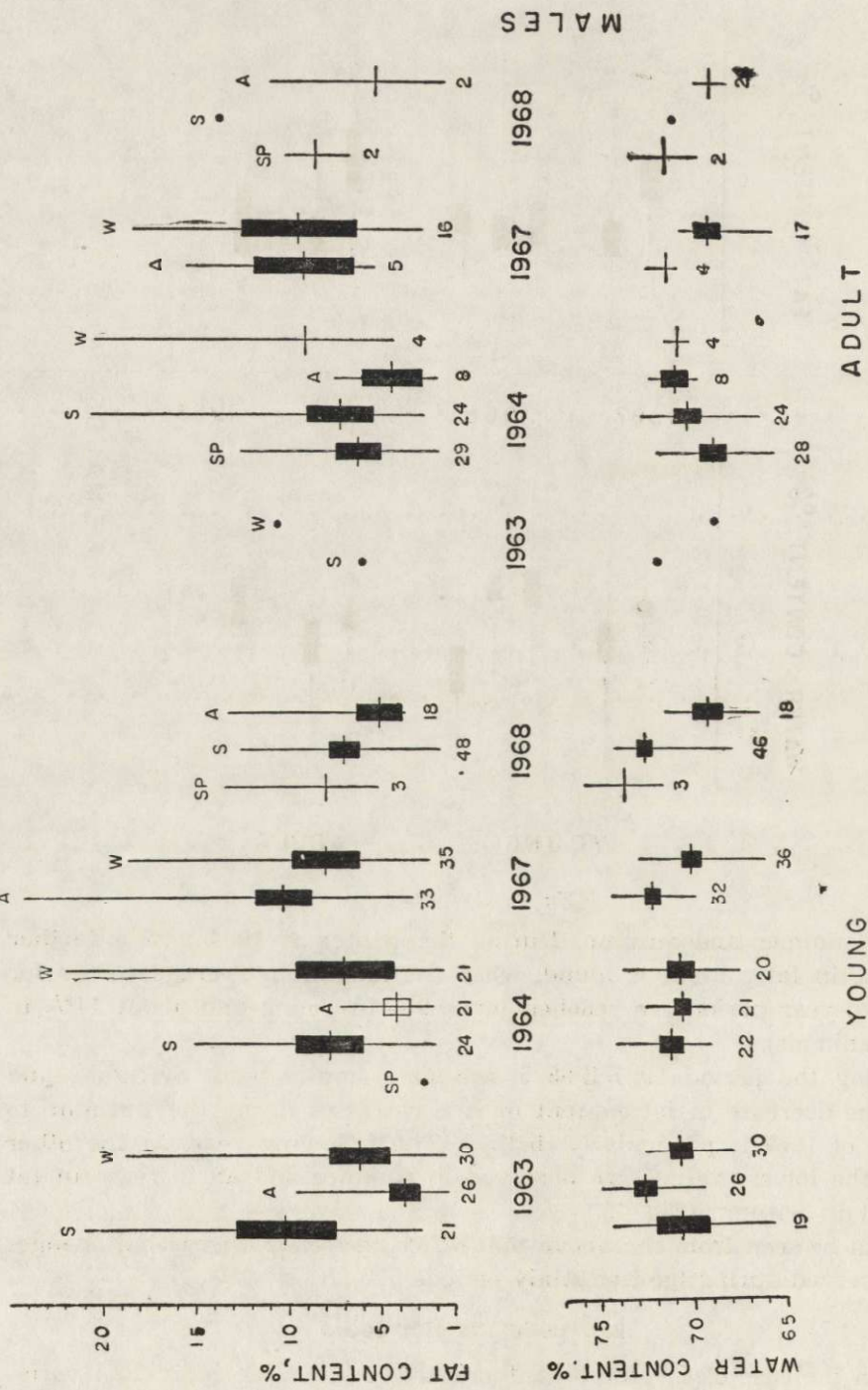


Fig. 3. Seasonal changes in fat and water contents in *Apodemus flavicollis*.
 Explanations of symbols as in Figs. 1 and 2.

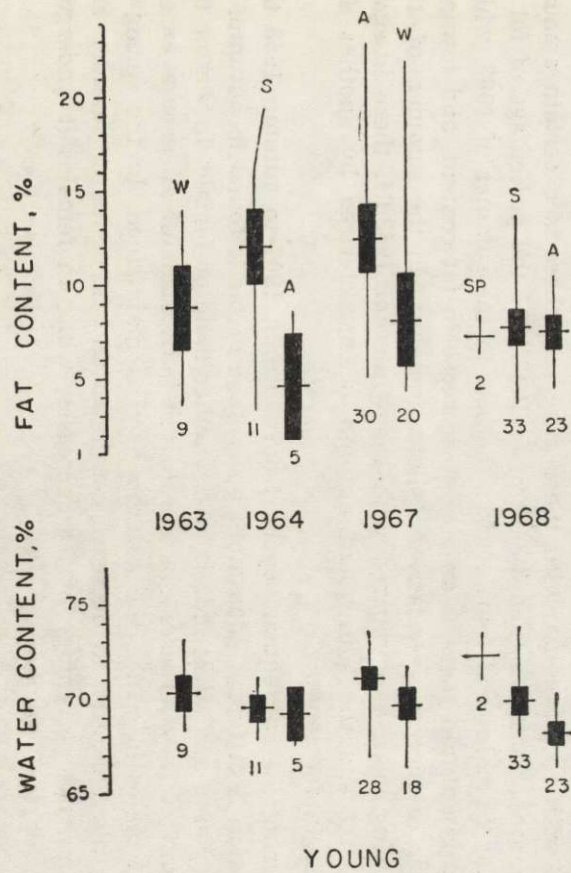
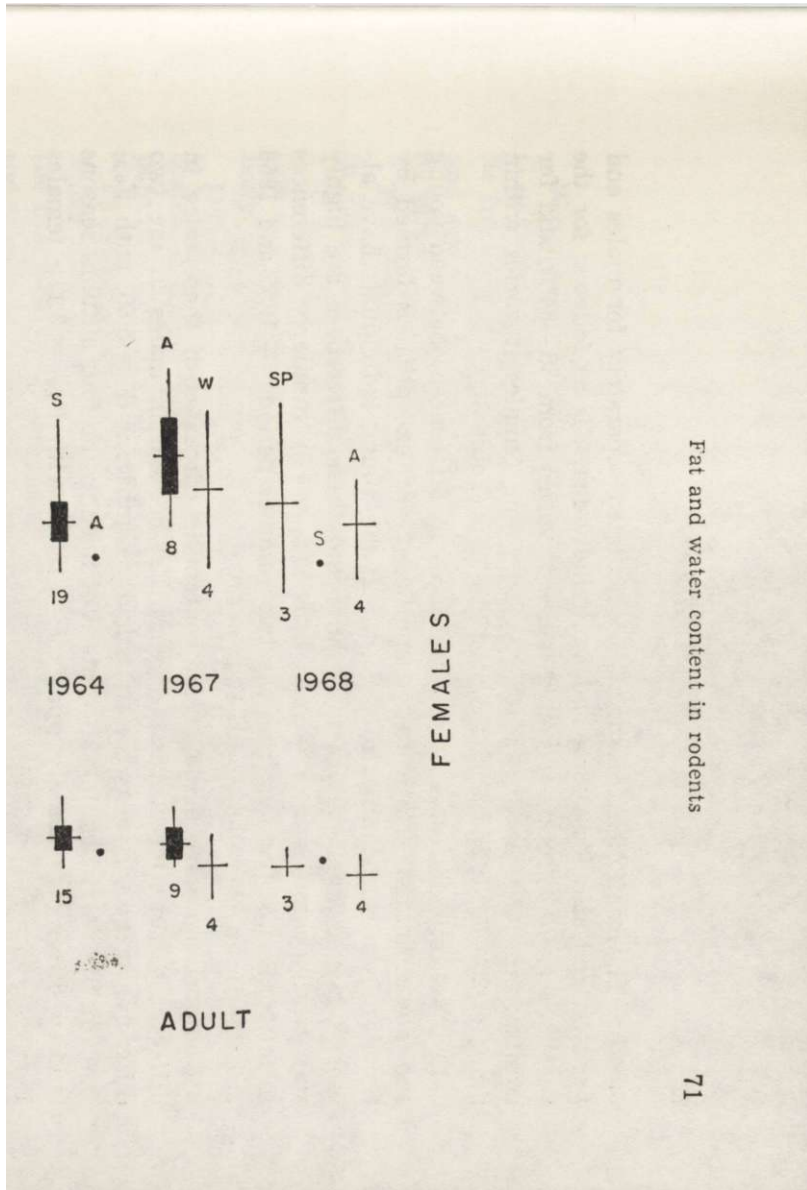


Fig. 3. Continued.



vicollis. The coefficient of variation calculated separately for males and females, and also for young and adult individuals, is as follows: for the various seasonal groups of young males it varies from 35—84%, and for adults from 28% to 63%. Similarly for young females it varies within limits of 25—64%, and adults from 27 to 32% (Table 3).

In practically no cases were differences in fat content between young and adult animals statistically significant. An exception is formed by females from the summer of 1964, when the young individuals have almost twice as much fat as the adults and these differences are highly statistically significant ($F = 12.8$, with $F_{0.05} = 4.0$). Similarly differences in fat content of females from the two summer periods — 1965 and 1968 are significant ($F = 6.83$, with $F_{0.05} = 4.0$).

Comparisons were made of fat content in carcasses of these mice in different seasons for successive years. Fat content in males in the two different spring seasons were statistically significant ($F = 5.60$, with $F_{0.05} = 4.16$). Similarly also the fat content of mice in the four autumn seasons studied differ significantly (males $F = 19.78$, with $F_{0.05} = 3.11$; females $F = 7.97$, with $F_{0.05} = 3.14$).

In the three summer periods compared, however, no significant differences were found in fat content of males, while in winter neither females nor males differed significantly in this respect.

As with *C. glareolus*, with these mice also there is a certain amount of seasonal variation (Fig. 3). In series 1963/1964 the percentage of fat is similar in males and females. It is highest in the summer of 1963, while towards autumn there is an abrupt decrease in fat content, and towards winter a successive relatively slight increase. In the summer of the following year, as compared with the winter of 1963/64, there is again more fat and the subsequent autumn is characterized by another decrease in fat content.

During the subsequent cycle from autumn 1967 to autumn 1968 the situation is different. Maximum percentage of fat is found in autumn, in both young and adult individuals, whether male or female. In winter the amount of fat decreases considerably in individuals of all groups except adult males in which the autumn level is maintained. In the spring of 1968 the tendency to decrease continues and in males in summer and autumn the percentage of fat decreases, while in females it undergoes no important changes.

Thus in the case of *A. flavicollis* the observations made of the bank vole in respect of differences in seasonal variations in the two different cycles studied are confirmed. In addition the character of seasonal variations in the two species of rodents is similar.

V. WATER CONTENT

Water content is a fairly constant value and similar in both species. In *C. glareolus* it varies within limits of 61.97—79.66%, and in *A. flavicollis* from 65.60% to 75.94%. The average values for the different seasonal and age groups come within the following limits: for *C. glareolus* from 69.92 to 72.68% and for *A. flavicollis* from 69.72 to 71.56% (Table 4).

The coefficient of variation for different seasonal groups distinguished in Fig. 2 and 3 may vary from 1.17—4.95% for *C. glareolus* and from 1.15 to 4.08% for *A. flavicollis*, and are for understandable reasons very low in comparison with, for instance, such coefficients of variation as for body weight or fat content.

Differences in water content in young and adult individuals, whether males or females, are not significant in any of the years or seasons compared for both species of animals.

In some seasons, however, significant differences can be observed in water content in animals from different capture years. For instance in the case of female *C. glareolus* water content in the autumn of 1967 was significantly higher (71.83%) than in the following year (68.40%) (Fig. 2) ($F = 10.90$, with $F_{0.05} = 3.98$). The case is the same with males. When material from four autumns is compared it can be seen that there is a different water content each autumn and that differences are statistically significant ($F = 14.05$, with $F_{0.05} = 2.67$) (Fig. 2).

With *A. flavicollis* no significant variations were observed in water content in carcasses of animals obtained in different years, but the same season (Fig. 3).

Average values of water content were calculated for the animals (Table 4) in material from all years jointly, and seasonal differences traced. It is clear from these comparisons that females of *C. glareolus* have the lowest percentage of water in winter. In spring the amount of water increases and the highest level is attained in summer. In autumn water content in the tissues again decreases. These differences, although only of the order of not quite 2.5 or 3.0%, are significant (*t* Student test). This applies to differences between summer and winter and summer and autumn (Table 4). In male voles the character of variations in water content of these animals is mainly similar in the different seasons, but these differences are statistically significant.

In *A. flavicollis* water content traced over seasons is similar to that in *C. glareolus*, as decrease in the water content is observed from summer to winter and differences in the percentage of water in carcasses in successive seasons are significant for males and not significant for females (Table 4).

Table 4

Seasonal changes in water content in *C. glareolus* and *A. flavicollis*. Statistically significant differences are indicated by an asterisk (Student *t* — test). Sp — Spring, S — Summer, A — Autumn, W — Winter.

Season	N	Min.	Max.	$\bar{x} \pm SD$	C.V.	between:	Difference %	t
<i>Clethrionomys glareolus</i>								
MALES								
Spring	86	64.05	75.87	71.24 ± 2.05	2.87	Sp — S	+0.17	P 0.05
Summer	139	66.23	76.61	71.41 ± 2.34	3.27	S — A	-0.24	P > 0.05
Autumn	140	64.48	76.38	71.17 ± 2.63	3.70	A — W	-0.31	P 0.05
Winter	132	65.21	75.26	70.86 ± 1.65	2.33	S — W	-0.55	0.05 > P > 0.01*
FEMALES								
Spring	25	68.14	78.25	72.54 ± 1.96	2.71	Sp — S	+0.14	P > 0.05
Summer	77	67.20	79.66	72.68 ± 1.90	2.61	S — A	-2.27	P < 0.001*
Autumn	74	61.97	75.38	70.41 ± 2.65	3.76	A — W	-0.49	P > 0.05
Winter	94	63.22	76.41	69.92 ± 2.55	3.65	S — W	-2.76	P < 0.001*
<i>Apodemus flavicollis</i>								
MALES								
Spring	33	65.61	75.94	70.37 ± 2.10	2.98	Sp — S	+1.19	P < 0.01*
Summer	113	65.60	74.62	71.56 ± 1.99	2.78	S — A	-0.10	P > 0.05
Autumn	111	66.35	75.06	71.46 ± 1.65	2.30	A — W	-1.19	P < 0.001*
Winter	108	65.76	74.03	70.32 ± 1.72	2.44	S — W	-1.24	P < 0.001*
FEMALES								
Spring	5	69.15	73.27	70.66 ± 1.63	2.30	Sp — S	-0.55	P 0.05
Summer	60	67.66	73.72	70.11 ± 1.45	2.06	S — A	-0.39	P > 0.05
Autumn	70	66.06	73.33	69.72 ± 1.89	2.71	A — W	+0.16	P 0.05
Winter	31	66.27	73.04	69.88 ± 1.60	2.28	S — W	-0.23	P 0.05

VI. CALORIC VALUE OF FAT

The caloric value of fat for the two species of animals was determined for all seasons. It was observed that there are no significant differences between values obtained from different capture years, and therefore this index was considered from the seasonal aspect only.

The caloric value of fat in *C. glareolus* in different seasons is as much as 0.6059—9.4867 kcal/g and is very similar to that in *A. flavicollis* 8.6785—9.3700 kcal/g (Table 5).

Some differences are observed between males and females, particularly in *A. flavicollis*. The average caloric value of fat is higher in females

Table 5
Variability of caloric value (in kcal/g) of the rodents' fat.

Season	N	Males		Females		
		$\bar{x} \pm SD$	C.V.	N	$\bar{x} \pm SD$	C.V.
<i>C. glareolus</i>						
Spring	10	9.4867 \pm 0.30	3.16	12	8.6908 \pm 0.45	5.14
Summer	12	9.2758 \pm 0.26	2.80	10	9.3322 \pm 0.40	4.30
Autumn	17	8.6059 \pm 0.55	6.44	23	8.8622 \pm 0.56	6.34
Winter	12	9.2692 \pm 0.48	5.22	14	9.2628 \pm 0.45	4.83
Total	51	9.0924 \pm 0.55	6.05	59	9.0020 \pm 0.54	6.00
<i>A. flavicollis</i>						
Spring	3	8.6933 \pm 1.05	13.11	3	9.3700 \pm 0.51	5.49
Summer	20	9.0900 \pm 0.93	10.22	9	9.1122 \pm 0.37	4.09
Autumn	26	8.6785 \pm 0.55	6.29	29	8.8493 \pm 0.72	8.13
Winter	25	8.9020 \pm 0.99	11.15	17	9.2212 \pm 0.44	4.73
Total	74	8.8658 \pm 0.50	6.25	58	9.0260 \pm 0.61	6.78

(9.0260 kcal/g) than in males (8.8658 kcal/g). In *C. glareolus* these values are almost uniform, differing by only 0.09 kcal/g in favour of males. It is therefore difficult to speak of any regularities in seasonal variations on the strength of the data contained in Table 5.

VII. DISCUSSION

Some data on fat content in the body of non-hibernating mammals are to be found in literature on gross body composition, a very wide range of fat content being given for species related to those discussed in the present studies. For instance Wolff & Bakay (1963) state that female laboratory mice of the yellow (*Aya*) strain contain 47.7% of fat, whereas females of the non-yellow strain (*aa*) only 15.6%. The range of variations in fat content in *Peromyscus polionotus* may be as great as from 15 to 27%, as shown by Connell's data (Golley, 1962). Aver-

age fat content for different groups of *Peromyscus leucopus noveboracensis* calculated by Sealander (1951) varies from 10.0 to 28.55%. The observations made by Hayward (1965) are also interesting, showing that different breeds of *Peromyscus* living under natural conditions have for lower fat content (2.72—10.09%) than animals adapted to laboratory conditions (10.0 to 52.21%). The data given for free-living *Peromyscus* are closest to those obtained in the present study. In the majority of cases, however, the fat content of carcasses of *C. glareolus* (averages for different groups from 4.84 to 11.61%) or *A. flavicollis* (respectively 2.77—13.71% of dry mass of carcass) were lower than the data given by the above authors. One of the species examined, *A. flavicollis*, was recently studied in this respect in the south of Poland (Sawicka-Kapusta, 1968), and the data obtained by this author on the fat content of these animals are also higher than those given in this study, being on an average for the various groups from 11.9 to 20.8% of dry weight.

The relatively lower degree of fat content in the rodent carcasses examined is obviously due to the way in which the animals were prepared for ether extraction. In our case, in connection with the other studies simultaneously conducted on the same animals, and the necessity for later determination of the age of animals, the head together with the brain were discarded, and this of course contains a relatively large amount of lipids. Part of the subcutaneous fat was removed together with the skin, which may, for instance, contain as much as 18% of fat (Sawicka-Kapusta, 1968), and in addition removed together with the mesenterium when excising the alimentary tract. The carcasses, however, contained deposits of perirenal fat, and fat in the inguinal region, between the scapulae, etc. In view of the lack of detailed data it is difficult to ascertain the order in which fat is deposited in the various regions of the body in the rodent species examined, and consequently to state when gross body fat has been taken into consideration in the studies.

Reciprocal comparison of results obtained by different authors is rendered extremely difficult by the application of different methods for extracting fat, and particularly by the different ways in which material was prepared. Most often whole animals from which the alimentary tract had been removed were used (e.g. Sawicka-Kapusta, 1968), but sometimes additionally with the skin removed. There is frequently absence of clear description of the way in which the material was prepared for extraction (Sealander, 1951; Hayward, 1965). Finally the fat content of animals is increasingly frequently expressed in percentages of *FFBW* (Hayward, 1965), but indices are also to be found in literature relating to fresh body mass (Hayward, 1965), indices of fat

content (= g of fat/g dry weight), or condition coefficients (Hsia-Wu-ping & Sun-Chung-lu, 1963). It would thus appear that there is particularly great need for establishing uniform procedure and study methods, if the data obtained are to be used for comparative purposes.

The chief purpose of the studies presented here was not discuss the absolute value of fat content in rodents, but to draw attention to the scale of variation in this parameter from different aspects, primarily depending on the seasonal and long-term cycle.

The problem of individual variations has not in principle been taken into consideration in the studies of this type made up to the present. The scale of individual variations presented in this study, expressed by variation coefficients of up to 53% in *C. glareolus* and up to 84% in *A. flavicollis*, show how greatly fat content may vary in rodents under natural conditions, and therefore how important sample size becomes. In research work of this type studies are frequently encountered giving the fat content of a small number of animals only (Wolff & Bakay, 1963; Buckner & Bergeron, 1972), which by no means necessarily describes the population of a given species in a given season. Thus, although the research procedure here also is laborious it is essential to obtain representative samples in order to ensure that results are reliable.

The majority of the authors referred to draw attention to the existence of seasonal differences in fat content of non-hibernating rodents. All are agreed as to the low fat content of insectivores in summer (Myrcha, 1969) and rodents (Sealander, 1951; Connell, after Golley, 1962; Hayward, 1965; Hsia-Wu-ping & Sun-Chung-lu, 1963). Sawicka-Kapusta (1968) has drawn a curve of variations in fat content in *A. flavicollis* in different seasons and confirms earlier observations made in respect of other species (genus *Peromyscus*). The data presented in the present study only partially confirm these observations, since it proved that the two species of rodents exhibited a significantly higher fat content in winter in two successive years, 1963 and 1964, this index increasing gradually over this period. Consequently samples from the two winters differed considerably in respect of the percentage of fat content (e.g. in male *C. glareolus* 7.27% and 9.90% — cf. Table 3). In the subsequent two-year study cycle (1967—1968) a decided and significant decrease in the fat content of the animals was observed in winter (particularly in 1967 — cf. Fig. 2 and 3). It can be seen from this that in two successive series of studies we may have to do with different courses of seasonal rhythm in the fat content of non-hibernating rodents.

The data presented (Fig. 1) show that the maximum degree of fat content in animals in a given year can be reached at almost any time of the year, if a longer study period is considered. This may be summer,

autumn or winter (cf. Figs. 2 and 3). It is thus essential to carry out long-term observations in order to grasp the whole scale of variations in the animals' fat content, whether to describe their condition or the caloric value of biomass at population level.

It was interesting to discover the considerable degree of synchronization in seasonal variations in the two species of rodents examined. Although these were representatives of two families differing as to food preferences, yet these two species exhibit relatively great similarity. Despite the fact that *C. glareolus* is a more polyphagous species than *A. flavicollis*, both are to a great extent grain-eaters, particularly in winter (Górecki & Gębczyńska, 1962; Drożdż, 1966; Holišova, 1971), and accumulate food stores. This most probably conditions the character and rhythm of the seasonal variations observed synchronously in *C. glareolus* and *A. flavicollis*, and also increase in fat content in these animals in winter, when the greater part of their food has a high caloric value.

The food supply conditions of these rodents will vary in a given year depending on intensity of fruiting of trees in deciduous forests of the temperate zone, which as is well known is subject to variation from year to year. It would thus seem that differences in degree of fat content in rodents accumulating stores of tree and shrub seeds for winter will be conditioned primarily by the actual states of their natural food supplies. This statement cannot of course be generalized to apply to all rodents, especially not to other *Microtidae* feeding chiefly on green food.

The material for the studies presented was obtained during the period 1963—1964 in the 9 ha study area, in which an attempt was made to supplement the rodents food supply by sprinkling oats in amounts which the animals can consume completely (up to 30 kg/week). Despite this no distinct differences in fat content of the animals were between 1963/64 period and the 1967/68 series, or in individuals obtained from the experimental and control areas. In view of the limited range of action of the increased food supply and the fairly low caloric value of oats (cf. Drożdż, 1966; Grodziński & Sawicka-Kapusta, 1970), this would not appear to be an adequate argument proving that there is no possibility of the current food supply effecting the degree of fat content (condition) in rodents.

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ZMIENNOŚĆ OTŁUSZCZENIA I ZAWARTOŚCI WODY U DWU GATUNKÓW GRYZONI

Streszczenie

Badano procentową zawartość tłuszczu w suchej masie tuszek (bez głowy, skóry i przewodu pokarmowego) dwu gatunków gryzoni, *C. glareolus* (N = 773) i *A. flavicollis* (N = 523). Zwierzęta łowiono w grądach Białowieskiego Parku Narodowego w dwu okresach: 1963—64 oraz 1967—68. Tuszki przygotowane do ekstrakcji etero-

wej stanowiły ponad 50% masy ciała *C. glareolus* i około 60% masy ciała *A. flavicollis* (Tabele 1, 2). Stwierdzono ogromną zmienność indywidualną stopnia otluszczenia zwierząt, w granicach od około 1 do 24% (Rys. 1, 2, 3). Średnie arytmetyczne procentowej zawartości tłuszczu wahały się w granicach od 4,8 do 11,6% dla poszczególnych grup sezonowych i wiekowych u *C. glareolus* i od 2,8 do 13,7% u *A. flavicollis* (Tabela 3). Współczynniki zmienności wynosiły od 14 do 53% u nornicy i 25–84% u myszy wielkookiej. Otluszczenie dorosłych gryzoni jest na ogół wyższe niż młodych, oraz samców wyższe niż samic, choć nie zawsze różnice te były statystycznie istotne. Różnice w stopniu otluszczenia w obrębie tego samego sezonu są większe w poszczególnych latach niż w obrębie różnych sezonów danego roku. Rytm zmian sezonowych jest podobny u obydwu gatunków i ma różny przebieg w różnych latach. (Ryc. 2, 3).

Zmienność koncentracji wody w tuszkach gryzoni jest znacznie mniejsza (C.V. wynosi od 1 do 5%) i wykazuje wyraźny rytm sezonowy z maksimum wiosną i latem a minimum zimą (Tabela 4).

Kaloryczność tłuszczu jest wartością stałą. Współczynniki zmienności wahały się u *C. glareolus* w granicach od 2,8 do 6,4% a u *A. flavicollis* od 4,1 do 13,1%. Średnie arytmetyczne dla grup sezonowych nie wykazują ukierunkowanych zmian (Tabela 5).

Dyskutowane są kwestie metod badania otluszczenia zwierząt oraz zagadnienie synchroniczności zmian sezonowych u gryzoni o podobnych stosunkach pokarmowych.