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Biomorphological Variability of the Population of *Clethrionomys glareolus* (Schreber, 1780) *

[With 25 Tables and 32 Figs.]

Analysis was made of variations in body weight and length and in age structure and reproduction dynamics of *C.glareolus* (Schreber, 1780) over a period of ten years (N=8040) and within the limited area of the Białowieża National Park. The existence of considerable variations in body dimensions in different years and seasons was demonstrated, and a critical assessment made of the significance of these characters in taxonomy of the species. Maximum body dimensions were observed in both sexes during the spring period. Sex dimorphism was expressed (with the exception of the autumn) by the greater body weight and length of females than males. Differences were found in the rate of growth and sexual maturation between the spring and autumn generations, the first of which exhibited rapid uninterrupted growth during the summer, and the second inhibition of growth and sexual maturation until the spring of the following calendar year. Individuals of this generation were characterised in addition by a greater capacity for survival during the autumn-winter period, and prolongation of the juvenile period. In 1954 the autumn generation exhibited different behaviour — owing to favourable climatic and food conditions the rate of growth of individuals was not inhibited. They rapidly attained sexual maturity and reproduction continued during the winter period. This contributed to the mass appearance of *C. glareolus* the following year (1955). The above data point to the different reaction of rodents to varying conditions in the external habitat.

* This paper is dedicated to the Memory of Professor Dr. August Dehnel.

I. INTRODUCTION

During the last few years there have appeared many theriological publications on *Microtinae*. This numerous group of small mammals in the Palearctic was given considerable attention from the theoretical and practical point of view.

The causes of lively interest in this group are various. Undoubtedly the substantial motives derive from the reproductive ability of these mammals, and their adaptability, closely connected with the factors of their ecology, and the harm they bring to agriculture.

Another more theoretical cause of interest in the above-mentioned group of *Micromammalia* resulting from improved, more precise and penetrating methods of investigation, is the necessity to revise the lower systematic units hitherto recognised. Some of them are the result of stereotyped studies executed several decades ago.

In the sub-family *Microtinae*, a respectable place, because of the multitude of works upon it, belongs to the genus *Clethrionomys* Tilesius, 1850. Numerously represented forms include almost the whole of Holarctic. In this genus are taxonomic "groups" such as: *glareolus, rutilus, nageri, rufucanus* with their attendent "subspecies", which are taken into consideration in the divisions of Millêr (1912), Hinton (1926), Ellerman (1941), Ognev (1950) and which still to be corrected. The last author mentioned, indeed, with a relatively large taxonomic ballast, devotes much space to the complexity of environmental factors and their consequences.

Schaefer (1935) and Stein (1951) very penetratingly call attention to the still frequently traditional and abstract character of interpretation of lower systematic units. They point out the ecological and populational character of morphological variability in individuals occupying a certain area.

Schwarz (1959) gives more extensive and more exhaustive comments in this field, noting the parallelism of individual and geographical variability in lower systematical units, among others in *Microtinae*. I wish to draw attention to the great adaptibility of these animals, which can be noticed in individual and geographical variability; not only such characteristic features as colour or proportions of the body, but also deeper, more "stabilized" elements of their organisms. Not considering these features of the organism, the author believes, sometimes leads to the incomplete or mistaken description of a given species or subspecies. He mentions many authors who in some degree helped to make systematic taxonomy more "plastic" and stabilized, both in reference to the form described and its relatives.

The balance of the last several years in reference to this problem gives us grounds for optimism.

Much notice is devoted to the most representative individual of this species — the bank vole. We know that this species includes almost the whole of Palearctic and is very adaptable. It can be found in various greatly-differing wooded environments.

This characteristic dynamism of the bank vole results from great adaptability, and the ability to eat absolutely any food (if necessary) (Wrangel, 1939; Naumov, 1948; Ognev. 1950; Koškina, 1957; Zejda, 1961; and others).

Publications on this species differ. Many of them are just fragmentary, describing a small sector of the subject; numerous, also, are works dealing with the problem on a large scale. There appear to be three basic trends in investigation: systematic and zoogeographical, ecological, and biomorphological. It would be difficult, taking into consideration the present state of methods of investigation, to make a more precise classification or description. Incontestable is the fact, that as regards the wild mammals (and others as well) these three above-mentioned trends, if followed simultaneously, give a better possibility of deeper knowledge of variability in a given species and the processes governing it.

The many-sided character of these speculations clearly stands out from former statistical analysis of the species, giving instead a plastic picture of the growth and the state of the individuals of the population in a given area.

In my study on *Clethrionomys glareolus* (Schreber, 1780) in the Białowieża National Park I decided to analyse the morphological variability of this species in its several aspects. I have taken into consideration chiefly those features which hitherto were given less notice, or worked on from different angles.

Having much material (more than 8,000 specimens) gathered over several years, I made efforts to consider the problem of the variability of the morphological features investigated from the following points of view: individual, their age, annual and seasonal. I devoted much attention to the changes in length and body weight, having in mind the taxonomic significance of these features.

I wanted to investigate the dynamics of population from the angle of the age of the individuals, the quantitative oscillation of both sexes, the intensity of their breeding, and the biological value of various generations in several analysed years.

At the end I discuss their mass appearances, and their consequences.

The above profile of research is essentially a continuation of the studies started by Dehnel (1949), in the Białowieża National Park and later continued by his pupils and co-workers (Adamczewska, Bazan-Kubik, Borowski, Caboń, Kubik, Pucek, Tarkowski, Wasilewski and others).

The chief aim of the research of this team is to obtain knowledge, from all possible angles, of forms in a given area in the Białowieża National Park both from the morphological angle and the functional. The substance of these investigations is the problem of biomorphological variability of *Micromammalia*.

I want to express special gratitude to my late Teacher, Professor Dr. August Dehnel, for his valuable help and consultations given during the preparation of this work.

I wish also to thank Dr. Marian Dąbek, from the Department of Mathematical Statistics at M. Curie-Skłodowska University (Lublin) for his valuable remarks and help during the statistical analysis of the material.

II. MATERIAL AND METHOD

The analysed collection of *Clethrionomys glareolus* (Schreber, 1780) comes from the National Park in Białowieża (BNP).

Systematic catching over several years supplied more than sufficient material for study. More than 8 thousand bank voles were collected from 1946 to 1955 on previously chosen capture areas in several different biotopes.

Detailed informations about methods of capture, description of 9 particular biotopes, their floral composition, characteristic features of the soil, thermic conditions etc. are given in the works of: Dehnel (1949), Borowski & Dehnel (1953), Matuszkiewicz (1954), Adamczewska (1960), Sidorowicz (1960).

To follow the possible morphological changes connected with the age of the specimens, the whole material was classified into several age groups.

Taking into consideration my own data and that from the works of Wrangel, 1939; Mohr, 1950; Prichodko, 1951; Sviridenko, 1959; Wasilewski, 1952; Stein, 1956; Koškina, 1955, 1957; Zejda, 1962, I established 5 age groups according to the structural state and growth of the first lower molar (M_1). The following age groups were considered: I — juvenis; II — subadultus; III — adultus I; IV — adultus II; V — senex.

The approximate length of life of each particular class was established. The publications of the authors cited greatly helped, on account of their penetrating treatment of this question.

On the whole the classifications are tinged, however, with subjectivism. Thus it is often difficult to establish the length of life or age of a particular specimen and the results sometimes disagree with reality. The fact that the generations born in spring have softer food and the generations born in autumn have harder food, chiefly tough seeds to eat, has a great influence on dentition. In consequence, where additional factors are not considered, data leading to establishment of the age of the specimens, based only on the formation of the dentition, may be problematic.

In this work, I attempt to connect the age of specimens with their sexual maturity, and length and weight of the body. For this purpose sexual organs, preserved in alcohol were dissected. Measurements of length and breadth of the testes and *vesica seminalis*, and also cornua of the uterus were made. The results of measurements were included in classes. Male specimens were divided into 6 classes (Table 1), females into 3. According to the size of the embryos, I established 5 phases of pregnancy.

Vesica seminalis in classes 1 to 4 are of very small size (width 0.57—1.99 mm), in the remaining groups (5—6) the sizes are from 2.5 to 5.0 mm. On the whole they are fully filled and have a meandering shape.

In the female groups the measures are: class 1 the width of uterus cornua extends from 0.4 to 0.8 mm, 2 — 0.9—1.6 mm, 3 — to 2.7 mm. In the first two groups the cornua show simple construction, and in the third they are irregular and folded.

In doubtful or particular cases the gonads were analysed by histological methods.

In the analysis of the variability the data concerning the length and weight of the body were taken into consideration. The problem was treated more widely (in various aspects) because of the considerable material and possibility of comparison. Variability in the length of bodies was studied on the material from the years 1946—1955, the weight on material from 1949—1955.

Table 1.

Classification of gonads (extremes of length and breadth of the testes).

Class of gonads	Lenght of testes mm	Breadth of testes mm
1	3.0 - 4.9	1.6 - 2.5
2	5.0 - 6.9	2.6 - 4.5
3	7.0 - 8.9	4.6 - 5.5
4	8.5 -10.9	5.6 - 6.9
5	11.0 -12.5	6.7 - 7.0
6	11.5 -14.5	6.9 - 7.7

The measurements were done in millimetres (mm.) and grams (g), according to established principles (D e h n e l, 1949; B o r o w s k i & D e h n e l, 1953).

Numerous figures, diagrams and histograms were made in order to give fuller documentation of the material, and to show a certain lability in their interpretation.

Among the drawbacks of the present work is the relatively high quantitative differentiation of the material. At different times, a different quantity of animals was available. Statistical tests were therefore necessary to evaluate the significance of the observations and to establish their proper interpretation.

To confirm the significance of the mean difference Student's Test (W e a t h e r b u r n, 1949) was employed.

Uniformity of proportions was tested using χ^2 for multi-class tables (S i e g e l, 1956).

Two divisional series were compared by the Kolmogorov-Smirnov test (S i e g e l, 1956), thus calculating the approximate value χ^2 (from the 2 degree of freedom) even for small quantities. In no case, however, were there any contradictory conclusions as regards the use, of the table of precise critical values, taken as $n = \min(n_1, n_2)$, where n_1 is the number of observations in the first divisional series, n_2 the number in the second series.

The material used can be found in the collections of the Mammals Research Institute of the Polish Academy of Sciences, in Białowieża.

III. VARIABILITY OF BODY LENGTH

In the relatively plentiful literature on the bank vole, biometric data are considered frequently.

Measurements, whether in mm or grams, clearly emphasize the sphere of morphological changes in the animal organism. Insofar as these data are analysed as a complex, making allowances for the environmental conditions, they allow for a wider understanding of the state of the population and its dynamics.

They clearly demonstrate the fine plasticity of the body's covering. They distinctly show the environmental dependence of form and the direction of individual growth of the given species.

There has been research on the analysis of measurements of length and body weight and the sphere of the variability of these features in *C. glareolus* more than once. The numerous publications in this field, however, often treated the problem marginally or did not give it the proper importance.

Table 2.
Variability of body length of *C. glareolus* in the years 1946—1955.

Year	n	Min. - Max	Difference between max. and min. values in mm	$\bar{x}$
1946	54	60 - 100	40	81.05
1947	248	66 - 112	46	87.30
1948	840	66 - 112	46	88.35
1949	139	58 - 100	42	88.77
1950	303	60 - 110	50	86.55
1951	36	68 - 104	36	86.85
1952	306	60 - 108	48	84.38
1953	1226	64 - 112	48	85.80
1954	674	64 - 102	38	82.82
1955	4249	64 - 114	50	86.08
1946 1955	8095	58 - 114	56	85.13

Many authors, such as: Zimmermann (1937), Naumov (1948), Kulajeva (1958), Stein (1956), Koškina (1957), Schwarz (1959), Zejda (1961), treated the problem more or less deeply. The character of these investigations and the conclusions proposed are often in strict dependence on the value of the materials. Scanty series of specimens from single years without record to the time period and place of traping and the effects of environmental factors, generally affect the objective value of these results negatively.

The relatively plentiful material at my disposal, caught over a period of several years, enables a fuller analysis to be made as also a definition of the values of measurements as indicators.

Taking into consideration the plasticity of growth of the animals investigated, their great vital metabolism (Schmalhauzen, 1935), I attempt to discuss the variability of length and body weight in several aspects: individual, age, annual, seasonal. The consequences of these results would be, in turn, attempts to establish which of the aspects mentioned is most significant and most closely associated with the field of oscillation of the measurements and body formation of the analysed individuals of the population.

The material presented in table 2 indicates the general variation of body-length in the various years. As can be seen from the table, the dispersion of body-length in the years from 1946 to 1955 varies considerably. The extreme values for the total number of specimens (more than 8000) are within the range 58—114 mm (Table 2, Fig. 1).

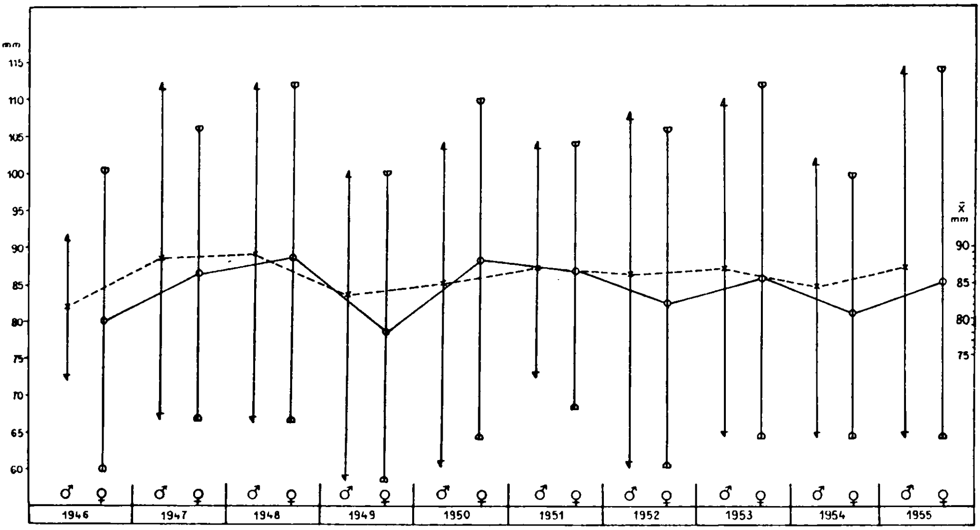


Fig. 1. Extreme and mean body lengths of *C. glareolus* in the various years with regard to sex.

However, in the several years, depending on the number of specimens captured, the limits of dispersion for body length vary. The less the number of specimens captured, the smaller the oscillation and the extremes noted. In the years with fewer specimens, up to 200 the range of length is not more than 42 mm. In other years, where more specimens were captured, when there were several hundred or even several thousand animals, the range of oscillation is up to 50 mm.

The dependence of the range of oscillation on the size of the sample of specimens, is in principle the consequence of the correct method of sampling.

Fig. 1 illustrates *inter alia* the above questions with regard also to the relations between males and females. Generally speaking there are here no special differences. In single years, except for 1946, the range of body-length for both sexes is practically identical. The extreme variations are not more than 5 mm. The striking difference between males and females as regards range of body-length in 1946 is probably due to the small sample of specimens obtained, only from the last months of the year.

It was calculated that the relation of variance of body-length during the years of investigation was different for either sex. Years in which the variances for males are greater than for females are more numerous (Table 3).

In three cases the reverse situation is observed, where females showed greater variance than males. The relation of variance is compared with the critical value of the variate *P*, read from Fisher's table with a 5% risk of error (column $F_{0.05}$).

Table 3.
Relation of variation of body-length, 1947—1955.

Year	Variance		Ratio of variance		$F_{0.05}$
	♂	♀	♂/♀	♀/♂	
1947	93.64	69.12	1.35		1.36
1948	86.76	78.94	1.10		1.19
1949	110.52	86.40	1.28		1.52
1950	81.72	77.04	1.06		1.39
1951	56.16	97.56	0.58	/1.74/	1.87
1952	91.80	73.80	1.24		1.31
1953	81.72	68.40	1.19		1.11
1954	44.64	51.12	0.87	/1.15/	1.22
1955	45.36	65.52	0 70	/1.44/	1.08

From this confrontation it appears that of 6 cases where the males show more variation than the females, four cases are significant.

This leads to the conclusion that differences between females and males in the respect are not random, both as regards greater variability of males as compared with females for certain years, as also contrarily for other years. There is no way, however, to state what caused the reversal of the relation of variability in the years 1951, 1954, 1955.

The mean body-length for the several years shows no special trend. From Table 2 we find that where there is a smaller number of specimens and small range (40 mm) the mean is 80.77 mm (1949). In other years, however, where the samples were similar, the mean was 86.50 mm. Similar results to the latter can, however, be seen also in years with a very large number of specimens. In 1953 (n = 1226) the mean was 85.80 mm, while in 1955 with 4249 specimens, the mean was 86.08 mm.

Student's test confirms that the observed longer body-length of males is significant for the years investigated (t = 6.0 for 8 degree of freedom).

In the histogram presented (Fig. 1), the horizontal lines (continous and broken, carried across the line of the body-length range for males and females) define the average values of body-length for both sexes. As can be seen from these data, the means in males for all the years are very similar. The curve shows great regularity without distinct oscillation. All the mean values are in the range 83.5—88.5 mm. In females, however, the mean body-length in the various years shows greater variation. The extreme values are in the range 78.3 to 88.5 mm. The graph (continuous line) is very irregular, showing a considerable drop in that line in certain years (1946, 1949).

Because of the great variation in body-length this feature was included 10 classes.

Table 4.
Dispersion of frequency of body-length, 1947—1955.

mm \ Year	1947	1948	1949	1950	1951	1952	1953	1954	1955	N	%
57.5	-	-	5.45	-	-	3.05	-	-	-	17	0.21
63.5	2.00	2.40	8.80	5.85	5.00	3.20	1.65	2.10	0.75	129	1.60
69.5	6.40	5.05	16.50	8.30	6.35	9.25	5.15	11.95	4.05	427	5.31
75.5	8.50	13.00	17.80	21.90	10.55	20.15	18.20	22.05	13.20	1183	14.71
81.5	27.20	27.80	23.25	31.85	35.25	33.30	35.10	34.35	39.65	2866	35.64
87.5	29.45	23.60	18.35	18.90	18.85	18.60	16.90	22.70	25.85	1953	24.29
93.5	13.55	12.20	7.55	6.60	13.30	7.20	12.60	16.05	9.70	824	10.25
99.5	12.25	12.55	2.30	5.50	13.05	4.30	8.25	0.80	5.40	519	6.45
105.5	2.80	2.75	-	0.90	-	0.95	1.80	-	1.20	105	1.31
111.5	0.70	0.65	-	-	-	-	0.35	-	0.20	18	0.22
n	248	840	139	303	56	306	1226	674	4249	8041	100.0

The question arose, as to how numerous (in %) the individuals were in the several years in which measurements were made, over that period of years.

From Table 4 it can be seen that in all years the largest percentage of specimens is to be found in two groups: 81.5—87.4 mm, and 87.5—93.4 mm. In the first group there were 35.64%, in the second 24.29%. In the collection of 8,000 specimens, from the whole range (57.5—112.0 mm) about 60% of individuals had body-lengths within the range 81.5—93.4 mm.

The groups of maximal and minimal dimensions in all years, as can be seen from the Table, have a very low percentage of specimens. In both extreme groups together, this is not more than 10%. The percentage of voles in groups with body-length less than 70 mm an higher than 105 mm is also very slight, not more than 2% for both such groups together.

Table 5.
Percentage proportion of males and females in the various classes of body-length.

Body length	57.5-63.4	63.5-69.4	69.5-75.4	75.5-81.4	81.5-87.4	87.5-93.4	93.5-99.4	99.5-105.4	105.5-111.4	111.5-114.0	n
Sex	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀
1947	- / -	2.0/2.0	6.7/6.1	4.7/12.8	16.7/32.7	29.3/29.6	20.0/7.1	15.3/9.2	4.6/1.0	0.7/ -	150/98
1948	- / -	1.5/3.3	3.5/6.6	7.8/18.2	22.0/33.6	24.4/22.8	17.0/7.4	20.1/5.0	3.0/2.5	0.7/0.6	477/363
1949	7.6/3.3	7.6/10.0	6.3/26.7	13.9/21.7	21.5/25.0	31.7/5.0	10.1/5.0	1.3/3.3	- / -	- / -	79/60
1950	2.2/ -	4.7/7.0	6.9/9.7	17.5/26.3	33.9/29.8	21.1/16.7	7.9/5.3	5.8/4.3	- /0.9	- / -	189/114
1951	- / -	- /5.0	2.7/10.0	11.1/10.0	30.5/40.0	27.7/10.0	16.6/10.0	11.1/15.0	- / -	- / -	36/20
1952	2.4/3.7	3.5/2.9	8.2/10.3	18.2/22.1	27.6/39.0	24.7/12.5	7.1/7.3	7.1/1.5	1.2/0.7	- / -	170/136
1953	- / -	2.0/1.3	4.0/6.3	14.0/22.4	28.9/41.3	21.2/12.6	16.2/9.0	11.9/4.6	1.5/2.1	0.3/0.4	703/523
1954	- / -	1.3/2.9	6.9/17.0	18.1/26.0	35.0/33.7	30.7/14.7	6.9/5.2	1.1/0.5	- / -	- / -	463/211
1955	- / -	0.6/0.9	2.9/5.2	11.6/14.8	38.9/40.4	31.4/20.3	9.9/9.5	3.9/6.9	0.6/1.8	0.2/0.2	2428/1821
%	0.21/0.21	1.40/1.88	4.07/7.05	12.53/17.78	33.64/38.46	28.39/18.54	11.48/8.52	7.03/5.65	1.04/1.67	0.21/0.24	4695/3346
N	10/7	66/63	191/236	588/595	579/1287	1333/620	539/285	330/189	49/56	10/8	8041

As in the general classification, the largest percentage of males is also contained in the group with body-length in the range 81.5—93.4 mm (Table 5). The females are most numerous in the groups with body-length in the ranges 75.5—81.5 and 81.5—87.4 mm (38.5%). Of 3346 females from the 8 years under investigation, ca. 75% were specimens with body-length in the range 75.5—93.4 mm (Fig. 2).

It should be noted that the limits of variation of body-length and the percentage state of individuals in the various groups of body-length in both sexes are closely parallel. This is distinctly seen by the fact that the greatest frequency both for males and females is for the group of measurement 81.5—87.5 mm (Fig. 2). Further, there is a gradual percentage regression, in the direction of the extreme values, maximal and minimal. The histogram simultaneously indicates the scope of the variation in body-length.

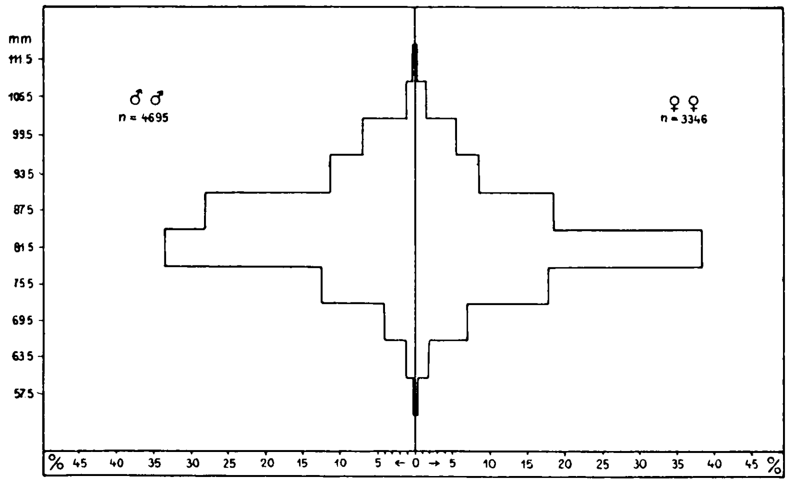


Fig. 2. Percentage oscillations of males and females in classes according to body length for all years together.

As in the general analysis in every year males and females were most numerous in the range 81.5—87.5 mm (Fig. 3). In all years, however, (with the exception of 1950), the females in this group were in the majority.

The situation in groups measuring more than 88 mm. is different. In this case, in all the the years males decidedly are in a percentage majority over females. For the period of 9 years, only 1949 and 1951 are slightly different. This is probably because these two years have a relatively small number of specimens.

The variation in body-length of C. *glareolus* in seasons and months is presented in Figs. 4—6. Analysing generally the system of polygons in all

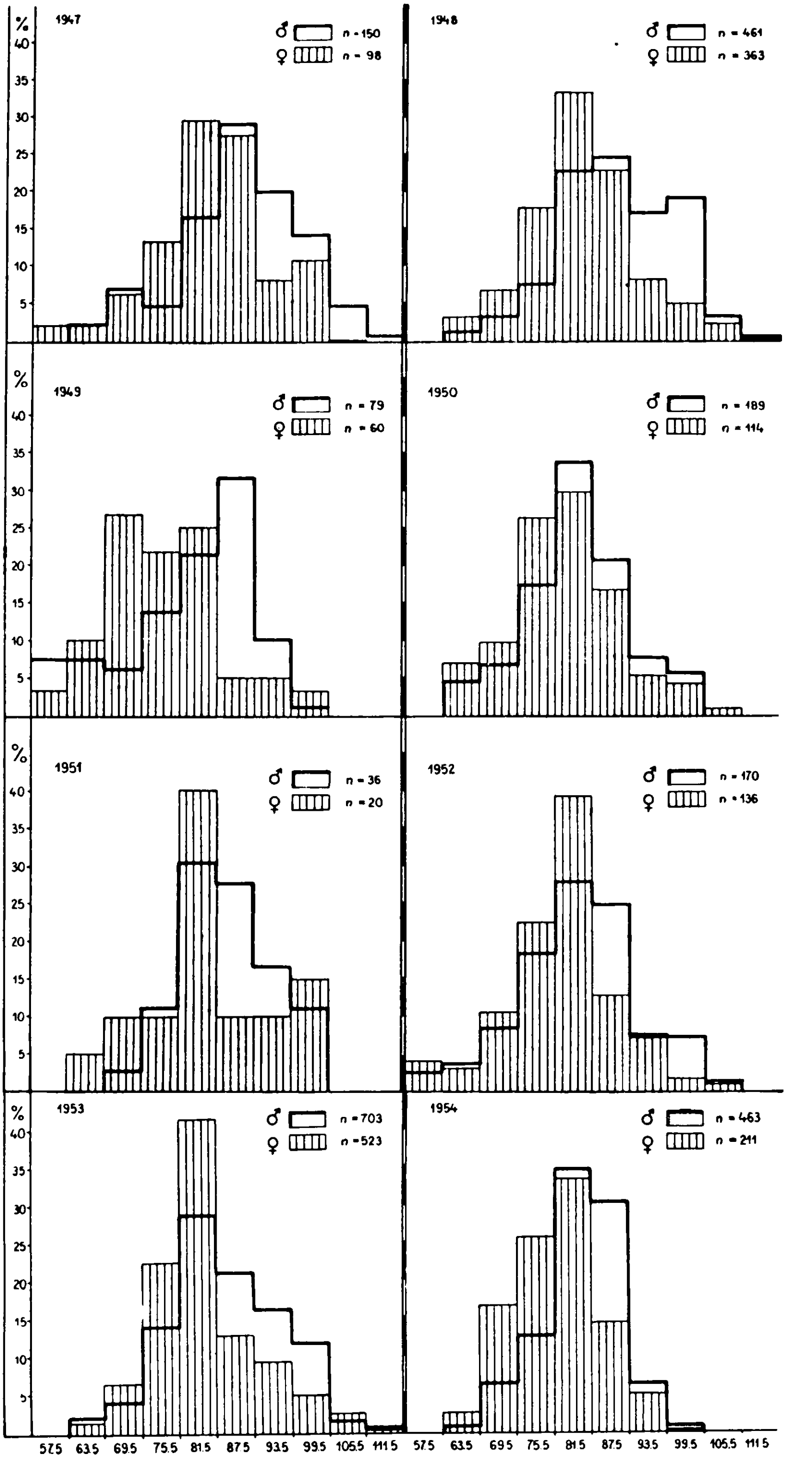


Fig. 3. Percentage oscillations of males and females in classes according to body length for the years 1947—1955.

years, the rather unusual graphs for some of the months can be observed. For example, in May, the body-length of the bank vole is much less in relation to the previous month. There is an equally interesting system of polygons at the place where, in the years 1950—1952 (Fig. 5), in June, all the graphs meet at the mean of 82.8—83.1 mm.

More reliable (because of the great number of specimens) are the results of the fairly regular and parallel system of the polygons (Fig. 6). There is a distinct rise in the curves with fairly high means — in the first quarter of the year. All graphs are highest for April. In the next month, the polygon shows a considerable fall, the tendencies of which keep it at a fairly low level for almost the remaining months.

Only in the collection of 1955 where there were a great many specimens (n = 4246), are the graphs more even. Over the whole year, the mean body-lengths are contained in the range 84.2—88.5 mm., but 3 decided rises in the graph can be seen on one level, in April, as already mentioned, and in January and September.

Table 5 is a supplement to the graphs described above: it illustrates mean body-length of voles in the various months, for all years under investigation together. This comparison shows even more clearly the character and direction of the variability of this feature. It indicates, *inter alia*, that in the sample coming from the years 1947—1955 the mean body-length in April (which indirectly could be learned from the graphs described earlier) is highest, over 90 mm. This difference is striking, in contrast to all the other months in all years of the investigation, where the mean is not more than 87.0 mm. From the data in Table 6, we cannot perceive any clear association between the number of animals in the sample and the size of the mean body measurements. Where there were many and few specimens in the analysed months (VI—IX) the means differed considerably.

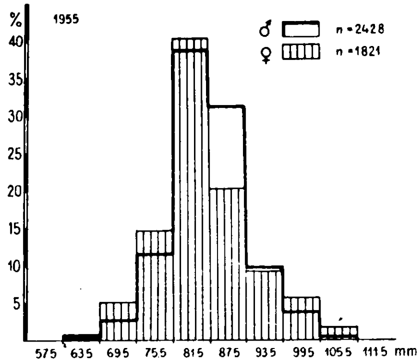
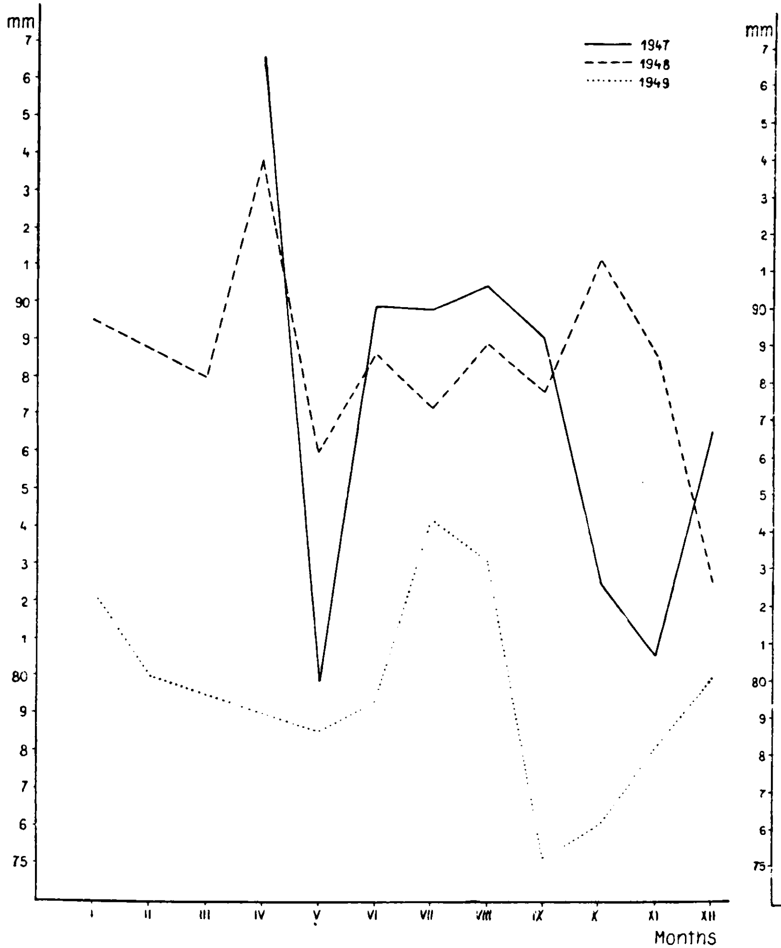


Fig. 3. Explanation on p. 128.



mm
7
6
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Months

Fig. 4

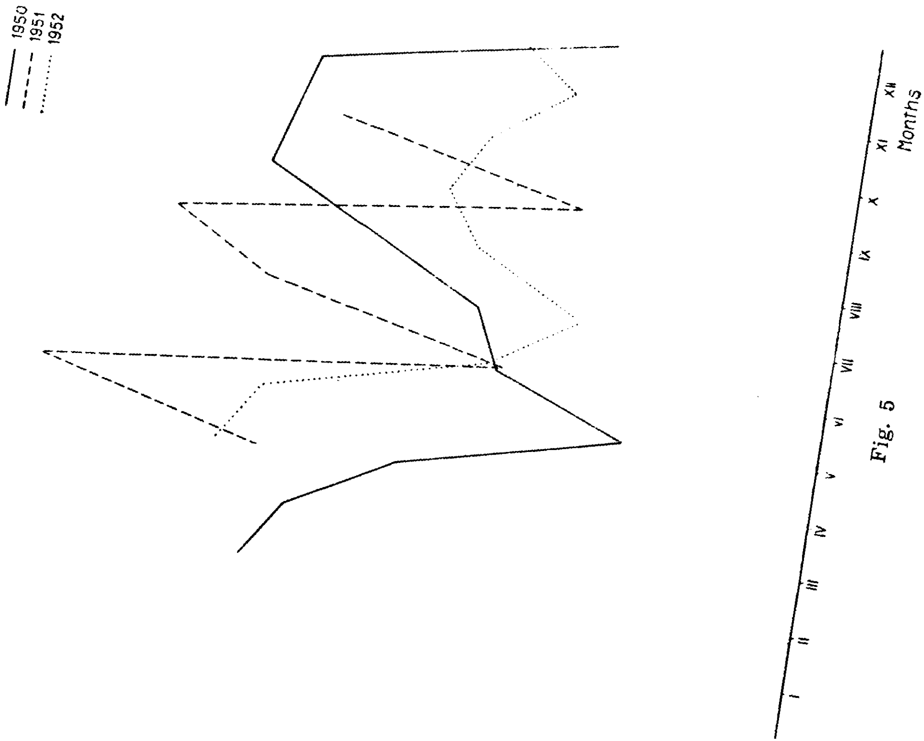


Fig. 5

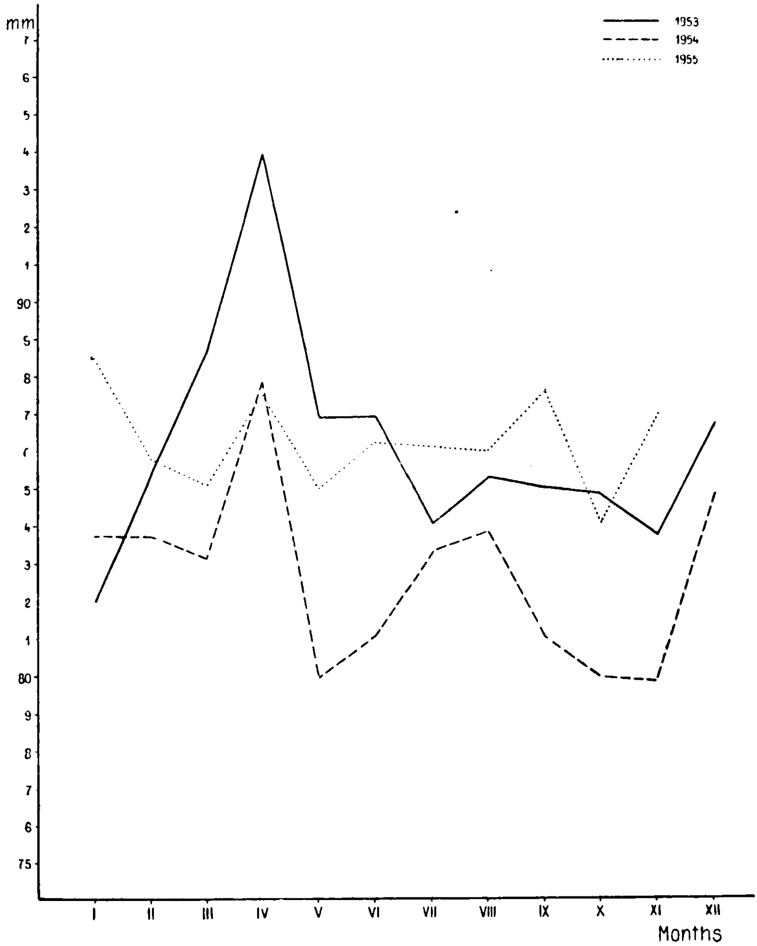


Fig. 6

Figs. 4—6. Variability of mean lengths in the months of 1947—1955.

Table 6.

Mean lengths of body of C. *glareolus* in the various months (total).

Months	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	$\bar{x}$
$\bar{x}$	85.19	85.97	86.59	90.67	84.29	84.65	85.44	86.71	84.63	83.98	83.61	83.67	85.45
%	0.97	1.77	2.26	3.22	8.41	19.29	22.13	14.36	14.43	3.08	8.00	1.95	100 %

A graphic picture of the great variability of the body-length of C. *glareolus* in the seasons of the investigated years, is given by Table 7 and Fig. 7. As can be learned from the data, in spring (III—V) in almost all years the specimens were the biggest. There are high means in each year and total mean ($\bar{x}$ = 87.10 mm) for this season (Table 7). Only the year 1948/1949 had a low mean in spring, 78.5 mm. This is a striking difference when compared with other means for this season, which are as much as 90 mm.

Fairly low means and total means are found in autumn and winter. Both these seasonal means, over a series of years, are within the range 81—89.0 mm., while the means for the total number of specimens are:

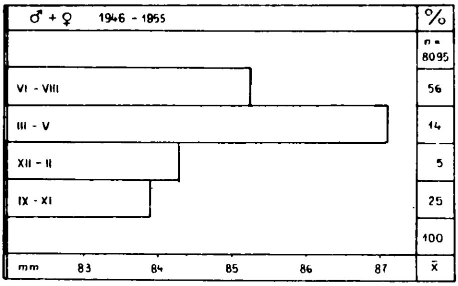


Fig. 7. Variability of mean lengths in the seasonal aspect for all years together.

Table 7.
Variability of means of body-length in the seasonal aspect for the years 1946—1955.

Years	%	Difference between Max and Min values in mm	$\Sigma\bar{x}$, mm	Season			
				IX - XI	XII - II	III - V	VI - VIII
1946/47	3.0	50	86.72	81.05	88.10	87.75	90.07
1947/48	10.0	46	85.79	84.10	81.57	89.27	88.23
1948/49	2.0	48	83.58	89.13	84.50	78.50	82.20
1949/50	4.0	46	82.31	76.40	81.00	87.53	84.33
1950/51	1.0	42	89.72	89.25	-	92.00	88.13
1951/52	2.0	48	85.55	84.65	-	89.30	82.50
1952/53	15.0	52	89.97	83.56	83.73	89.83	82.77
1953/54	8.0	48	83.94	84.60	84.73	83.67	82.77
1954/55	39.0	50	84.64	80.03	86.43	85.90	86.20
1955	16.0	46	-	86.33	-	-	-
Total	100.0	56	85.13	83.91	84.29	87.10	85.24

autumn, 83.91 mm and practically identical in winter, 84.29. There is a slightly higher total mean in summer, over 85 mm.

The above data (Table 7, Fig. 7) indicate that, with the exception of spring, in all seasons of individual years, the average measurements of body-length are very closely similar. This allows us to assume that in the three other seasons there is a relatively large number of young specimens

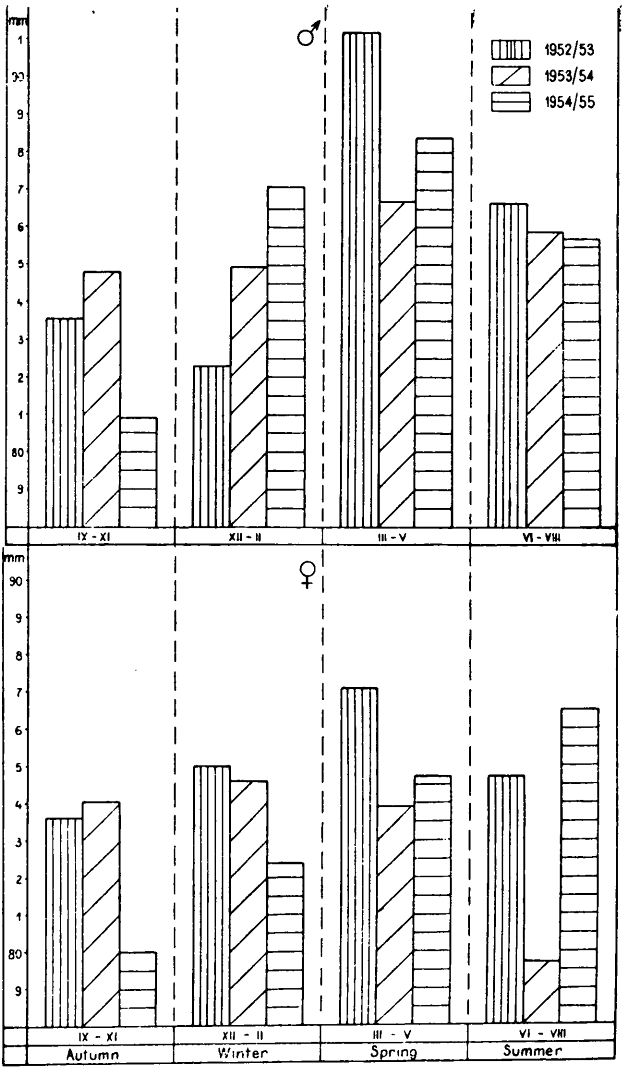


Fig. 8. Variability of mean lengths of males and females in the seasonal aspect.

among the animal population. In spring, however, the high mean would indicate a majority of mature individuals, fully-grown.

Analysing the males (Fig. 8) we notice a majority of high means in spring, as compared to other seasons. This allows us to assume that the majority of males shows stabilization of growth in this season. Indirectly it is also possible to assume that there is a majority of adults, or mature males capable of breeding. (Analysis made in Sections IV and V supports this assumption).

The most similar means, expressed in practically identical graphs, can be seen in summer. The mean body-lengths of males in all three years in this season is relatively low and fairly uniform. In the remaining seasons of the various years, the picture is not so uniform (Fig. 8).

Females (Fig. 8) are also largest in spring, although this difference is not so marked as in males. The means most frequently oscillate in the range 83.5—86.5 mm. Only in summer 1953/1954 and 1954/1955, the means are 80.0 mm or less.

Table 8.

Sphere of variability of body-weight of *C. glareolus* in the years 1949—1955.

Year	n	Min. - Max.	Difference between max and min values in g	$\bar{x}$
1949	138	5.0 - 27.0	22.0	14.31
1950	298	6.0 - 30.0	24.0	16.03
1951	57	6.0 - 23.0	17.0	14.50
1952	312	6.0 - 24.0	18.0	14.47
1953	1221	7.0 - 32.0	25.0	16.02
1954	674	7.0 - 26.0	19.0	14.00
1955	4243	7.0 - 35.0	28.0	15.41
Total	6943	5.0 - 35.0	30.0	14.96

Table 9.

Relation of variation of body-weight in the years 1949—1955.

Year	Variance		Ratio of variance		$F_{0.05}$
	♂	♀	♂/♀	♂/♀	
1949	19.44	21.33	0.91	/1.10/	1.48
1950	22.86	21.06	1.09		1.32
1951	13.32	20.88	0.64	/1.57/	1.88
1952	10.98	12.06	0.91	/1.10/	1.30
1953	25.92	20.25	1.28		1.16
1954	7.65	11.70	0.65	/1.53/	1.22
1955	11.61	17.73	0.65	/1.53/	1.08

The year 1954/1955 shows a fairly characteristic graph (Fig. 8). In autumn (1954) there can be seen a "progressive increase" in body-length, ending in a rise of means in the summer of 1955. The mean body-length of females in this season is 86.5 mm.

A similar picture (with the exception of summer) can be seen in 1952/1953. Contrasting with this is the year 1953/1954, where the level of means in summer ($\bar{x}$ = 79.0 mm) is very low and highest in autumn and spring.

IV. VARIABILITY OF BODY WEIGHT

The second significant feature with taxonomical importance, which simultaneously reflects the physical condition of specimens of the population, is data on the body-weight and weight of its organs.

In generalizing on the individual variability in body-weight of specimens in the years 1949—1955, we may state that there is a considerable range of variation.

Table 8 shows that the range of body-weight of voles was from 5.0 to 35 g. This refers to all investigated years together. The greatest range (25 g, 28 g) was found in 1953 and 1955; both these years afforded many

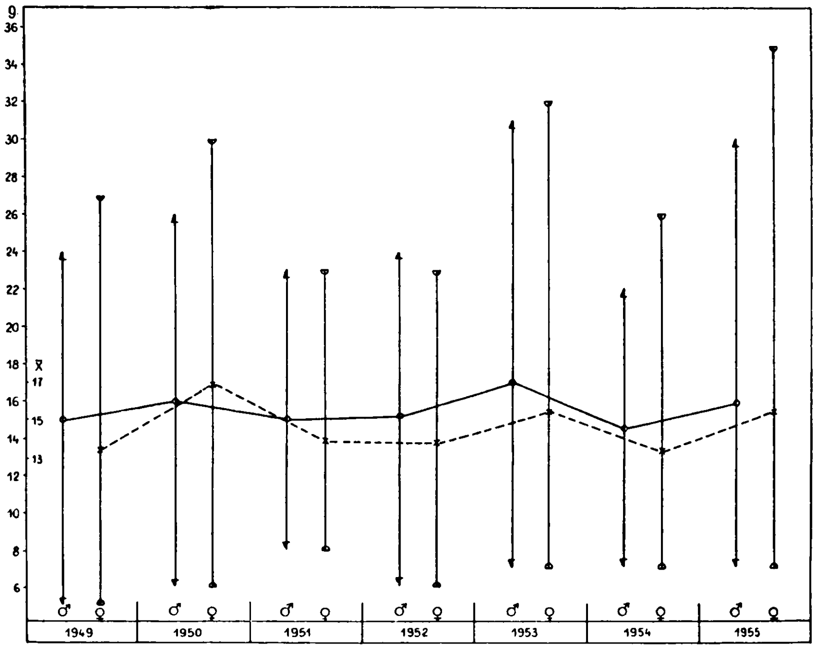


Fig. 9. Extremes and mean weights of *C. glareolus* in the various years with regard to sex.

specimens. In 1953 there were 1221 specimens, in 1955 more than 4000 specimens. However, even years in which a comparatively small number of specimens were collected, also show considerable oscillation, as is seen in Table 8. In 1949, 1950, where there were not more than 300 new specimens, the body-weight oscillates between 6 and 30 grams.

We also observe (Fig. 9) a distinctly greater range of oscillation in body-weight in females than in males, and usually in the upper limits of the range. Only in years with a small number of specimens (1951, 1952) the relationship is somewhat different. In 1951 the range for both sexes is identical (8—23 g.) and in 1952 the males are slightly (1 g.) heavier.

The variances calculated for each year for both sexes oscillate in the ranges 7.65—25.92 for males and 11.70—21.33 for females. There is a certain agreement in oscillation of variances for both sexes; there are years of low variance in both sexes and years of greater variance. There are, however, no years in the period of investigation where we may observe decidedly differing variances in both sexes.

In the seven years under investigation, in only two cases males have a slightly greater variance than females. After calculation of the relation of variances for both sexes it appears that in only three cases in years exceptionally well supplied with specimens, these relations are significantly different from unity. In these three years of significant differences in variances, two show a greater variance of females over males, while the other shows the reverse.

Table 10.

Percentage proportion of individuals in the various classes of body-weight.

Range \ Year	1949	1950	1951	1952	1953	1954	1955	N	%
5.0 - 6.4	4.35	2.01	-	2.24	-	-	-	19	0.27
6.5 - 9.4	16.67	10.40	10.53	4.81	3.18	5.35	2.50	257	3.70
9.5 - 12.4	15.94	13.42	17.54	16.99	11.70	19.28	15.71	1064	15.32
12.5 - 15.4	19.56	32.55	26.32	49.04	36.53	41.83	41.46	2777	39.99
15.5 - 18.4	28.98	22.48	24.56	16.35	17.44	26.11	24.00	1578	22.72
18.5 - 21.4	10.14	9.06	15.79	7.69	9.34	6.38	8.87	607	8.74
21.5 - 24.4	3.62	5.03	5.26	2.88	11.70	0.75	5.16	397	5.74
24.5 - 27.4	0.72	4.70	-	-	8.03	0.30	1.62	184	2.65
27.5 - 30.4	-	0.34	-	-	1.97	-	0.59	50	0.72
30.5 - 33.4	-	-	-	-	0.16	-	0.09	6	0.09
33.5 - 35.0	-	-	-	-	-	-	0.09	4	0.06
n	138	298	57	312	1221	674	4243	6943	100.0

Table 8 shows the mean body-weights in the several years; we see from it that in years with great range of body-weight the mean body-weight is higher, whether or not the year provided many specimens. In extremes of 24—28 g, means are on the level of 15.4 to 16.0 g; where the range is lower than 22.0 g. the means are not higher than 14.5 g.

From this general analysis of weight data it appears that independently of the range of body-weight and number of specimens the mean body-weights in the years investigated are more or less equal.

Fig. 9 may serve as illustration of these relations, where two polygons (horizontal lines — continuous for males and broken for females) indicate the great regularity of means of body-weight in both sexes. In females, although there is a greater range of body-weight, the mean weights are lower and remain on two uniform levels — ca 14 g, and over 15 g. With the exception of 1950, in all years the mean body weights of males are greater than those of females.

The difference in means varies from 0.18 to 2.31 g. After Student's test, we receive the value $t = 3.22$ for 6 degrees of freedom, as the critical value $t_{0.05} = 2.02$. This value is highly significant and indicates a considerable difference between males and females in this respect.

Table 10 shows that in dividing the material discussed into a series of weight groups, the majority of specimens falls into three classes. The largest percentage (39.99%) is found in the group with body-weight in the range 12.5—15.4 g. The next largest group (22.7%) has a range of 15.5—18.4 g. The third group (more than 15% of specimens) has a range of 9.5—12.4 g. Generally speaking of a collection of more than 7,000 specimens of bank voles, from a number of years, more than 78% have their body-

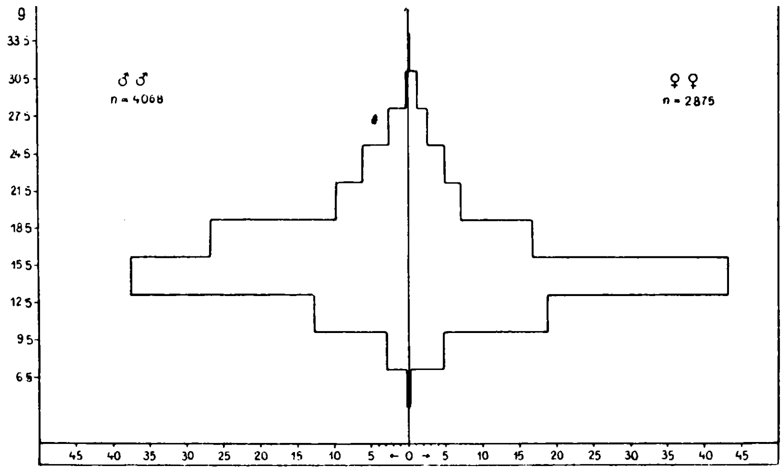


Fig. 10. Percentage oscillation of specimens of both sexes in the various classes of body weight for all years together.

weight in the range 9.5—18.4 g. Less than 22% of specimens fall into the remaining 7 classes of weight. This is a relatively low percentage, especially to be found in the extremes. Thus, in groups of body-weight less than 9.5 g, there are only 4% of individuals, while in groups from 21.5 g to 33 g of body-weight there are not more than 10% of the whole collection.

There is an interesting similarity in the percentage numbers of the whole in the weight classes and length of body class (compare Table 4). There is an identical number of classes and considerable range for these two features. While for each feature the greatest percentage number (78% and 69% respectively) is represented in three classes.

Fig. 10 shows the percentage number of males and females in the various weight classes with regard to the whole series of years. In years

Table 11.
Dispersion of frequency of males and females in classes of body-weight, 1949—1955.

Body wt.	5.0-6.4	6.5-9.4	9.5-12.4	12.5-15.4	15.5-18.4	18.5-21.4	21.5-24.4	24.5-27.4	27.5-30.4	30.5-33.4	33.5-35.5	N	
Sex	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂ / ♀♀	♂♂	♀♀
1949	5.1/3.3	10.3/25.0	10.3/23.3	20.5/18.4	35.9/20.0	14.1/5.0	3.8/3.3	- /0.7	- / -	/ -	- / -	78	60
1950	2.7/0.9	8.4/13.3	13.5/13.3	29.2/38.0	23.2/21.2	11.9/4.4	5.9/3.5	4.8/4.4	- /0.9	- / -	- / -	185	113
1951	- / -	5.1/22.2	15.4/22.2	25.6/27.8	33.3/5.5	15.4/16.6	5.1/5.5	- / -	- / -	- / -	- / -	39	18
1952	1.7/2.9	4.0/5.7	12.7/22.3	50.8/46.7	19.6/12.2	7.5/7.9	3.4/2.1	- / -	- / -	- / -	- / -	173	139
1953	- / -	3.3/3.1	9.1/15.3	28.4/47.5	17.5/17.4	12.9/4.4	16.7/4.8	10.4/4.8	1.6/2.5	0.1/0.2	- / -	704	517
1954	- / -	3.4/9.8	15.1/28.9	41.3/41.7	32.4/11.8	7.0/4.9	0.2/2.0	- /0.9	- / -	- / -	- / -	470	204
1955	- / -	2.1/3.1	13.5/18.6	40.0/43.3	29.0/17.3	9.4/8.2	4.7/5.7	1.9/2.2	0.1/1.2	- /0.2	- /0.2	2419	1824
N	12/7	122/135	523/541	1532/1245	1094/484	403/204	256/141	111/73	14/36	1/5	- /4	4068	2875
%	0.29/0.24	3.00/4.69	12.86/18.82	37.68/43.32	26.90/16.84	9.90/7.09	6.28/4.90	2.73/2.54	0.34/1.25	0.02/0.17	-/0.14	6943	

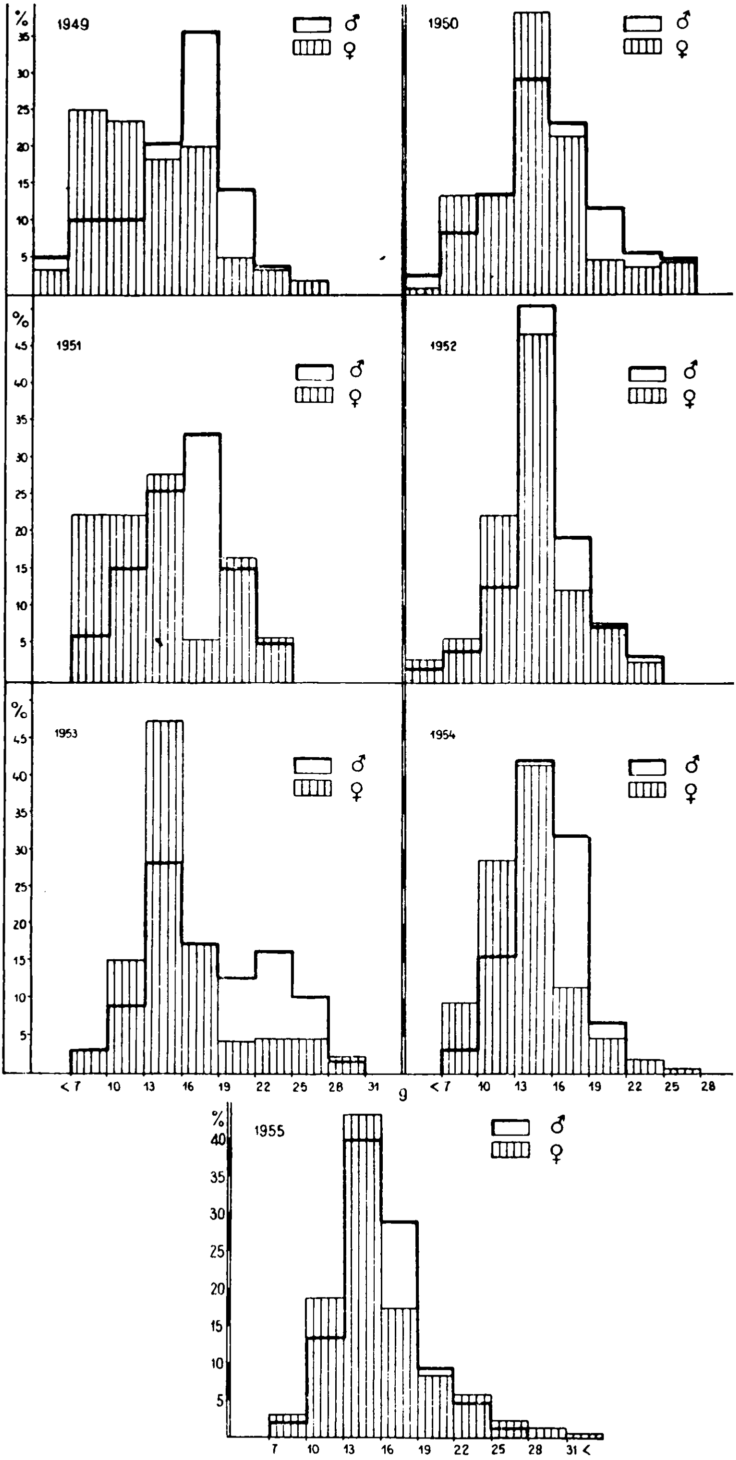
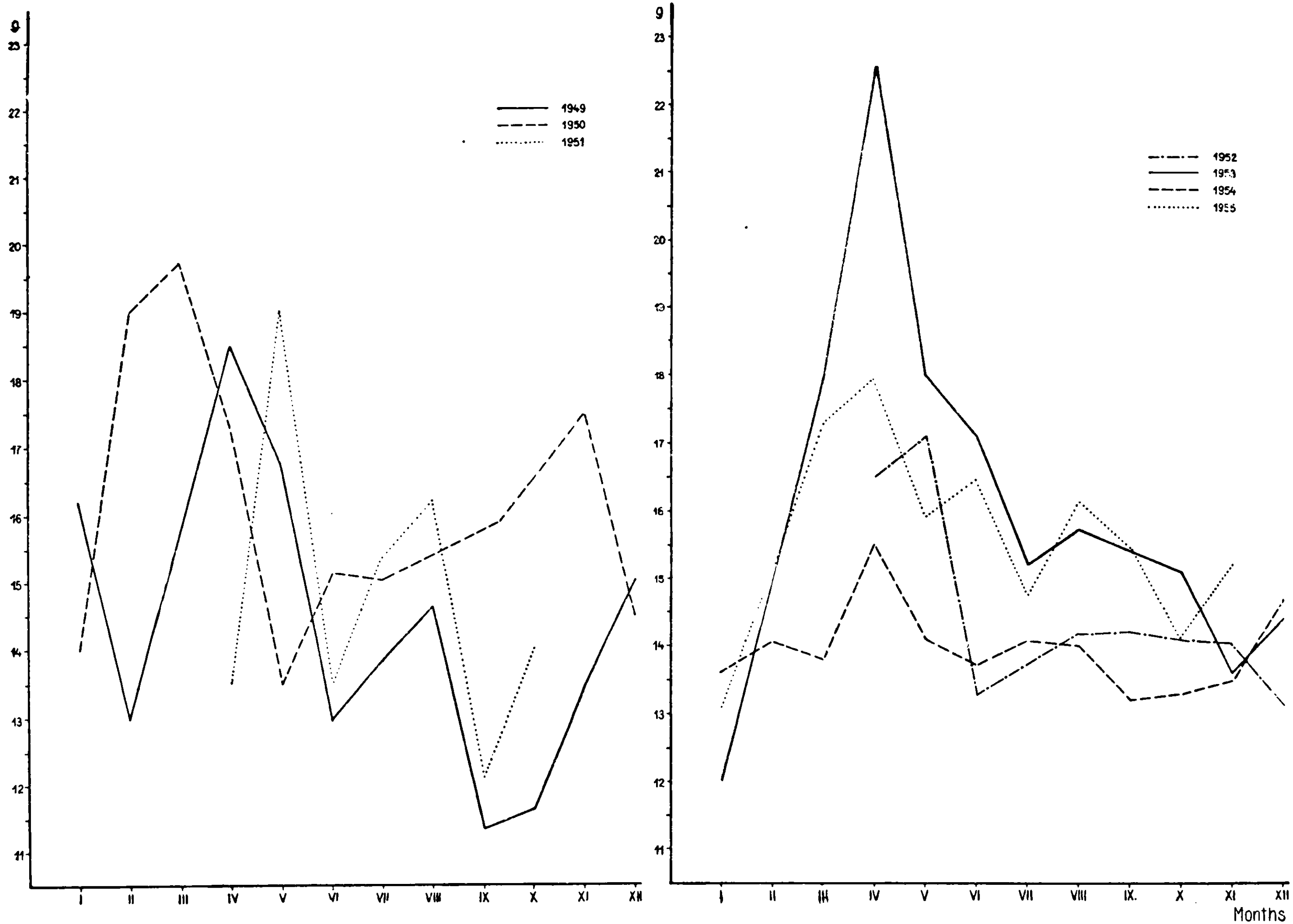


Fig. 11. Percentage oscillation of males and females in the various classes of weight in the years 1949—1955.



Figs. 12—13. *Variability of* mean weights in the various months of 1949—1955.

where there were many specimens (1953, 1955), especially in groups with the biggest body-weight, the females clearly predominate. This is probably due to the fact that there are the greatest numbers of pregnant females in these classes. (This will be discussed later in the present work). The years 1949 and 1951 (smallest number of specimens) show certain differences. In both these years there is a clearly greater percentage proportion of females in the smallest groups (6.5—12.5 g). The greatest percentage of males, however, is found in the 15.5—18.5 g group. These two years, in contrast with the others, show a greatly differing picture on the histogram.

It should also be mentioned (Table 11), that in the three most numerous groups: 9.5—12.4 g, 12.5—15.4 g, and 15.5—18.4 g the percentage pro-

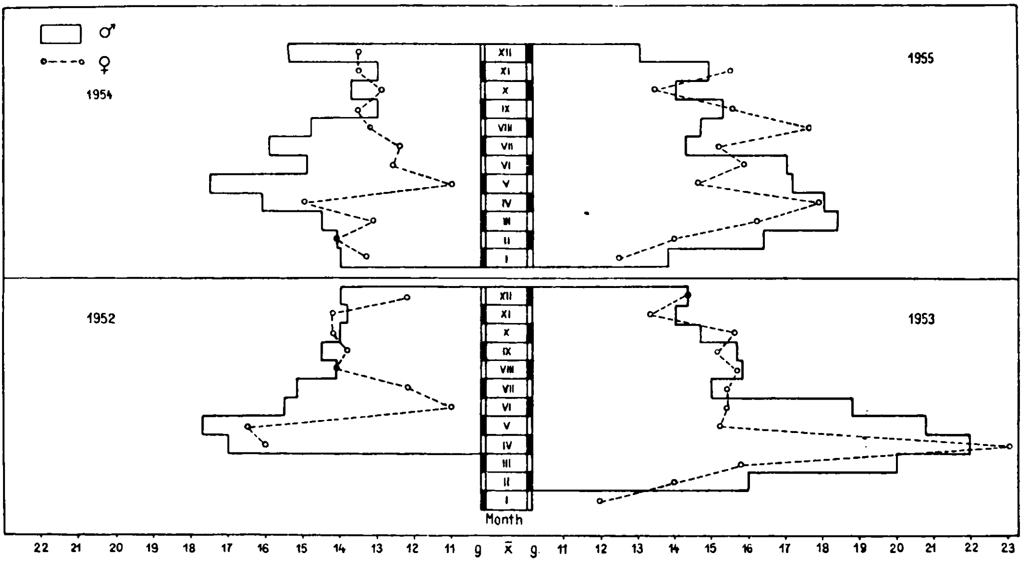


Fig. 14. Mean weight of males and females in the various months of a series of years.

portion of males and females is frequently very similar. These three groups together contain 77.44% of males and 78.98% of females.

In the total picture (Fig. 11) there is a very obvious similarity in the dispersion of frequency in both sexes, despite their differing numerical proportions. The highest columns are in the 12.5—15.5 g class; these then follows a gradual slackening of frequency in the direction of groups with greater and lesser body-weight.

Variability in body-weight of the bank vole in the various months and seasons of the analysed years is fairly great. As can be seen from the graphs and histograms presented, especially for 1949—1951 (Fig. 12), the mean body-weights show great variation in the several months.

Generally speaking, however, almost all graphs from June onwards are within the range 13.0—16.5 g. This can be most clearly seen on Fig. 13, where the years 1952—1955 are shown. In March, April and May, however, the graphs for all years investigated, in general remain in the upper

Table 12.
Mean weights of *C. glareolus* in various months of all years taken together.

Months	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
$\bar{x}$	13.80	15.26	17.20	17.41	16.36	14.60	14.59	15.18	13.89	13.74	14.55	14.13
%	1.02	2.12	2.53	2.95	7.61	17.32	24.49	12.40	15.86	3.12	8.48	2.10

Table 13.
Variability of mean values of body-weight in the seasonal aspect for the years 1949—1955.

Year	%	Difference between max. and min. values in g	Seasons			
			IX – XI	XII – II	III – V	VI – VIII
1949	1.07	20	–	15.2	17.3	13.8
1949/50	4.97	25	13.2	16.4	16.2	15.2
1950/51	0.99	18	18.6	14.0	16.2	15.0
1951/52	2.30	18	12.7	–	16.3	13.7
1952/53	17.09	26	14.1	13.4	19.6	16.0
1953/54	9.02	21	14.6	14.0	14.5	14.0
1954/55	45.03	28	13.3	14.3	17.0	15.8
1955	19.53	21	15.0	–	–	–
Total	100.00	30.0	14.5	14.5	16.7	14.7

Table 14.
Mean weights of males and females in seasonal aspect.

Years	Sex	Season			
		IX – XI	XII – II	III – V	VI – VIII
1952/1953	♂♂	14.13	15.00	21.00	16.50
	♀♀	14.08	12.75	18.00	15.50
1953/1954	♂♂	14.50	14.20	16.00	15.20
	♀♀	14.70	13.90	13.00	12.70
1954/1955	♂♂	13.20	15.20	17.90	15.30
	♀♀	13.50	13.50	16.20	16.20

range. In January and February, with the exception of 1949, the means are low and do not exceed 15.5 g.

The positions of the polygons and columns showing the level of means of body-weights for both sexes (Fig. 14) are fairly similar. Obvious differences can, however, be seen in these years (1952—1955) in May and

June, where females, in contrast with males, exhibit a considerable fall in means. Only 1955 in summer and autumn shows a different picture, where the body-weight of females is greater than that of males.

It can generally be noticed that the means of body-weight are less in females for the various months of the series of investigated years.

Table 12 illustrates the mean body-weight of the bank vole in the various months of all the years investigated (1949—1955) together. In this Table the mean body-weights are highest in March, April and May, and are markedly lower in all the remaining months. In the first case, the means are in the range 16.4—17.4 g, in the other, not more than 15.3 g.

The percentage proportion of specimens in the various months of all the years investigated together, as shown in Table 12, allows us to assume, *inter alia*, that there are no clear connections between the numbers of specimens and the size of the weight means. Where there is a low percentage number in the given months, there may be means in the lower and upper weight ranges, or vice versa. The same refers to means of body-length.

In comparing the Table discussed above with the similar Table for body-length (Table 6), certain interesting similarities of results become obvious.

Variability in body weight in seasons can be seen in Table 13. As supplement the weight dispersion and percentage number of individuals in all seasons investigated, is also included. Attention is drawn especially to spring, comparing the data in the Tables. In all years analyzed the mean body-weights in this season are usually higher than in the remaining seasons. This can be seen, *inter alia*, by means of the total mean which is about 17 g in this season. The remaining seasons have total means of not more than 15 g. The relatively low means and total means for autumn, winter and summer are fairly uniform. Over the years investigated, the weight means in these three seasons were in the range 13—16 g. Only in autumn 1950 did the means rise above this range, reaching 18.6 g.

There are no observable significant relations between the level of means of weight and the percentage proportion of specimens at different seasons in the series of years (Table 13). It may thus be assumed that a greater or lesser number of specimens captured in a given season, independently of the limits of the range of body-weights, does not, essentially, affect the interpretation of the results.

An analysis of the variability of body-weight in its seasonal aspect with respect to either sex is shown in Table 14. Of the most numerously represented years shown, we see that the mean weights of autumn in both sexes are very similar and remain in the range 13—14 grams. In the remaining seasons of the years investigated the mean weights of males are usually greater — up to 21.0 g, while in females they do not exceed 18 g. Fig. 15 indicates that in all the years investigated (except for IX—XI, 1953), we observe a gradual rise in means from autumn onwards, slightly greater in winter, and considerably higher in summer. In autumn there is a distinct fall in the level of means, giving a graph similar to the winter graph.

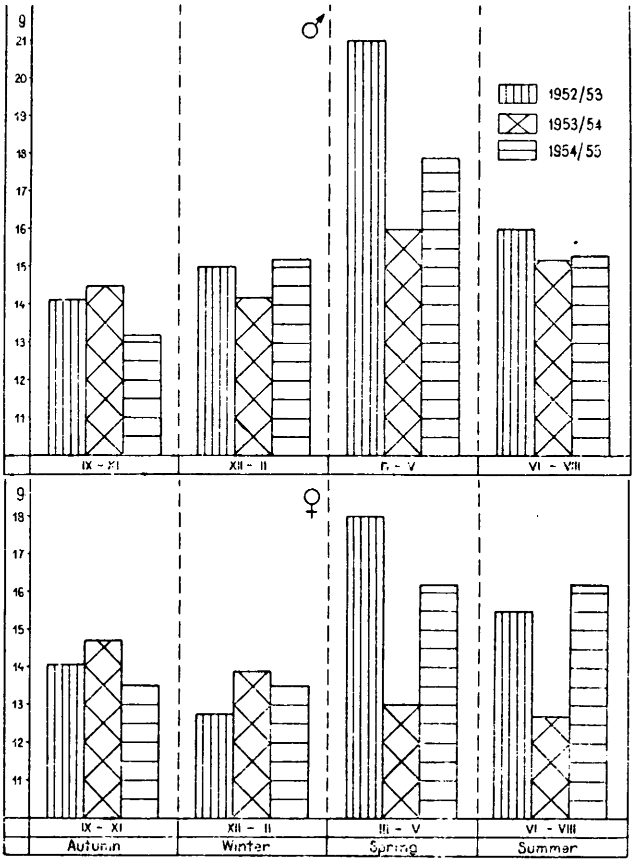


Fig. 15. Variability of mean weight of males and females in seasons for all years together.

In females, however, (Fig. 15) these relations are more differentiated. Thus, the year 1953/1954 shows a gradual fall in means, beginning from the highest point (14.7 g) in autumn, to the lowest point (12.7 g) in summer. In other years the columns are at their lowest in winter and highest in autumn. The highest level of means can be seen, however, in spring (18.0 g), and a slightly lower (16.2 g) in summer. The graphs are a contrast to those for males.

V. VARIABILITY IN LENGTH AND WEIGHT IN THE ASPECT OF AGE

Taking into account the age structure of the bank vole population, an analysis of the variability of length and weight of body in both sexes was carried out. Table 15 illustrates the number of individuals in the various classes of body-length with regard to the age factor. From it we see that the greatest number of young individuals (juv.) have body-length within the range 70—99 mm. In subadults, both male and female, these figures are larger especially at the lower extremes: 76 mm. Adults I and II, fully

Table 15.

Dispersion of numbers in classes of body-weight with regard to age and sex for all years together.

Age group	Sex	Head and body length mm										n	$\bar{x}$
		58	64	70	76	82	88	94	100	106	112		
juv	♂♂	13	49	149	392	978	574	115	11	-	-	2281	84.4
	♀♀	2	42	166	381	795	307	65	16	-	-	1774	83.3
subad	♂♂	-	1	13	73	286	238	44	4	-	-	659	86.6
	♀♀	-	1	14	73	188	84	32	25	2	-	419	86.3
adult I	♂♂	-	-	-	13	62	93	39	14	-	-	221	89.9
	♀♀	-	-	3	11	51	40	40	15	2	-	162	90.3
adult II	♂♂	-	-	-	15	36	84	95	70	4	-	304	94.1
	♀♀	-	-	1	9	28	24	34	34	8	2	140	94.1
senex	♂♂	-	-	-	7	28	67	87	79	17	2	287	95.9
	♀♀	-	-	-	7	18	8	32	26	17	1	109	96.4
n	♂♂	13	50	162	500	1390	1056	380	178	21	2	3752	
n	♀♀	2	43	184	481	1080	463	203	116	29	3	2604	
N	♂/♀	15	93	346	981	2470	1519	583	294	50	5	6356	
%	♂/♀	0.24	1.47	5.44	15.44	38.85	23.89	9.17	4.62	0.79	0.08		

formed with stabilized growth, have a much larger range of measurements. Both males and females of this age-group are within the classes of 82—105 mm. The oldest individuals, however (group V, senex), are sometimes up to 112 mm long. Generally speaking, the majority (60%) of specimens of all age groups together, is contained within the range 82.0—93.9 mm.

The numbers in the extreme classes in the Table under discussion are interesting. The young (juv.) have a range of oscillation in body-length of

60—105 mm. In the older voles, in the successive age-groups, the length becomes increasingly greater.

Analysing all the investigated years together (Table 15) it can be said that the mean values of body-length in the various age-groups are fairly markedly differentiated. This can be seen especially clearly in the groups juvenis and subadult, where in the former the mean for males is 84.9 mm, and in the later 86.6 mm. The females also show marked differentiation

Table 16.

Variability of mean body-lengths of males and females in age-groups with regard to extremes of size and numbers of individuals.

Year		1949	1950	1951	1952	1953	1954	1955
juv	♂	12.7	13.6	12.8	15.0	14.0	13.6	14.3
	♀	10.4	13.0	11.0	14.0	13.7	11.7	13.7
	Min - Max	6 - 20.0	6 - 26.0	8 - 19.0	7 - 21.0	7 - 28.0	7 - 21.0	7 - 29.0
	n ♂ / ♀	46/40	103/73	18/9	58/37	265/287	202/83	1548/880
subad	♂	17.6	15.7	16.0	15.1	15.1	15.7	15.3
	♀	16.9	15.7	16.6	15.0	14.6	15.8	15.7
	Min - Max	12 - 20.0	8 - 25.0	8 - 23.0	12 - 19.0	7 - 24.0	10 - 22.0	7 - 28.0
	n ♂ / ♀	15/8	44/23	14/8	22/9	113/98	94/40	346/220
adult I	♂	20.0	22.8	-	19.5	19.1	14.6	17.2
	♀	20.2	21.1	-	18.7	15.2	16.7	17.8
	Min - Max	14 - 27.0	13 - 27.0	-	12 - 23.0	10 - 26.0	11 - 26.0	12 - 29.0
	n ♂ / ♀	5/6	14/8	-	2/7	21/17	16/11	175/112
adult II	♂	15.9	22.4	19.7	18.5	22.7	14.3	20.4
	♀	16.5	21.2	-	-	23.4	13.8	21.0
	Min - Max	14 - 17.0	17 - 26.0	18 - 21.0	20 - 22.0	13 - 32.0	11 - 22.0	10 - 33.0
	n ♂ / ♀	3/2	9/4	4/ -	4/ -	129/41	38/25	120/63
senex	♂	19.7	20.5	21.2	22.0	23.3	16.5	21.8
	♀	-	30.0	15.0	-	23.7	14.5	23.1
	Min - Max	19 - 22.0	15 - 30.0	15 - 23.0	21 - 24.0	13 - 31.0	10 - 25.0	15 - 35.0
	n ♂ / ♀	4/ -	4/1	4/1	4/ -	140/41	56/23	78/63
N		73/56	174/108	40/17	90/53	668/484	406/182	2267/1338

in these two age-groups. In adults and older specimens the means are within the range 89.9—96.4 mm.

Table 16 illustrates the mean body-length in years. The mean body-length in males (juv.) is even but low, not more than 95.8 mm. The lowest mean in this age-group is found in 1949: 78.4 mm. The females appear to be smaller. The mean for them is not higher than 84.0 mm, and in some cases is lower than 80.0 mm.

In the subadults, the mean body-length appears to rise; the lowest extreme is 84.5 mm in males and 83.4 mm in females. The highest extremes are 88.5 mm (♂♂) and 87.3 mm (♀♀). Only 1951 shows a considerable increase for females, up to 94.0 mm. In the remaining age-groups, (adults I—II, senex), the means show a gradual rise, occasionally even attaining more than 100 mm. These are usually higher than in the young groups (juv. — subadult) and also of a higher level in males.

A good illustration of the composition and levels of the means in the various years in both sexes in defined age-groups can be found in Fig. 16. Here a great similarity between the graphs of both sexes is obvious. Most frequently the graphs (broken line) defining the level of means of body length in females are lower than the corresponding graphs for males. It is possible visually to assume that the males in all age-groups usually have a rather longer body-length than the females.

A further illustration of the question is found in Fig. 17, which shows a more detailed relation of the means of body-length in both sexes in the aspect of age. This histogram clearly shows the relatively large correlation between size of body and age of the bank voles in the years investigated. In all years, especially in the age-groups juv. and subad. there are clear tendencies to increase. With few exceptions, in all age-groups there is a gradual rise of means from the lowest in juvenis (75—85 mm) ending in adults and the old (adult II and senex). The total means for all years within the various age-groups and their results entitle us to make this classification.

The question of body-weight in connection with the various age-groups is rather less clear. As can, however, be seen from the Tables and histograms there are certain similarities between the length of body, and the weight. There can be seen a fairly clearly similarity in the general range of weight in specimens of various ages and established modal values (Table 17).

A large group of specimens (juv.) can be found in weight classes from 7 g to 18 g. In slightly older voles (subad.) there is a movement of the modal values, which sets the numbers in the weight classes 13—18 g.

In adults and the old (adult I—II and senex), however, the individuals of these numbers are dispersed and show no special grouping in any of the classes. It is possible to conclude, however, that these individuals are usually heavier than the young. The extension of the extreme values in the various age-groups, both in upper and lower extremes, is fairly large.

From Table 17 it appears that the weight range in the young animals (juvenile) is 6.0—7.0 g, to 30 g. In the next age-groups, the numbers in the extreme classes are affected to a greater or lesser degree. This means that the oldest (senex) are found in the weight classes: 13—15 g to 34—35 g.

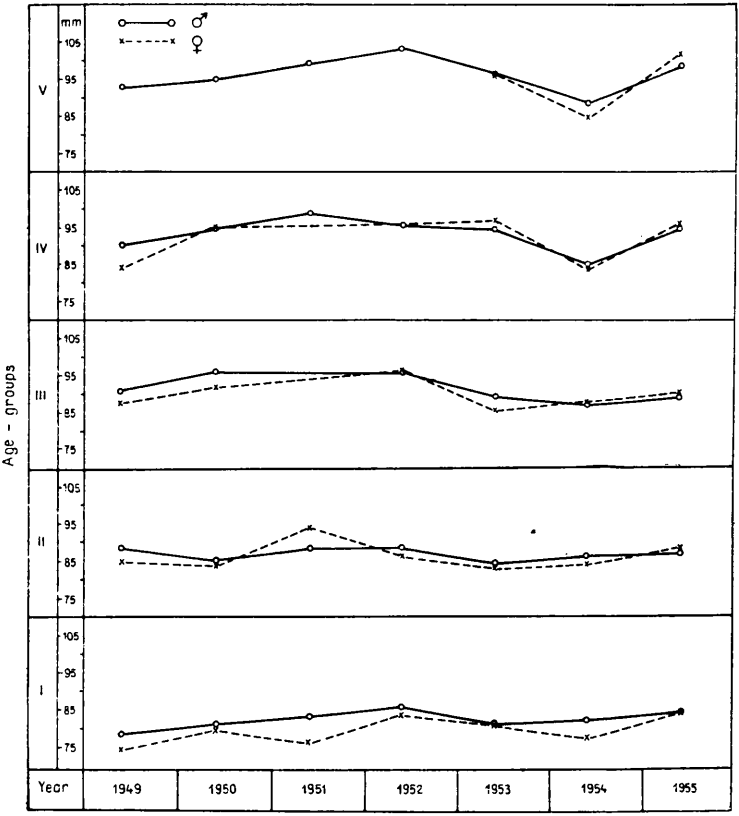
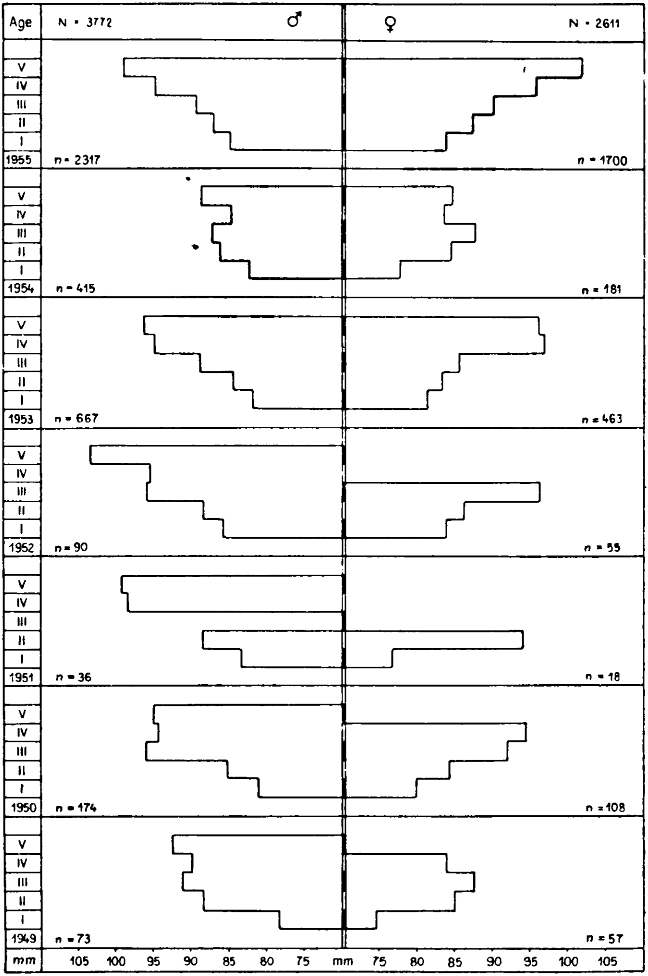


Fig. 16. Mean length in age-groups with regard to sex.

Fig. 17. Mean lengths of males and females in age-groups with regard to numbers in the years. →



Age
N = 3772
♂
♀
N = 2611
V
IV
III
II
I
1955
n = 2317
n = 1700
1954
n = 415
n = 181
1953
n = 667
n = 463
1952
n = 90
n = 55
1951
n = 36
n = 18
1950
n = 174
n = 108
1949
n = 73
n = 57
mm
105
100
95
90
85
80
75
mm
75
80
85
90
95
100
105

Table 17.

Dispersion of numbers in the various classes of weight, with regard to age and sex for all years together (1949—1955).

Age group	Sex	Body weight g. 4.0	7	10	13	16	19	22	25	28	31	34	n	$\bar{x}$
juv	♂	8	109	404	1005	578	88	7	2	-	-	-	2201	14.2
	♀	3	109	367	666	210	37	9	7	1	-	-	1409	13.5
subad	♂	-	3	58	274	268	40	5	-	-	-	-	648	15.4
	♀	-	3	48	193	103	34	19	5	1	-	-	406	15.5
adult I	♂	-	-	12	60	79	45	27	10	-	-	-	233	17.6
	♀	-	-	11	42	51	25	21	8	3	-	-	161	17.7
adult II	♂	-	-	6	33	38	89	98	38	5	-	-	307	20.6
	♀	-	-	9	19	24	25	24	25	6	3	-	135	20.3
senex	♂	-	-	1	24	41	70	89	53	11	1	-	290	21.4
	♀	-	-	-	20	11	18	19	18	6	-	1	93	20.9
n	♂♂	8	112	481	1396	1004	332	226	103	16	1	-	3679	
n	♀♀	3	112	435	940	399	139	92	63	17	3	1	2204	
N	♂/♀	11	224	916	2336	1403	471	318	166	33	4	1	5883	
%	♂/♀	0.19	3.81	15.57	39.71	23.85	8.00	5.40	2.82	0.56	0.07	0.02		

Table 18.

Variability of mean weights of males and females in age-groups with regard to weight distribution and numbers in years.

Year		1949	1950	1951	1952	1953	1954	1955
juv	♂	78.4	81.1	83.4	85.8	81.9	82.3	84.9
	♀	74.7	79.9	76.6	84.0	81.5	77.7	83.9
	Min.-Max.	58 - 98	60 - 104	64 - 96	62 - 104	64 - 102	66 - 98	60 - 111
	n ♂/♀	46/38	103/74	18/10	58/39	265/283	197/79	1609/1259
subad	♂	88.4	85.2	88.5	88.5	84.5	86.1	87.0
	♀	85.0	84.2	94.0	86.2	83.4	84.5	87.3
	Min.-Max.	72 - 100	66 - 100	73 - 104	78 - 100	72 - 110	70 - 100	68 - 108
	n ♂/♀	15/12	45/22	11/8	22/9	110/105	103/40	348/224
adult I	♂	91.2	96.0	-	96.0	88.9	87.3	89.2
	♀	87.6	92.0	-	96.3	85.6	87.6	90.2
	Min.-Max.	80 - 100	80 - 102	-	86 - 106	78 - 96	80 - 98	70 - 106
	n ♂/♀	5/5	14/8	-	2/7	21/17	18/10	161/115
adult II	♂	90.0	94.4	98.5	95.5	94.9	84.7	94.8
	♀	84.0	94.5	-	-	96.9	83.6	95.9
	Min.-Max.	84 - 90	84 - 105	94 - 104	88 - 100	78 - 110	74 - 102	76 - 112
	n ♂/♀	3/2	8/4	4/-	4/-	128/44	40/28	118/62
senex	♂	92.5	95.0	99.3	103.5	96.3	88.6	99.0
	♀	-	-	-	-	96.2	84.6	102.0
	Min.-Max.	88 - 98	82 - 102	94 - 102	102 - 108	78 - 112	78 - 98	84 - 112
	n ♂/♀	4/-	4/1	3/1	4/-	135/43	57/24	81/40
N		73/57	174/108	36/18	90/55	667/492	415/181	2317/1700

As in the analysis of body-length, there are here two general weight-groupings. The first, of the young (juv. and subad.) and the second of the adult (adult I and II) and old (senex). The general means of weight (Tab. 17) referring to age-groups from all years together, can serve as evidence of the differentiation of body-weight in connection with the age of specimens. In both sexes a distinct increase of means of weight can be seen, beginning with the young (juv.) males, 14.2 g, females 13.5 g, ending with the old (senex), where the means of body-weight are: males 27.4 g, females 20.9 g.

As can be seen from the analysis of the total collection of captured voles, when following the mean values for weight and length within the various age-groups, a certain parallelism of both these features with the age-groups is observable. This is, however, a matter for discussion.

Table 18 shows the means of body-weight in years. It illustrates in a detailed manner the values of weight means within the various age--groups. This indicates, *inter alia,* a more or less regular rise in weight means in both sexes in the various years. Thus, in individuals in the first class (juv.), the weight means are in the range 10.4 — 15.0 g. In slightly older individuals (subad.) they are from 14.6 to 16.9 g. In the next two age groups they are in the ranges 15.2 — 18.9 and 22.8 — 23.4 g respectively. In old individuals, however, (senex) the mean body weights in the various years are in the range 19.7 to 23.7 g.

Analysing the course of variability of body weight and length, we observe a definite similarity in the rise in mean values within the various classes over the years investigated. This similarity certainly indicates the reliability of the interpretation of the weight and length data in the description of the bank vole population.

To illustrate more clearly the similarity of the levels of means of weight and length in the various age-groups in the series of years, the author presents several figures (Figs. 18, 19, 20, 21). They show the tendencies to increase the mean values of both features in age-groups and clearly indicate their great correlation in almost all years. Fig. 21 also appears interesting. It partly summarizes the whole of the analysis of length and weight for the bank voles in the various age-groups. It is certainly an interesting illustration, indicating the dependence of both these features on the age of the individual, both as regards males and females.

Analysing this question in detail, the author made a total comparison of every age-group of the divisional series of all the summarized material, not divided into the several years. The mean lengths and weights in the various age-groups were also calculated. An obvious extension of numerical series for groups III, IV, and V, is visible in comparison with the former, both for length and weight for the two sexes. It is typical that the

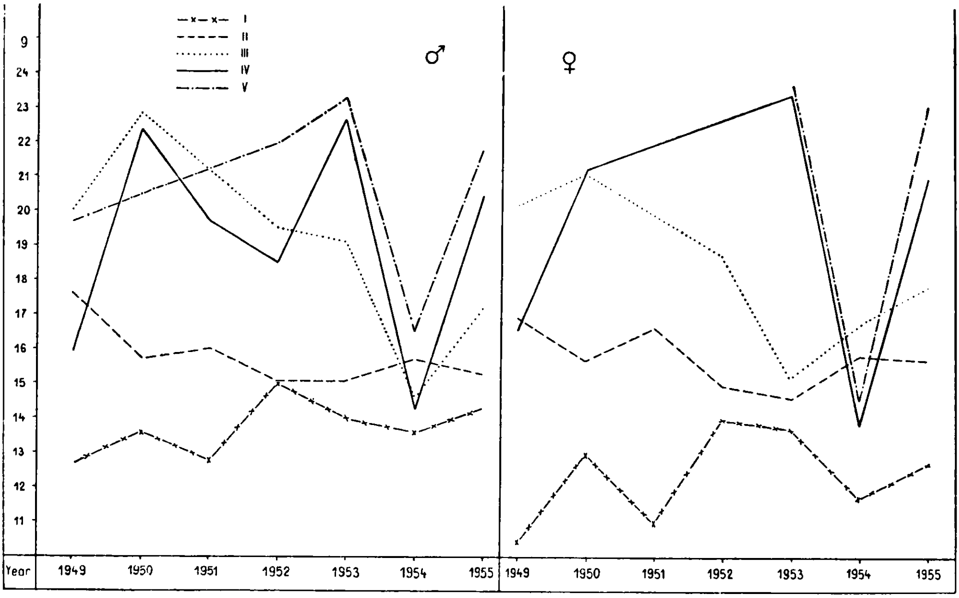


Fig. 18. Mean weight of males and females in the various years with regard to age.

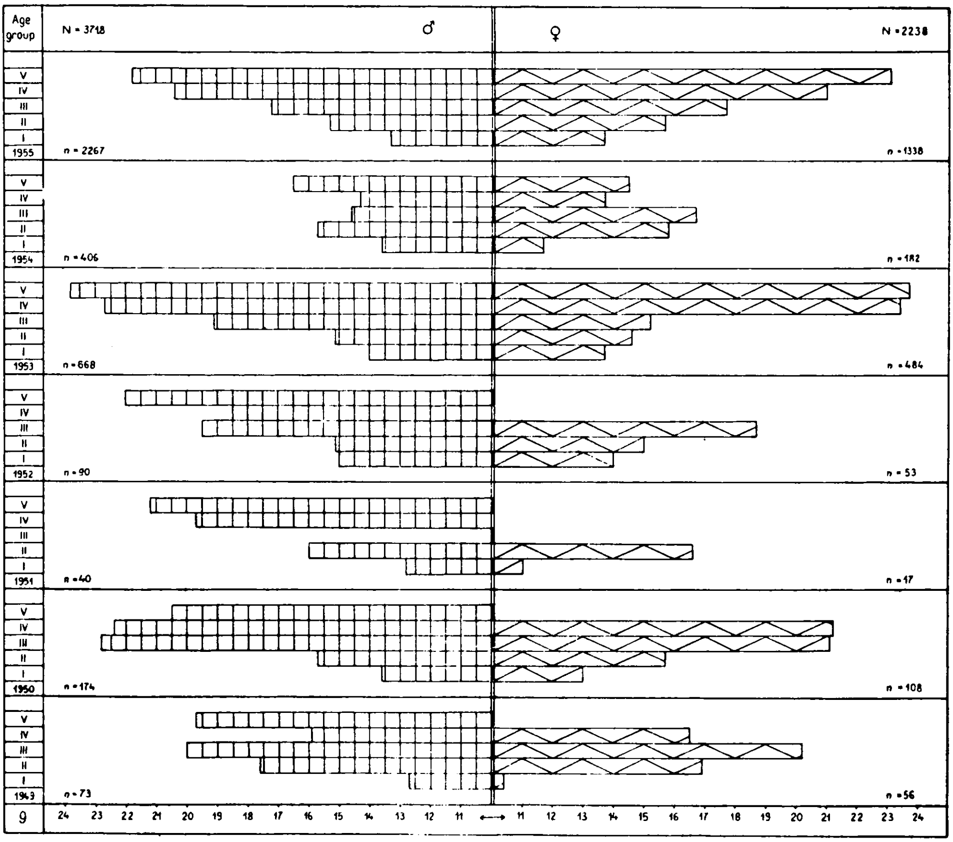


Fig. 19. Mean weight in age-groups with regard to sex and numbers in the years.

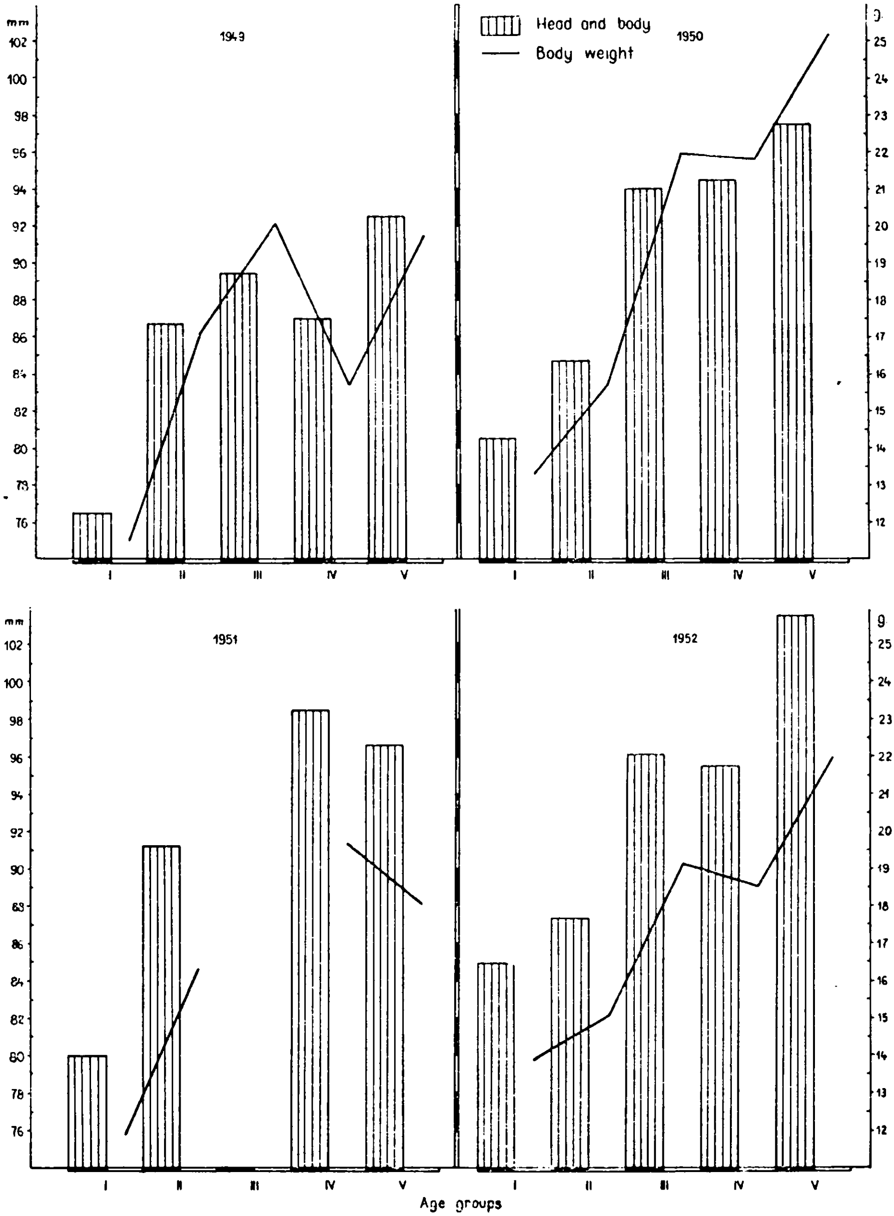


Fig. 20. Similarity of means of length and weight in the various age-groups in the years 1949—1955.

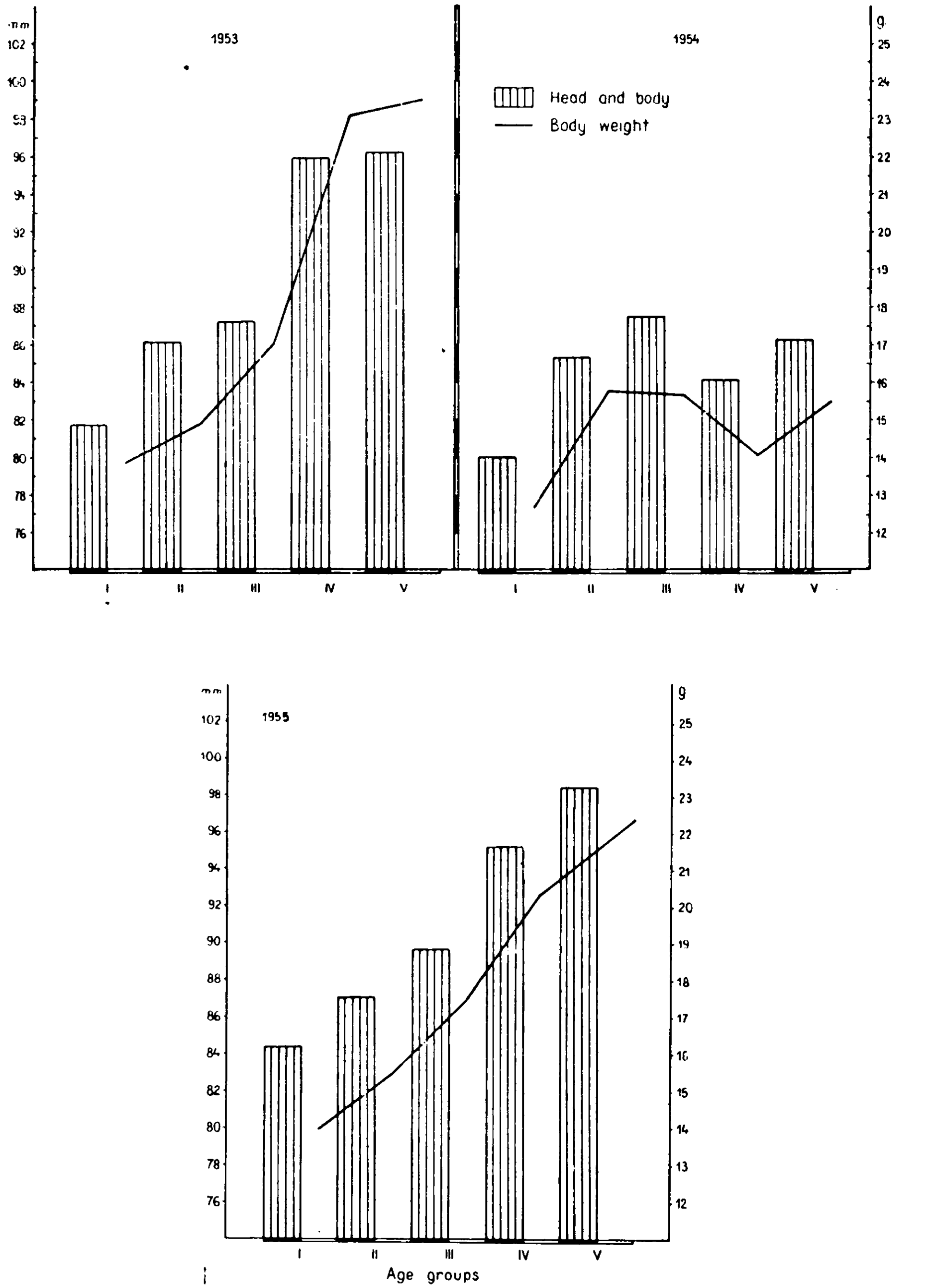

1953
1954
1955
Head and body
Body weight
mm
g
I
II
III
IV
V
Age groups

Fig. 20.

fall in tempo of growth is sharper in males than in females between group II (subad.) and group III (adult I). Carrying out the test of Kolmogorov-Smirnov, of pairs of neighbouring age-groups for length and weight, we obtain the following results (Table 19). The growth continues to the fourth age-group, both as regards length and body-weight. It is

Table 19.
Increase in length and weight with regard to neighbouring pairs of age-groups.

Age group	Head and body ♂♂	Head and body ♀♀	Body weight ♂♂	Body weight ♀♀
I II	35.96	20.58	63.30	57.95
II III	34.02	30.99	54.09	34.07
III IV	51.15	13.16	83.64	19.98
IV V	5.64	4.81	4.21	0.57

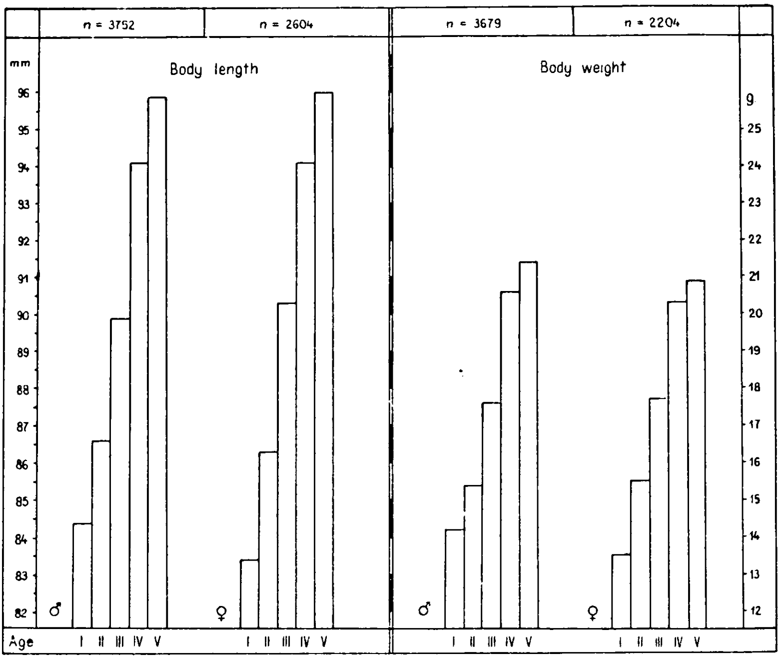


Fig. 21. Means of length and weight of males and females in the various age-groups for all years together.

also interesting to note the great difference in comparing groups III and IV for the males, whereas we observe no such difference in females although the K.-S. test gives a significant result. Thus, ♀♀ rose more slowly, while ♂♂ rose faster.

The means mentioned above indicate that the increase in length and weight with age is more even in ♀♀ than in ♂♂ (Tables 15 & 17). These differences between the sexes are seen most in the 1st age-group, but are very slight in the remaining age-groups. A topological test showed that only in the 1st age-group differences between males and females; both as to length ($\chi^2 = 6.43$ for 1 degree of freedom) and to weight ($\chi^2 = 7.12$ for 1 d. f.) are statistically significant. In the remaining age-groups χ^2 values are markedly less than 2, and thus differences are not significant.

VI. AGE STRUCTURE OF THE POPULATION

A closer knowledge of the age structure of a population analysed is a significant element in the investigation of the biology of a given species. Morphologists, taxonomist, ecologists and modern physiologists consider it as an important element fully justified methodically.

As we know, the methods of determining age are for *Micromammalia*, based on several criteria. These are considered with relation to the given species. For some species, biometric criteria are used, for others, morphological features or functional states, for others, all criteria together.

Over the last few years several publications have devoted space to the analysis of the age of *C. glareolus*. The age of these animals has been linked with such features as length and weight, formation and measurements of the skull, or corresponding formation of teeth roots. Naturally, however, in all schemes of classifications, the subjectivism of the author is unavoidable. Nevertheless, analysis of the age of the bank vole based on their dental root system as a stable element only slightly responding to external factors, seems to be the most reliable and makes for a greater objectivism in the appraisal of the age structure of the population.

The question has been dealt with in detail by: Zimmermann (1937), Wrangel (1939), Mohr (1949), Prychodko (1951), Sviridenko (1959), Wasilewski (1952), Zejda (1961), Mazák (1963). Their works should be treated as a serious contribution to the establishment of criteria for the age of *C. glareolus*. The similarity of results in this field, obtained by the authors mentioned above, allows us to assume that the method of analysis employed is correct.

As we know, the length of life of the bank vole in natural conditions is estimated at 16—18 months. If the young are born in spring in a given year, we assume that, at the maximum, they live until autumn the following year. During this time they grow intensively, mature sexually and breed. The tempo of growth and maturation of the individuals doubtless depends on a number of factors, both genetic (Chitty, 1952; Stein, 1956), and environmental (Naumov, 1948; Mohr, 1959; Ognev, 1950; Schwarz, 1960) and others. It is known that the sum of these factors affects the biological value of individuals in the various generations. It also decides on the dynamics of the whole population.

The number of individuals of varying age, and the keeping of correct proportions in this sphere is a significant indication of the state of a given population. The material analysed on *C. glareolus* in the years 1949—1955 indicates the fairly large majority of the young in the population. As can be seen from Table 20, of the total number of more than 6,000 specimens about 63.4% are young, with teeth which have not yet appeared. They are not more than two months old. 37% of specimens fall into the remaining 4 age-groups (Fig. 22). The percentage proportion of males and females in the juveniles group includes almost 2/3 of the area of the circle (Fig. 23). The percentage of males and females in the subadult group is, for the

Table 20.

Age structure of the population of *C. glareolus* expressed in percentages.

Year	Age groups					
	I	II	III	IV	V	n
1949	64.6	21.0	7.5	3.7	3.0	133
1950	62.6	23.5	7.7	4.5	1.7	285
1951	48.2	37.9	–	6.8	6.8	58
1952	67.1	21.2	6.1	2.7	2.7	146
1953	47.3	19.1	3.2	14.9	15.5	1168
1954	44.8	22.0	4.8	11.2	15.9	622
1955	70.8	14.1	7.0	4.5	3.6	4060
N 1949–55	4089	1087	400	453	443	6472
%	63.37	16.84	6.20	7.02	6.86	100.00

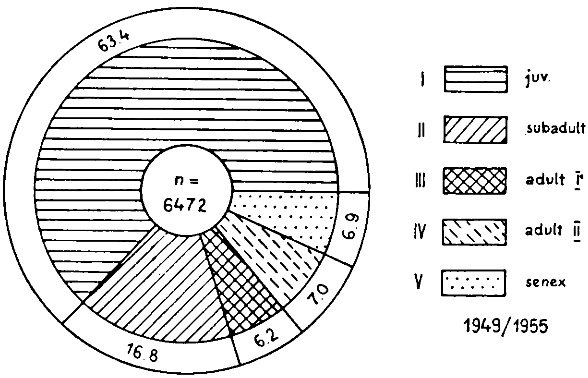


Fig. 22. Age structure of the population of *C. glareolus* expressed in percentages for the whole population captured.

former, 17.4%, for the latter 15.9%. In the remaining age-groups (Table 21) a gradual percentage "decrease" is noticeable, which in the last group (V, senex), is least numerous (males — 8.1%, females — 5.0%).

Similar relations between the various age-groups in both sexes suggests the question: Is repartition into the various age-groups identical for both sexes? In order to answer the question χ^2 test for homogeneity was carried out on the combined material from all years investigated, taking into

Table 21.
Frequency of males and females in the various age-groups.

Age group	I		II		III		IV		V		I - V 1949–55 N
Sex	n	%	n	%	n	%	n	%	n	%	
♂♂	2297	60.18	666	17.44	237	6.20	312	8.17	311	8.14	3823
♀♀	1792	67.73	421	15.90	163	6.16	141	5.32	132	4.96	2649

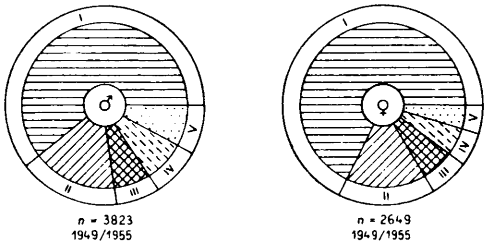


Fig. 23. Age structure of the population with regard to sex for all years together.

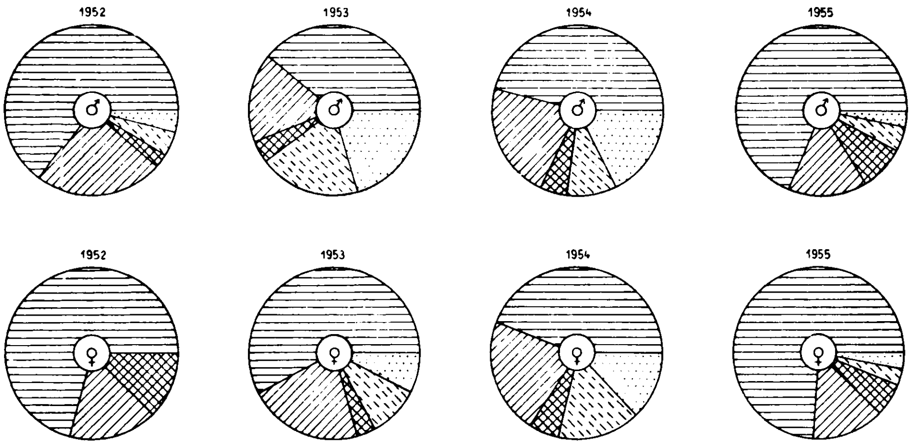


Fig. 24, 25. Proportions of males and females in the various age-groups in the years 1952—1955.

consideration in the classification — sex and age. The result obtained was $\chi^2 = 2.57$ for 4 degrees of freedom, where the critical value with a 5% risk of error is $\chi^2 = 9.49$, and does not indicate any differences in repartition in the age-agroups in both sexes.

The distinct numerical advantage of the young in groups I, II, usually in all years, to a certain extent reflects the character of the population analysed.

From a more through analysis of the age structure and numerical relationship of both sexes in various age groups we learn that there are quite large oscillations of these data in the years with the greatest number of captured specimens. As can be seen from Fig. 24, in 1952 young males (juv. and subad.) form more than 88% of the whole collection. In successive years more typical numerically, they also form a high percentage. In 1953 it is 55%, in 1954, 70%, and in 1955 more than 80%. The numerical proportions of the adults (adult I—II) and senex show considerable oscillation in the years discussed. In 1953 the percentage of males in this age-category is fairly high, altogether more than 40%. 1954 reveals a slightly lower percentage in both groups. The percentage figures for a year with a small number of specimens (1952) and for a year very well represented (1955) are interesting. In both cases the numbers, proportionally, are very similar in all groups. More than 4/5 of the collection consists of young males (juv. and subad.) 2—4 months old, and a mere 1/5 falls into the remaining three age-groups. To these last belong adult males (adult I—II) aged 5—11 months and senex, 16—17 months.

Similarly, for females, there is also a considerable majority of young females over the years. From Fig. 25 we see that the majority of females in the population are from the groups juvenis and subadult (70—85%). There is a comparatively low percentage of adult and senex females. Only 1954 differs from the remaining years with a comparatively high proportion of older females.

When we compare this with the similar picture for males (Fig. 24) the characteristic similarity of the graphs for both sexes in some years is obvious. 1954 and 1955 present an almost identical picture, very similar (especially as regards the young) to 1952. 1953, however, presents a very different picture where there is a considerable majority of adult males (adult II) and old males (senex) in comparison with females of the same age-group.

Examining the several years more closely and carrying out χ^2 test for homogeneity for every year separately, the following were the results:

$$1949\ \chi^2 = 3.56; \qquad 1950\ \chi^2 = 2.53;$$
$$1951\ \chi^2 = 2.30; \qquad 1952\ \chi^2 = 2.86;$$
$$1953\ \chi^2 = 69.47; \qquad 1954\ \chi^2 = 5.83;$$
$$1955\ \chi^2 = 4.27;$$

For all these variates χ^2 there are 4 degrees of freedom, of which the critical value $\chi^2_{0.05} = 9.49$. The result for 1953 alone is significant. Thus we conclude that, apart from 1953, in all the years investigated the repartitions of males and females into the various age-groups are the same. 1953 is characteristic in having a majority of females in age group I but in other age-groups the majority of males occurs; as in the remaining years.

The numerical proportions of males to females of various ages at the different seasons of the year present an interesting picture. As can be seen from Fig. 26, more than 90% of young males (juv. and subad.) are found in summer and autumn. Their percentage in spring and winter is minimal (5.8% and 3.4% respectively). The above data concern all years together. Analysing the years of investigation from this angle, we note a great similarity of results. In all the years here considered (1952—1955), in spring there was a minimal proportion of young specimens. The same situation is repeated in winter, except for 1954/1955, where the number of males in this age group was fairly high (more than 25%).

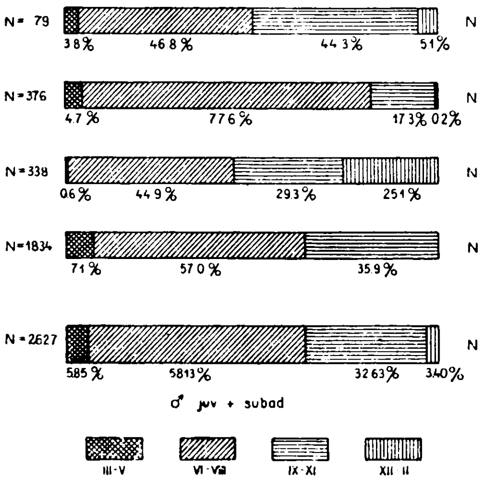


Fig. 26.

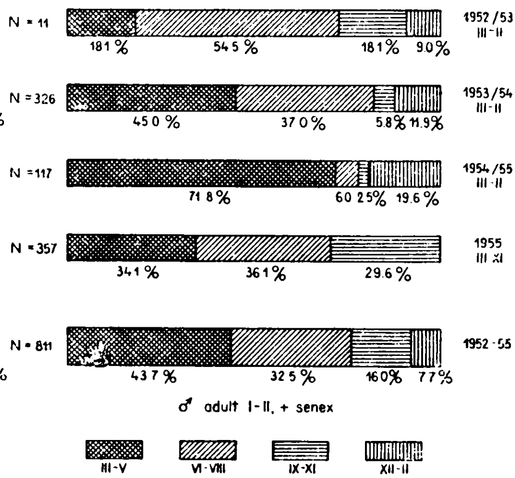


Fig. 27.

Fig. 26. Percentage proportion of young males (juv. and subad.) in the seasons of a series of years.

Fig. 27. Percentage of adults and old males (adult I—II) (senex) in the seasons of a series of years.

The numerical relationships of adult and old males groups III—V vary in different seasons. The majority of specimens (Fig. 27) occurs in spring (43%). A smaller proportion (32.5%) is found in summer, while in autumn only 16% is captured. In winter, however, the total percentage number of specimens captured is not more than 8%. This varies, as we see when analysing the various years. A particularly striking difference in numbers is seen in spring 1954, when more than 70% of adult and old males are found. As for the remaining seasons of that year, a relatively large percentage (19%) of individuals in these age-groups was found in winter 1954/1955, while in summer and autumn together the number taken is not more than 8%. The numbers and proportions within the various age-groups in the seasons discussed are clearly different as compared with

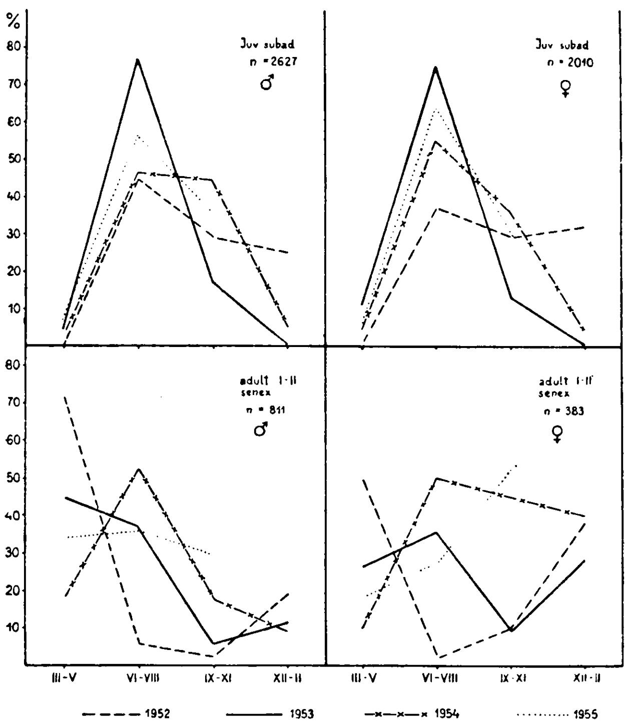


Fig. 28. Frequency of voles in the various seasons, 1952—1955, with regard to age and sex.

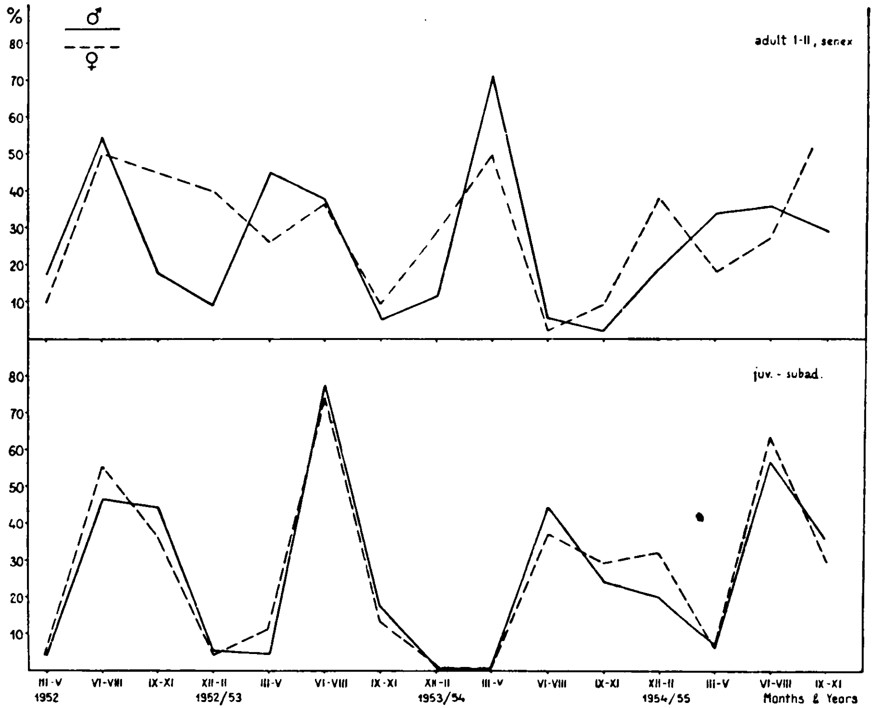


Fig. 29. Age structure of the population with regard to the seasons of the successive years.

other analysed years. In all remaining years, adult (I—II) and old (senex) males are most numerous in spring and summer. They are specimens who had spent one, more rarely two, winter periods.

A similar proportion of age-groups is observable in the females caught in the various seasons (Figs. 28, 29). As in the case of the males, there is a preponderance of young (juv. and subad.) females in the summer and autumn (altogether more than 90%). Analysing the various years, we see considerable similarity with the generation of the year 1953/1954, when in summer there were more than 74% of young females. Winter 1954/1955 is relatively well represented in young females (25%).

As regards adult and old females the numbers in the various seasons are fairly even. From the total data it appears that in spring, summer and autumn the numbers are within the range 25—33%. Only in winter are they below 15%. In some years, however, there are greater or lesser variations from this scheme, especially in 1954, (as with the males) where in summer and autumn there is less than 12%. In those seasons in other years, these proportions differ markedly, both summer and autumn are well-represented.

The relative proportions of both sexes in the various years for the defined age-groups depend on the age of the specimens. After carrying out tests χ^2 for homogeneity in the defined age-groups and the various years (1949—1955), the following results were obtained: for age-group I — $\chi^2 = 39.77$; II — $\chi^2 = 15.74$; III — $\chi^2 = 6.27$; IV — $\chi^2 = 10.06$.

For age-group V — no test was carried out, since there were too few specimens. All variables χ^2 have 6 degrees of freedom. Critical value $\chi^2_{0.05} = 12.59$. From the above data, it appears that the years differed among themselves as regards the relation of sex especially in age-group juvenis, and to a lesser degree in subadult. In the remaining two groups, however, we can observe no essential differences in these relations.

VII. THE DYNAMICS OF REPRODUCTION

The question of breeding in small mammals has particular significance in an analysis of the density of population in a given area. This is closely connected with the question of oscillation and numbers of a given generation over several years and seasons.

In the case of the bank vole, *Clethrionomys glareolus* (Schreber), a fairly common inhabitant of our forests, which plays an important role in biocenosis in periods of mass occurrence, this topic is doubtless a valuable one. Several authors have devoted much space to these questions, *inter alia:* Heptner (1947), Formozov (1948), Naumov (1948), Ognev (1950), Koškina (1957), Kulajeva (1958), Sviridenko (1959), Schwarz (1959). They gave us several valuable elements in the knowledge of the processes of breeding and their biocenotic significance. Together with the numerous and frequently exhaustive work of the European authors: Brambel & Rowlands (1936), Rowlands (1936), Zimmermann (1937), Wrangel (1939), Turček (1954), Stein (1956), Kalela (1957), Zejda (1962) and others, they form a noteworthy record of achievements to date in this field. The value of the work of the authors here mentioned, especially the recent, is so far significant because the results of their investigations are frequently based on long series of observations with, simultaneously, good documentation of the material. This certainly brings greater objectivity to the interpretation of results and drawing of conclusions.

The literature of Poland in this field is fairly numerous, especially within the last 10 years. It is, however, chiefly concerned with other species of *Micromammalia:* Kowalski, 1950; Borowski & Dehnel, 1953; Kubik, 1952; 1953; 1960; Dehnel, 1952; Bazan, 1956; Tarkowski, 1956; Wasilewski, 1960; Grodziński, 1957; Skuratowicz, 1957; Pucek, 1959; Adamczewska, 1961; Dynowski, 1963, and others. Concerning *C. glareolus,* however, to date there has not been a full consideration of the breeding of these mammals, especially as regards the morphological variability of the gonads, varying breeding tempo at various seasons in different years and breeding predispositions of individuals of the various generations and their consequences. The questions mentioned above, which certainly have significance in the dynamics of the population also concern, to a large extent, the entirety of these questions connected with the biology of breeding in the forms analysed, and will be discussed in this chapter.

The problems of the breeding of *C. glareolus*, as touched on by the present author, form only a small part of the wider problem of the biology of breeding in *Micromammalia,* but this part has considerable theoretical and practical values.

Within the various age-groups (Table I), in males, the testes in transverse section show considerable variation. They vary in size from 3.0 to more than 14.0 mm. Similarly, the size of *vesica seminalis* varies from 1.7 to 10.0 mm with, in the upper range, the length of the testes from 11.5—14.5 mm. From histological examination of sections, we assume that the males reach full sexual activity when the testes are from 10—11 mm long. This allows us to define more accurately at what age males are sexually active, and what proportion of such males can be found in the various seasons and years.

Fig. 30 presents the percentage proportion of males of various ages, with consideration of their degree of sexual maturity from the most numerously represented years. From the graphs it appears that the young (juv. and subad.) with the smallest testes (class I) are the most numerously represented in all years except 1954. They form from 60% to 90% of the total of young males of the given year. The graphs then show a sharp fall in the remaining classes of gonads (2, 3, 4) within the boundaries 2—1%. A slight rise in the curves can be seen in the class of the largest testes (5, 6) where the number of males is not more than 20%. The above data indicate that among young males (juv. and subad.) of the years 1952, 1955 was a majority of sexually immature specimens. The percentage of active sexually mature males was minimal.

1954 shows a completely different picture in the graphs. Young males with the smallest testes are very few (10%). Those with the largest testes (classes 5, 6) assumed to be sexually active, were found to be 50% of the population.

As regards adult and old males (adult I, II, senex), the majority (70—80%) of individuals is sexually active. The graph rises sharply for the group with the largest gonads (classes 5, 6). However, in groups with minimally grown testes, the curve falls; the number of such individuals is not more than 25%. Only 1954 shows (as with the young) a slightly different character. There was 50% of sexually active individuals, the remainder were immature with more or less well-developed testes.

The polygons present a fairly characteristic picture (Fig. 30). In the young (juv. and subad.) the graphs rise highest in all years for the group with the least-developed gonads (class 1). For the adult and old the graph

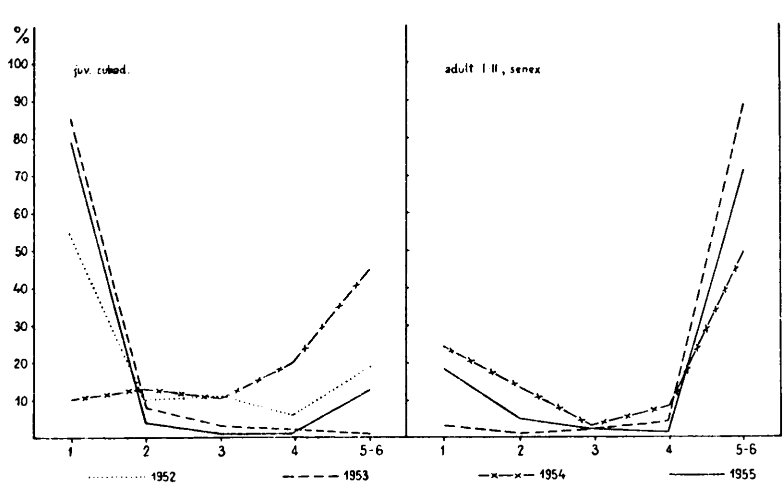


Fig. 30. Sexual maturity of males (classes according to gonads), 1952—1955, with regard to the age of specimens.

peaks occur in the group with the largest testes (classes 5, 6). In the non-extreme classes of gonads the graphs are clearly indefinite, as the percentages of such individuals are slight, not more than 6—7%.

The differing picture for 1954 becomes clear if we analyse the intensity of maturation of specimens during the various seasons of the year and consider the climatic conditions during that time. From the data in Fig. 31 it appears that the largest percentage of young males (juv. and subad.) with least-developed testes (classes 1, 2) is found in summer and autumn (about 80%). In summer, when the largest number of newborn animals appears, rutting generally extends over all months of that season. In autumn, however, the tempo of sexual maturity is to some degree inhibited and dependent on climactic conditions and food available in the given year. Our example here may be the three successive years 1953, 1954, 1955 (Table 22). Favourable climatic conditions and abundance of food in summer and autumn 1954 and winter 1954/1955 (Adamczewska, 1961; Sidorowicz, 1960) undoubtedly speeded the tempo of the growth of the gonads, which in consequence might lead to a quicker commencement of sexual activity. As can be seen from Table 22, more than 70% of young males in summer in the first 2—4 months of life were capable of breeding. The development of testes and *vesica seminalis* clearly indicated this.

Similarly in autumn of that year, where of 99 specimens about 50% of young males was sexually active. Winter 1954/1955 deserves attention. Here we find a clear majority of mature young males capable of breeding (altogether more than 80%). This is striking when compared with the years 1953, 1955, where in all the seasons mentioned above the numerical relationships are reversed. The majority of young males with underdeveloped testes and small percentage of males with the largest size of testes

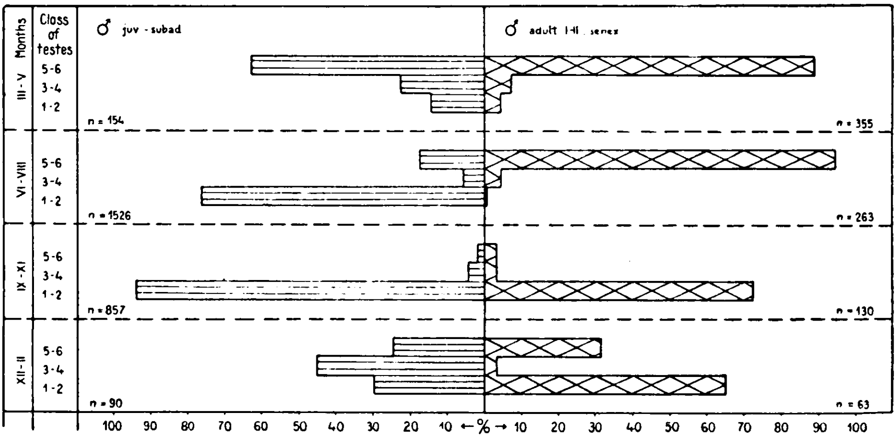


Fig. 31. Percentage proportion of males in varying phases of sexual maturity with regard to age and the seasons of the series of years.

in these seasons clearly indicates a decrease in the tempo of sexual maturation. This is marked in autumn, where there are almost no maturing young males capable of breeding (Table 22 and Fig. 31).

Fig. 31 shows a contrasting picture in spring. This period, of course, has a special role in the breeding of rodents. After the winter rest period there occurs a period of intense breeding in adults and the old. However, the young in especially favourable winter and pre-spring conditions may be active in the spring rutting. From the general analysis of that season (Fig. 31) it appears that the role of sexually active (classes 5, 6) young males (juv. and subad.) in this period is quite large, about 70%. But this question, when the spring in various years is compared (Table 22) appears in a different light. We then observe a great dissimilarity of results, probably dictated by various environmental conditions (weather, food, base, etc.). Thus, considering the well-represented years 1953—1955, we see that only in spring 1955 was there a majority of young sexually mature males. In other years however, either the young had not yet appeared (in

Table 22.

Sexual maturity of males in the various seasons of the years 1952—1955.

Season	Year	juv - subad			n	adult I - II			n	senex			n	N
		1-2	3-4	5-6		1-2	3-4	5-6		1-2	3-4	5-6		
Spring	1952	-	1	2	3	-	-	1	1	-	-	1	1	5
	1953	11	7	-	18	1	5	89	95	-	-	52	52	165
	1954	-	1	1	2	10	4	8	22	6	13	43	62	86
	1955	11	26	94	131	-	-	113	113	-	-	9	9	151
N	1952/55	22	35	97	154	11	9	211	231	6	13	105	124	509
%		14.3	22.7	63.0	30.2	4.8	3.9	91.3	45.4	4.8	10.5	83.9	24.4	100.0
Summer	1952	10	14	13	37	-	-	4	4	-	-	2	2	43
	1953	273	14	5	292	-	-	47	47	-	9	65	74	413
	1954	11	37	104	152	-	-	3	3	-	-	4	4	159
	1955	876	23	145	1044	1	2	76	79	1	1	48	50	1174
N	1952/55	1170	88	267	1525	1	2	130	133	1	10	119	130	1789
%		76.7	5.8	17.5	85.2	0.7	1.5	97.8	.7.4	0.7	7.7	91.6	7.3	100.0
Autumn	1952	35	-	-	35	-	-	1	1	-	-	1	1	37
	1953	63	2	-	65	6	1	1	8	3	5	3	11	84
	1954	49	33	17	99	-	-	2	2	-	-	1	1	102
	1955	657	1	-	658	80	3	4	87	7	8	4	19	764
N	1952/55	804	36	17	857	86	4	8	98	10	13	9	32	987
%		93.8	4.2	2.0	86.9	87.7	4.1	8.2	9.9	31.2	40.6	28.1	3.2	100.0
Winter	1952/53	4	-	-	4	-	1	-	1	-	-	-	-	5
	1953/54	1	-	-	1	30	-	-	30	9	-	-	9	40
	1954/55	22	41	22	85	2	1	20	23	-	-	-	-	108
N	1952/55	27	41	22	90	32	2	20	54	9	-	-	9	153
%		30.0	45.5	24.4	58.8	59.2	3.7	37.0	35.3	100.0	-	-	5.9	100.0

1954 the rutting took place in late spring) or as in 1953 the majority of males in this season was sexually inactive.

Analysis of the various seasons in the different years (Table 22) shows that the percentage of sexually active males varies considerably (as it does with regard to the young). This table shows, *inter alia*, that in spring 1953 and 1955 almost 100% of adult and old males were capable of breeding. In 1954, however, the number of adult sexually acitve males was barely 35%.

An even more characteristic oscillation is seen in winter, where in one year (1953/1954) there were 100% of adult and old males with a regressive state of the gonads (in classes 1, 2), while in winter 1954/1955 more than 90% were capable of breeding. The gonads of these specimens were of maximal size (classes 5,6). Histological examination indicated that these males took part in winter breeding.

With these facts in mind, we can state that the picture presented by Fig. 31 and Table 22 indicate a dissimilarity in the interpretations of the results. Fig. 31, illustrating the intensity of breeding of the males in the seasons of all analysed years together, shows that there is a considerable percentage of young males, capable of breeding in spring, and a very small percentage in summer and autumn. Table 22 shows this topic with consideration of the various years separately and draws attention to the great oscillation in this respect. It shows that in the various years taken singly, the percentage of sexually active males in certain seasons undergoes greater or lesser oscillation. The tempo of maturation in the young or the state of accidental degeneration in young males show significant differentiation. The oscillations here demonstrated have no corresponding reflection of the existing relations in the histogram, which treats the question only on a general plane, as it is concerned with the various seasons altogether, not singly, and without taking any other aspects into consideration. Thus, the picture presented by Fig. 31 indicating the large percentage in spring of sexually active young males, is rather relative. If the data for 1955 (Table 22) were not included in this general picture, the results would then be quite different. They would show that the number of young males capable of breeding in spring was very slight. Similar, though less characteristic dissimilarities of this type were shown for other analysed seasons of that year.

As can be seen, all interpretations (frequently made for several species based only on massed general data, without consideration of various aspects) may be rather problematical.

From the analysis of the various seasons of several years (1952—1955) we may conclude that the part played by young males (juv., subad.) in breeding changes from year to year and in the various seasons of the year. The factors affecting these changes are fairly widely commented. The interpretations made of these problems vary according to the material the authors had at their disposal. As a rule, however, as regards spring, intensity of breeding and the greater part played by young or adult voles, are explained as due to favourable atmospheric conditions and abundance of food. This may also be the consequence of unbroken sexual activity which occasionally takes place in the preceding autumn-winter season. Stein (1956) and Zejda (1962) drew attention to this. They caught fully-active specimens in the winter months.

The material analysed, especially as regards the two years 1954, 1955, to some extent allows to confirm the thesis of the two above-mentioned authors. Thanks to good weather and food conditions in the summer-autumn season of 1954 and in winter and spring 1955, the sexual acitivity of young and adult males was definitely more intensive. The fairly large percentage (Table 22) of males with maximal-size gonads (classes 5,6) in all above-mentioned seasons confirms this.

This permanent intensified part played by sexually-active males in breeding doubtless significantly affected the density of the population and mass appearance of the species in summer and autumn 1955. This special rise in the birth-rate, despite relatively optimal ecological conditions, adversely affected the sexual maturation of young specimens born during these periods. Both in summer and autumn 1955 the percentage of young males (juv. and subad.) with the smallest gonads (classes 1, 2) was very great (85—99%). This would indicate a certain developmental stagnation, probably arisen either because of the intensified rivalry between the animals (for food) which continues both in the adolescent as well as in the postnatal phase (Naumov, 1948; Formozov, 1948); or because of certain different genetic predispositions (Chitty, 1952; Stein, 1956).

Both interpretations are possible, especially if we consider the fairly characteristic data on length and weigth of individuals born in this period (Fig. 32). As compared with the previous year (1954), individuals from these two seasons, especially autumn 1955, were relatively heavy and long. The average body-length in voles in summer is 87.1 mm (in 1954, $\bar{x}$ = 84.1 mm), in autumn it is 87.8 mm (in 1954 it was 81.1 mm). As regards body-weigth in the first case the average was not more than 15.8 g (1954, $\bar{x}$ = 14.8 g), in the second it was 15.0 g (1954, $\bar{x}$ = 13.0 g). These differences may indicate that the growing factor in the young generation in summer and spring in 1955 "directed" all its dynamism towards increasing the general "constitutional" mass of the body, at the cost of other elements, as in this case, breeding. In 1954, however, the reverse is true. Where the body-mass of individuals born in the two seasons here discussed is small, there is a decidedly quick development of sexual organs, which in turn leads to a fairly high percentage of young males capable of reproduction.

From the above interpretation of rather differentiated data, certain conclusions may be drawn. Namely, the first concerns what plays a significant role in the rise in population and prognosis of mass appearances of the species in the following calendar year, the second concerns what affects the numerical regress of the population.

In the first case this would concern specimens born in summer and autumn 1954, which, as has been mentioned, have a quick development of the gonads and intensified sexual activity. This generation, with such dynamic morphofunctional reproductive properties and relatively optimal density of population and a favourable complex of environmental factors (*inter alia* good weather extending over the winter-spring season) undoubtedly increased the population of the bank vole. The large part

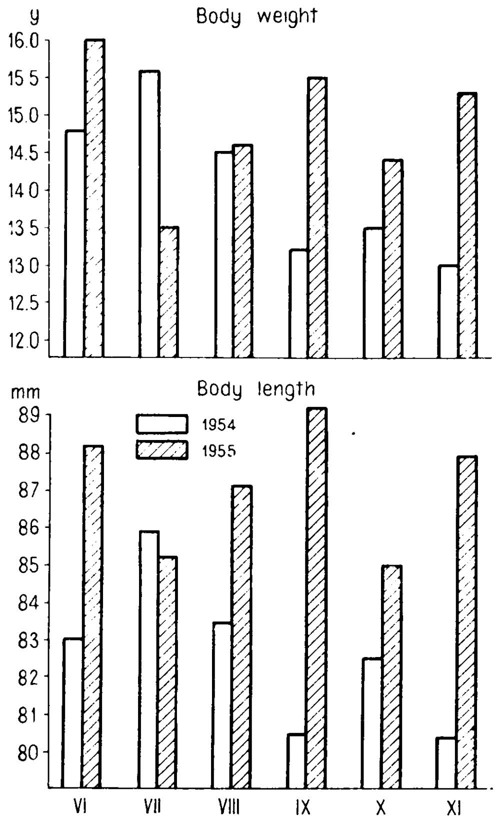


Fig. 32. Mean length and weight in the various months of the summer-autumn seasons 1954—1955.

played by this generation in the dynamics of breeding in the seasons mentioned was reflected in a marked manner on the following very numerous generation, leading to the mass appearance of these mammals in the following calendar year, 1955. This generation could be defined, on the one hand, as biologically valuable, guaranteeing the preservation and stabilization of the species, but on the other hand it could be defined as economically harmful since it increased the density of the population, which indirectly affects forest exploitation.

These are two aspects of the same problem, indicating the varying significance of one generation. They show, too, that the reproductive predestination of individuals from even one generation may affect significantly the dynamics of the whole population.

The above thesis is seen in its proper values when the results of the summer season, and especially, the autumn of 1955 are considered. In place of sexually active young males (1954), we here meet a numerous

Table 23.

Sexual maturity of females in the various seasons with regard to age-group.

Season	Year	juv. - subad.			n	adult I - II			n	senex			n	N
		I	II	III		I	II	III		I	II	III		
Spring	1952	1	1	-	2	1	-	-	1	-	-	-	-	3
	1953	34	10	1	45	1	9	3	13	-	-	-	-	58
	1954	-	1	-	1	4	-	-	4	16	1	1	18	23
	1955	2	10	-	12	-	8	-	8	-	1	1	2	22
N	1952-55	37	22	1	60	6	17	3	26	16	2	2	20	106
%		61.7	36.7	1.7	56.6	23.1	65.4	11.5	24.5	80.0	10.0	10.0	18.9	100.0
Summer	1952	19	6	-	25	-	3	2	5	-	-	-	-	30
	1953	258	28	-	286	2	5	3	10	1	11	7	19	315
	1954	17	21	4	42	-	-	-	-	-	-	-	-	42
	1955	675	29	16	720	4	16	4	24	-	8	3	11	755
N	1952-55	969	84	20	1073	6	24	9	39	1	19	10	30	1142
%		90.3	7.8	1.9	94.0	15.4	61.5	23.1	3.4	3.3	63.3	33.3	2.6	100.0
Autumn	1952	16	1	-	17	-	-	-	-	-	-	-	-	17
	1953	54	3	-	57	5	2	-	7	1	3	1	5	69
	1954	29	7	3	39	-	-	-	-	-	-	-	-	39
	1955	372	1	-	373	60	20	2	82	3	9	12	24	479
N	1952-55	471	12	3	486	65	22	2	89	4	12	13	29	604
%		96.9	2.5	0.6	80.5	73.0	24.7	2.2	14.7	13.8	41.4	44.8	4.8	100.0
Winter	1952/53	2	-	-	2	2	1	-	3	-	-	-	-	5
	1953/54	3	-	-	3	19	-	-	19	11	-	-	11	33
	1954/55	18	9	2	29	1	9	1	11	-	-	-	-	40
N	1952-55	23	9	2	34	22	10	1	33	11	-	-	11	78
%		67.6	26.5	5.9	43.6	66.7	30.3	3.0	42.3	100.0	-	-	14.1	100.0

infantile generation, sexually immature. Probably the above fact and less favourable complex of environmental conditions in this period caused the decrease of population in 1956. The small number of specimens captured in that year could, to some extent, confirm this thesis.

The part played by females in breeding, both young and adult in the various years analysed is essentially similar to that of males. The numbers of sexually inactive young females with minimal-size gonads are large in all years. From Table 23 we conclude that in the years 1953 and 1955 a considerable proportion of young females (juv. and subad.) did not take part in breeding. In the years mentioned, of a relatively large number of individuals (more than 1,000 females in 1955) more than 90% females were characterized by a minimal development of gonads (class 1). A very small number of mature, sexually acitve females in this age-group was found — not more than 2%. 1954 shows a somewhat different picture. More than 51% of females had minimal measurements for the horns of the uterus, 39% were in the maturing phase (class 2) and 10% were capable of reproduction. Thus, in comparison with young males of this year (Fig. 30) females give the impression of a slower tempo of maturation.

However, the results of comparisons of both sexes in the years 1953 and 1955 are fairly similar. In the first and second case the role of the young in breeding is very small. The problem is very different in appearance with regard to adult and old females (Table 23).

In comparison with males, distinguished by a majority of sexually-active individuals, the females show considerable quantitative variations in this sphere. We find a relatively large number of adult and old (adult I-II, senex) females in the regressive or resting phase of gonads. Thus the number of females with minimal and average measurements of the horns of the uterus is fairly large in all the years analysed. There is, however, a very small number of sexually active females in the various years; in 1953 there were 24.5% (of adult and old together), in other years, as in 1954, only 3.5%, in 1955, 7.5%.

Similar quantitative variations (Table 23) are found when the question is examined in the seasonal aspect. Both young and adult females in the various seasons of the series (1952—1955) are most numerously represented in groups with minimally developed gonads (classes 1, 2). The number of females capable of reproduction (class 3) is very small. Data contained in the table referred to are based only upon the degree of development and the formation of the horns of the uterus and do not allow us to draw reliable conclusions on the tempo of maturation and reproductive activity of the females. They show only the general numerical relations of females, with a greater or lesser degree of formation of the reproductive organs, both at various ages, and deriving from various years and seasons in a given year.

Undoubtedly fuller results may be obtained from analysis of pregnant females as regards the dynamics of reproduction and its intensity (Brambel & Rowlands, 1936; Wrangel, 1939; Naumov, 1948; Zejda, 1962).

With regard to the age of females and their part in reproduction (Table 24) it may be said that the greatest percentage, 44.2% falls into the first two age-groups, juvenis and subadult. This concerns all years together.

However, from the analysis of the various years it appears that these relations undergo considerable variations. Thus, in 1953, there were barely 10% of young and pregnant females (juv. and subad.), in 1954 88%, and in 1955 more than 47%. There were also considerable percentage oscillations of pregnant females in the remaining age-groups. Especially obvious differences are observable in the percentages for 1954. In comparison with the neighbouring years there is a decided numerical majority of young pregnant females and a low proportion of pregnant females in the remaining age-groups, which may indicate the slightly different character of the dynamics of reproduction in this year. Support for such an interpretation can be found in the tables (Table 25) where there is a quantitative analysis of pregnant females of various age-groups with consideration of the various months of the given year. From this comparison it appears that the majority of pregnant females in 1954 in all age-groups, is to be found in summer (40%) and autumn (50%).

Table 24.
Percentage proportion of pregnant females in 1953—1955 with regard to age-group.

Age / Year	juv.- - subad.	adult. I - II	senex	N	n	%
1953	10.2	51.3	38.5	487	39	8.0
1954	88.0	8.0	4.0	168	25	14.0
1955	47.3	44.6	8.1	1350	74	5.0
Total	61	55	22	2005	138	
Percent of pregnant females	44.2	39.8	15.9			

The picture is very different for 1953 and 1955, where the majority of pregnant females can be found in spring and early summer. But as from July 1953 and August 1955, in all remaining summer and autumn months the percentage of pregnant females is very small, only 7% and 25% respectively. The majority of young females in 1954 is pregnant and takes part in reproduction in summer and autumn. Also the role played by that generation is completely different, especially as compared with the neighbouring years 1953, 1955.

The above results allow us to assume that the intensity of reproduction in young females in 1954 was more or less evenly distributed in both seasons, summer and autumn, with prolongation of the breeding season because of favourable weather and food conditions, in winter also. These facts should be treated as to some extent significant in defining the reproductive predestination of the various generations and the roles they might play in determining the quantity and quality of the generations in the next calendar year. In the case discussed, the very numerous population of 1955 would be an expression of this. The generations of adult and old females where the concentration of breeding was chiefly in spring, led to the lowering of the numbers of the population in the following year. An index in this field may be the relatively moderate number of specimens captured in 1954 and 1956.

The above considerations would have a certain significance: if the decrease noticed in the essential expansion by reproduction in the adult and old were taken into account (N a u m o v, 1948; S t e i n, 1953, 1956; S c h w a r z, 1959; Z e j d a, 1962).

Table 25.

Number of pregnant females in the various months of 1955 with regard to age.

Year	Age group	Months II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	N	%
1953	I + II	-	-	-	1	2	1	-	-	-	-	-	4	10.2
	III	-	-	-	-	-	-	-	-	-	-	-	-	-
	IV	-	-	6	7	7	-	-	-	-	-	-	20	51.3
	V	-	-	3	4	6	-	1	1	-	-	-	15	38.5
	n	-	-	9	12	15	1	1	1	-	-	-	39	100.0
	%	-	-	23.1	30.7	38.5	2.6	2.6	2.6	-	-	-	100.0	
1954	I + II	-	-	-	-	3	3	3	3	2	6	2	22	88.0
	III	-	-	-	-	-	-	-	1	-	1	-	2	8.0
	IV	-	-	-	-	-	-	-	-	-	-	-	-	-
	V	-	-	-	-	1	-	-	-	-	-	-	1	4.0
	n	-	-	-	-	4	3	3	4	2	7	2	25	100.0
	%	-	-	-	-	16.0	12.0	12.0	16.0	8.0	28.0	8.0	100.0	
1955	I + II	-	-	1	8	17	9	-	-	-	-	-	35	47.3
	III	1	4	6	2	4	4	-	-	-	-	-	21	28.3
	IV	-	1	5	1	3	2	-	-	-	-	-	12	16.2
	V	-	-	-	1	2	3	-	-	-	-	-	6	8.1
	n	1	5	12	12	26	18	-	-	-	-	-	74	100.0
	%	1.3	6.7	16.2	16.2	35.1	24.3	-	-	-	-	-	100.0	
Total	N I - V	1	5	21	24	45	22	4	5	2	7	2	138	
	%	0.7	3.6	15.2	17.4	32.6	15.9	2.9	3.6	1.4	5.0	1.4	100.0	

The remarks made above are rather working hypotheses. We know that in the definition of the value of a population or generation in a given year, a number of fairly significant factors are considered. In connection with the analysis of the males, it was remarked here that the time period or season of the year is closely connected to climactic and nutritive conditions. The sum of these factors influences, to a large extent, the biological value of the specimens of a given generation, the condition of these mammals and their reproductive predestination.

VIII. DISCUSSION AND CONCLUSIONS

In the analysis of the population of the bank vole in Białowieża a number of questions connected with the morphological variability of certain features with taxonomic and constitutional significance were discussed.

Namely, from the analysis made of the length and body-weight under the aspects of age, season, year, and the individual, it appears that the variability of these features is relatively large. It is, however, difficult to establish any rules determining their variability. The following factors show that the problem is fairly complicated: considerable numerical fluctuations in the various years, great range of dispersion, oscillations of the average values for weight and length in the various years, seasons and months. Any conclusions or hypotheses in this sphere may be rather subjective. One thing can be stated certainly: both length and weight show considerable plasticity and a wide field of variation in the species investigated.

The considerable range of variability in body-weight and length, based upon abundant material captured over a period of years in the Białowieża National Park, essentially indicates the variability of these features on the population level. From a purely morphological point of view it indicates only a section of variability limited in time and space (Stein, 1951; Kubik, 1957). It chiefly indicates the individual and geographical variability of the bank vole population in a defined area (Dehnel, 1949; Schwarz, 1959).

That view-point, the result of careful morphobiometric analysis of the material, compels us critically to evaluate the criteria of body-length as a taxonomic index. These is no doubt that the mean values or ranges accepted for many subspecies of *Clethrionomys*, can be successfully linked to the variability of the Białowieża form discussed. Wasilewski (1952) also stated this in a craniometric analysis of this species. As regards other species of *Micromammalia*, similar remarks are to be found in the work of Dehnel (1949), Borowski & Dehnel (1953), Kubik (1952), Adamczėwska (1959).

Schwarz (1959) giving numerous examples (based on literature) of individual and geographical variability of morphological features in various subspecies and species of vertebrates, points out that it is necessary to learn in what proportion genetic nonhomogeneity of a population within a defined subspecies appears in geographical variability of the species as a whole. He states that the description of a subspecies indicates the norm of variability of a population, and that, in the appearance of individual variabilities within the subspecies, a distinct parallelism with geographical variability within the species can be observed. This parallelism is readily observable within the numerous subspecies of a species and is a mark of their common links with the species.

With a view to the above statements, and results obtained by the analysis of variability in the Białowieża population of the bank vole it clearly perceived that the diagnostic value of morphological features of a series of subspecies of a species is fairly relative. The problem undoubtedly requires further investigation.

A reflection of the condition and age composition of the population investigated is, *inter alia,* their weight and length. While taking into account the critical remarks in this field made by Stein (1938), Heptner (1947), Naumov (1951), Turček (1954), Sviridenko (1959), it is nevertheless permissible to state that these features, at least generally, have a value and throw light on the dynamics of the population investigated. The results obtained allow us to assume that both weight and length of males and females are an indicator of growth in relation to age. This growth is greatest in the age-groups I-II (juv. and subad.) and can also be observed in older individuals (adult I-II, senex). The above data would thus demonstrate that the features mentioned might serve as indicators in defining the age-structure of the population, though naturally with certain corrections.

There was found a fairly distinct synchronization of weight with length in the several investigated years and seasons. The oscillations of mean values of both features in different seasons of a series of years indicate, to some degree, the physical condition and tempo of growth in individuals of the various generations.

As a result of the analysis of the various seasons of the series of years investigated, it was found that individuals of the spring generation reveal swifter growth (higher mean weight and length) as compared to the autumn generation. In individuals of the autumn generation the growth to some extent ceases, attaining its maximum only in spring of the following year. In this period the growth both of the spring and the autumn generation (of the previous year) is intensive. This leads to a relatively even optimal level of means of weight and length in the summer.[1])

From the above facts it would be possible to make some conclusions interesting from the point of view of gerontology. Namely, that individuals born in autumn show a "two-phase" growth capacity. Thanks to a typical accidental interval, they go through a second phase of intensive growth and development in the spring of the following calendar year. This kind of "second childhood" of the autumn-born generation, "kept up" by the

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[1]) Investigations carried out simultaneously on morphohistological variability of the thymus of *C. glareolus* (Bazan-Kubik, in litt.) also showed a differing type of development of this gland in both generations.

winter, certainly classes them among the biologically more predestinated individuals in a population. The life of these individuals as an analysis of the age structure of the population shows, is somewhat longer than that of the spring generation. This allows us to assume (remembering the connection of the proces of ageing with intensity of metabolic processes) (S c h w a r z, 1959, 1963) that lowering of the metabolic rate of the whole organism in winter, especially in the young, which have "held back" temporarily in development, affects their life-span for the better. The spring "renewal" of the organism of these mammals, their intensive growth and development in this period, makes this generation morphologically more stable and biologically expansive. This certainly indicates the different "life stress" upon individuals of the two generations.

This apparently ideal system, a type of adaptive syndrome of the organism, repeating itself over a series of years and giving the impression of a rule, sometimes, however, shows certain variations. Thus, in 1954 and 1955, especially in autumn 1954, it is obvious that exceptions to this rule may have significance in the population dynamics. As can be seen from an analysis of the material, the above-mentioned characteristic inhibition of development in the autumn generation is here clearly partial. Namely, there is intensified sexual activity in individuals of this generation, with simultaneous inhibition of growth, both as regards length and weight of the body. It appears that the increased sexual activity of the autumn generation is not met (as we learn from the analysis of breeding) in other years investigated, and thus throws an additional light on the direction and sphere of adaptation of the organism of these mammals. This compels us to a wider treatment of this question: a consideration not merely of an adaptive syndrome of the organism in its strictly morphofunctional form, but also of the differentiated reaction of individuals to variable factors of the external environment and their consequences.

It should be assumed that the uninhibited reproductive capacity of the autumn generation of 1954 (thanks, *inter alia*, to favourable weather and food conditions), continued into the winter season, formed the main part of the very numerous population in the following calendar year. The mass appearance of bank vole in 1955 was doubtless a consequence of this relatively rarely met, in other years, reproductive ability of individuals of the population.

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ZMIENNOŚĆ BIOMORFOLOGICZNA POPULACJI *CLETHRIONOMYS GLAREOLUS* (SCHREBER, 1780)

Streszczenie

Przeprowadzone badania dotyczyły biomorfologicznej zmienności populacji *Clethrionomys glareolus* (Schreber, 1780), pochodzących z Białowieskiego Parku Narodowego.

Licznie reprezentowany zbiór (N = 8040) z lat 1946—1955 posłużył jako materiał do analizy zmienności ciężaru i długości ciała, struktury wieku oraz dynamiki rozrodu. Przy rozpatrywaniu powyższych zagadnień uwzględniono zmiany w aspekcie indywidualnym, wiekowym, rocznikowym i środowiskowym.

Cały materiał sklasyfikowano pod względem wieku na 5 grup, przyjmując za kryterium stopień rozwoju korzeni zębów trzonowych, głównie M_1. Przy analizie długości i ciężaru ciała uwzględniono szereg przedziałów klasowych. Dynamikę rozrodu poparto analizą morfologiczną gonad.

Wskazano na zróżnicowany charakter zmienności ciężaru i długości ciała (Tab. 2—19, Ryc. 1—21). Uzyskane rezultaty badań pozwoliły na krytyczną ocenę obu tych cech w taksonomice systematycznej.

Podkreślono dużą zmienność oraz zakres rozpiętości ciężaru i długości ciała osobników obu płci w różnych latach i sezonach. Ogólna analiza danych wykazała, że największe zgrupowanie ilościowe samców w populacji zawarte było przy modalnych wartościach szeregów rozdzielczych. Samice natomiast przeważały procentowo w niższych i najwyższych przedziałach klasowych. W poszczególnych jednak rocznikach, stosunki te ulegały mniejszym lub większym wahaniom.

Wyraźną zmienność obu cech uzyskano przy analizie poszczególnych miesięcy i sezonów rozpatrywanych lat. Zarówno samice jak i samce wykazują najwyższą długość i ciężar ciała w miesiącach wiosennych.

Poza okresem jesiennym we wszystkich pozostałych sezonach samice wykazywały większą długość i ciężar ciała niż samce.

Stwierdzono wyraźną zbieżność długości i ciężaru ciała osobników populacji w poszczególnych analizowanych rocznikach i sezonach. Z poziomu i oscylacji wartości średnich obu cech z różnych sezonów, wnioskowano o stanie kondycyjnym i tempie wzrostu osobników poszczególnych pokoleń.

Uzyskane wyniki pozwoliły przyjąć, że młode osobniki generacji wiosennej wykazywały z reguły szybszy, nieprzerwany wzrost (wyższe średnie długości i ciężaru ciała, szybsze dojrzewanie płciowe) w porównaniu do generacji jesiennej. U tych ostatnich tempo wzrostu i dojrzewania ulegało pewnemu przyhamowaniu, osiągając swoje maksimum wiosną następnego roku kalendarzowego. Ta „dwufazowość" rozwoju przedłużała w pewnym stopniu okres młodociany, co w konsekwencji prowadziło do lepszej morfofunkcjonalnej stabilizacji ustroju. Generacja ta odznaczała się większą przeżywalnością w porównaniu z wiosenną.

Stwierdzenia powyższe, podbudowane danymi analizy struktury wieku (Tab. 20—21, Ryc. 22—29) oraz dynamiki rozrodu (Tab. 22—25, Ryc. 30—31) pozwoliły określić generację jesienną jako życiowo bardziej ekspansywną i odporną na wpływy środowiska zewnętrznego.

Na przestrzeni szeregu analizowanych roczników stwierdzono odmienny charakter rozwoju jesiennej generacji rocznika 1954. Wykazano mianowicie, szybkie tempo dojrzewania płciowego i szybkie zakończenie wzrostu osobników bez drugiej fazy „odnowy" w sezonie wiosennym następnego roku kalendarzowego. Przyjęto, że niezahamowana zdolność rozrodcza tej generacji (dzięki sprzyjającym warunkom klimatycznym i żywieniowym) przeciągająca się również na sezon zimowy, wydatnie przyczyniła się do masowego pojawu tych ssaków. Stanowiła ona trzon bardzo licznej populacji w następnym roku kalendarzowym. W sensie ekonomicznym oceniono tę generację jako szkodliwą, mającą ujemne znaczenie w gospodarce.

Drugi aspekt tego zagadnienia to biologiczna ocena wartości wyżej przytoczonych faktów. Pozwala ona wydaje się na głębsze wysnuwanie wniosków co do określenia czynników kierujących rozwojem osobniczym gatunku. Wskazuje bowiem nie tylko na zespól przystosowawczy ustroju w jego ściśle morfologicznej postaci, lecz również zróżnicowaną reakcję osobników na zmianę warunków środowiska zewnętrznego oraz konsekwencji z tym związanych.