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Growth, Variations and Age Criteria in *Apodemus agrarius* (Pallas, 1771)

[With 7 Tables & 8 Figs.]

Using analysis of body and skull measurements, and also wear of teeth and weight of dry mass of eye lens as a basis, a description is given of growth and age changes in *Apodemus agrarius*. It was found that changes in the degree of wear of teeth and increase in eye lens weight are most closely parallel with the age of these mice. Intercorrelation is also greatest between absolute age and eye lens weight (r — .959) in individuals of known age. Estimates of age on the basis of wear of the teeth are less accurate, while among the measurements which can be made on live animals body weight is burdened with serious error when used for defining age, due to its connection with physiological and phenological changes. Tail length is less subject to these variations, but its rate of growth slows down considerably as early as after the age of three months. Condylobasal length of the skull gives a very good description of growth variation in individuals, while the diastema is closer to age variation. The other dimensions increase only slightly and for a very short period during the animal's life. All measurements exhibit considerable variation, masking growth changes, particularly in the case of measurements subject to little increase. Calculation of correlations between all the measurements for 922 individuals showed that Cb is correlated to the greatest degree with all the other measurements. Correlation coefficients analysed by the dendrite method indicate that there are three groups of measurements which are markedly intercorrelated, according to the type of increase and aging of the animals: 1. eye lens weight and wear of teeth, 2. body weight and length, tail length, Cb length and length of diastema, 3. breadth of braincase, height of brain-case measured *per* and *inter bullae* and length of the upper row of teeth. It was found that the rate of increase in body weight is twice as quick in individuals born in spring and the first half of summer as in those born in the autumn. A change in growth rate in different generations occurs with different degrees of intensity in different measurements.

1. INTRODUCTION

The main purpose of this study was to gain an idea of the interrelations between some morphological characteristics of *Apodemus agrarius* during the animals' life under natural conditions and to determine which of the characteristics best corresponds to the actual age of an animal, and what regularities are in the individual growth of this species.

Not all the various parts of animal's organism grow evenly during its life, and this causes a change in body proportions. Examination of the interrelations between characteristics subject to change during the animal's life, and the degree to which the various characteristics variate in the time which they undergo changes, forms an important point in these studies.

In order correctly to assess the age of a species it is necessary to make use of characteristics which vary most parallel to length of life. Such characteristics will be on the one hand measurements of those parts of the body and skeleton which increase during the whole of the animal's life, giving positive correlation with age, and on the other hand characteristics subject to gradual wear. As estimates of age based on all characteristics are always burdened with some degree of error, it is necessary to establish the order of characteristics according to degree of error, as this makes it possible to choose the most accurate criterion.

The subject of these studies was *Apodemus agrarius* (Pallas, 1771), a common species occurring in humid forests and undergrowths, in meadows and parks (Chełkowska, 1969; Zejda, 1967). Sviridenko (1947) states that field mice caught in the foothills of the Caucasus Mountains had reached the age of three years. Varšavskij

& Krylova (1948) caught field mice of similar age; in the geographical zone of Central Europe such old individuals were not found among them. The data given by Haitlinger (1962) show that *A. agrarius* may live 18 months under field conditions.

It is more difficult to assess age in small mammals than in large species, as it is impossible to use, for instance, quantitative methods based on growth, varying qualitatively in summer and winter, of certain bones (Klevezal & Klainenberg, 1967), and therefore age is often assessed on the basis of wear of the teeth. Varšavskij & Krylova (1948) distinguish four classes of wear for *A. agrarius*, Haitlinger (1962) five clases of wear, but neither of these two scales coincides exactly with the material presented below. Body size and the size of various bones (Adamczewska-Andrzejewska, 1971) or indices calculated on the basis of several measurements (Lidicker & MacLean, 1971), are commonly used as criteria for assessing age. Age is now estimated very widely on the basis of the weight of dry mass of the eye lens (Lord, 1959), and this has been applied to *A. agrarius* also (Adamczewska-Andrzejewska 1971).

It is of great importance in field studies to determine the age of animals but the majority of the methods referred to can be applied only after the animal's death. This is the reason why many authors use simply body weight, despite the numerous criticisms of this method (Naumov, 1936, 1937; Plater-Plachocki, 1937; Rall, 1939 *et al.*). Sviridenko (1947, 1949) classifies material according to body weight for *A. agrarius*.

2. MATERIAL AND METHODS

For the purposes of the present study 1210 individuals of *A. agrarius* (455 ♀♀ and 755 ♂♂) were caught over a period of two years 15th April 1965 to 30th April 1967, in the Łazienki Park and the Botanical Gardens in Warsaw. There were frames, hothouses, beds containing seedlings and seed stores in the areas where the captures were made. These areas were surrounded by undergrowth in which the traps were set, and did not form a uniform capture area.

The mice were caught in live-traps, using oat as bait, and inspection of the traps was made once daily. The traps were blocked open and filled oats on Saturdays, then set again on Monday, that is, captures were made effectively 5 days a week. The number of functioning traps varied according to the gardening operations being carried out in the trapping areas. The maximum number of traps in operation during the summer months was 150, but in winter this was reduced to 50. A large part of the traps were destroyed by persons unknown, which altered the number from day to day.

The live mice were taken to the laboratory, anaesthetized and after the length of head and body, and the tail had been measured, and animals weighed on a spring balance with accuracy to 0.5 g, they were next dissected and the state of activity of the gonads examined. The skulls were prepared and after they had been cleaned 6 measurements were made on them: condylobasal length, diastema, upper row of teeth, maximum breadth of brain-case, height of skull *per bullae* and height of skull *inter bullae*, using a slide-rule with accuracy to 0.1 mm. The degree of wear of the teeth was determined according to the originally established model. Teeth were examined under a microscope with 25.5 × magnification. The eyes were removed during dissection and kept in 10% water solution of formaldehyde, then after at least 10 days the lens were excised, rinsed in distilled water, and dried for 48 hours at 80°C, after which the two lens were weighed together on a torsion balance with accuracy to 0.1 mg.

Statistical calculations relating to body and skull measurements were made on ZAM-21 and GIER computers, using for this purpose only those individuals for which none of the measurements were missing.

In addition to the material taken to the laboratory after the first trapping and killed, some of the animals were marked by toeclipping and released, body weight and state of sexual activity being recorded at each capture. It was chiefly young individuals with body weights of less than 15 g which were caught first. Pregnant and nursing females were also marked, mainly to ensure that population numbers were not reduced by catching them and removing them from the area. During the summer and autumn months, when large numbers were caught daily, females over 15 g in weight were also marked. A total number of 510 individuals were marked. Capture of marked individuals was arranged so as to ensure that a full range of individuals survived in the area for the longest possible time, while simultaneously giving the intermediate stages of growth. Of all the marked mice 121 individuals were caught and removed either on purpose or accidentally (*e.g.* they died in the trap), and of this number only 65 were marked as young animals and lived in the area under inspection for at least 1 month.

Table 1

Variations in body and skull measurements for the whole of the study material (number of males = 755, females = 455).

Measurement	Min.	Max.	Avg.±error	S.D.	Min.	Max.	Avg.±error	S.D.
			Males				Females	
Lens weight	2.7	14.2	8.26±.01	2.29	3.1	13.5	8.02±.12	2.33
Tooth wear	2.0	6.0	3.86±.04	0.99	1.0	6.0	3.72±.05	0.98
Head & body	63.0	114.0	86.74±.34	8.23	58.0	103.0	80.73±.43	8.14
Tail	53.0	94.0	74.40±.27	6.38	43.0	88.0	70.73±.37	6.88
Body weight	8.0	36.5	22.12±.22	5.26	7.0	36.0	18.28±.28	5.22
Cb. length	19.0	24.9	22.03±.04	1.03	17.4	24.0	21.45±.06	1.15
Diastema	5.4	7.9	6.56±.02	0.39	5.0	7.8	6.36±.02	0.44
Maximum brain-case breadth	8.1	11.6	10.67±.01	0.31	8.6	11.3	10.51±.02	0.33
Maxillary tooth row	3.0	4.9	3.82±.01	0.15	3.4	4.8	3.79±.01	0.15
Brain-case height (*per bullae*)	7.9	10.7	8.69±.01	0.27	7.7	10.7	8.60±.02	0.32
Brain-case depth (*inter bullae*)	6.1	8.5	7.39±.01	0.27	7.7	10.7	7.26±.02	0.32

The four pregnant females caught produced young, 12 of which were reared in the laboratory and weighed at the age of 7, 14 and 28 days in order to find body weight during the period of life in the nest.

For working purposes the material was arranged in accordance with the so-called »genetic system«[1] (Dehnel, 1949), which consists in arranging all individuals in classes of value of the given measurement in successive months of occurrence of the given generation. These tables were used to trace both growth of individuals in time and the distribution of monthly averages.

3. DISTRIBUTION OF MEASUREMENT VALUES OVER THE YEARLY CYCLE

The range of body dimension values and their variations in the population may describe a given group of animals from the morphological aspect (Table 1). The changes which take place over the yearly cycle, both in the range and in the average values of measurements, gives a certain picture of the growth and development of individuals in time and the possibility of identifying generations (Fig. 1).

Table 2

Ranges of eye lens weight in composition with absolute age of mice.

Age in months	Lens wt.	Age class
< 2	1.9— 5.5	I
3— 4	5.6— 8.5	II
5— 6	8.6—10.3	III
7— 8	10.4—11.3	IV
9—10	11.4—12.2	V
11—12	12.3—13.0	VI
12>	13.1>	VII

Analysis of the whole material showed that the weight of the dry mass of eye lens gives the most objective estimate of age of all the measurements examined in this paper. Consequently it was possible to plot the growth curve of the lens for the marked individuals as the character of the lens permitted the establishment of six two-month age classes. The classes of lens weight established in this way formed a basis for distinguishing age classes of individuals for all the other measurements analysed here (Table 2).

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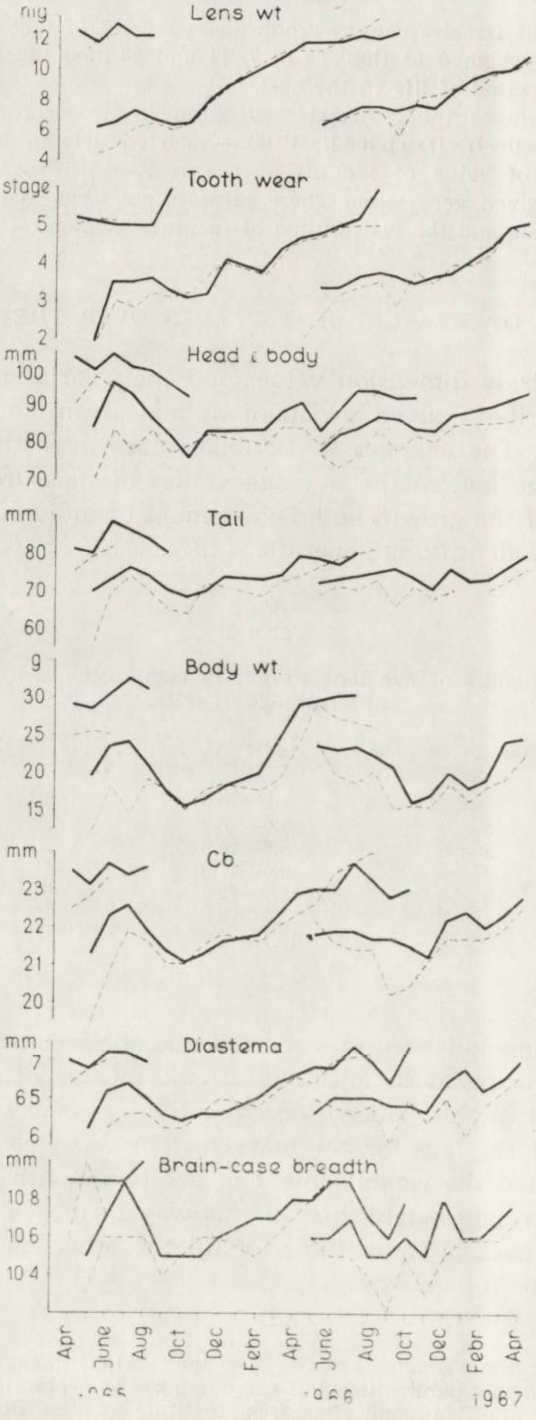
[1] The tables of the »genetic system« for the various measurements have not been enclosed with this publication, but are available as typescript from the author, in the library of the Mammals Research Institute of the Polish Academy of Sciences in Białowieża and in the library of Warsaw University.


Lens wt
mg
12
10
8
6
4
Tooth wear
stage
5
4
3
2
Head & body
mm
100
90
80
70
Tail
mm
80
70
60
Body wt.
g
30
25
20
15
Cb
mm
23
22
21
20
Diastema
mm
7
6.5
6
Brain-case breadth
mm
10.8
10.6
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Apr
June
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1965
1966
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Fig. 1.

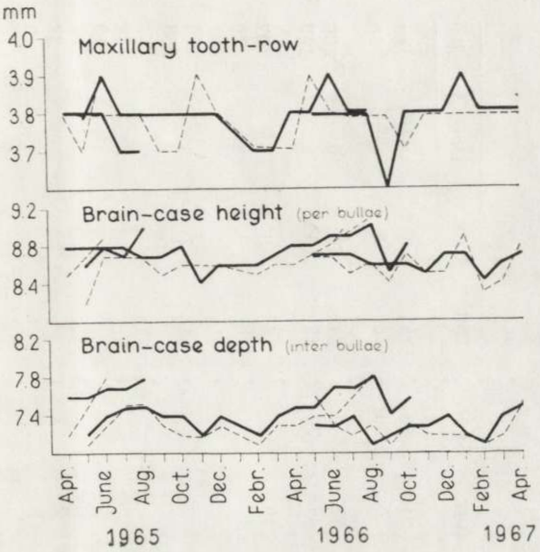

Fig. 1. Curves plotted from monthly averages of measurements calculated separately for individuals belonging to one generation. The continuous line indicates averages for ♂♂, the dotted line — ♀♀.

3.1. Weight of Dry Mass of Eye Lens

Individuals belonging to age classes determined on the basis of lens weight are clearly distributed into two separate generations: young animals born in spring and old adults. Constant lens growth is very distinct in both generations (Table 3).

The distribution of frequencies of individuals reveals two peaks (Fig. 2). The first peak occurs at 7 mg in males and 6 mg in females, the second peak of numbers is greater in females than in males. An attempt may be made at interpreting the decline of the curves of this distribution at values of 9 mg and 10 mg by the fact that this is the upper limit of values for the lens in young individuals born in the current year the start of the range of values for older individuals. In this case the extreme classes with the lowest numbers correspond to the winter pause in reproduction. Young individuals, practically speaking, begin to appear in May, but individuals with the lowest lens weights are not encountered until September. Entry of young individuals into the population continues from May to October or November. Growth of the lens is gradual and parallel for the lower and upper limits of range of measurement during the winter months. It is not until near the end of the old adults'

Table 3

Distribution of material in monthly intervals according to age classes determined on basis of growth curve of eye lens weight.
M — males, F — females.

Age	Sex	Jan.	Feb.	March.	Apr l.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	n
I	M					3	7	4	21	19	5	4		63
	F				2	4	2	4	16	20	3	5		56
II	M					14	61	52	73	40	24	20	6	290
	F	1				1	19	18	44	25	29	14	8	159
III	M	3	11	11	5	2	2	13	19	11	5	9	6	97
	F		8	16	8			4	10	4	8	6	6	70
IV	M		4	19	14	12	1	1				2		53
	F		6	12	15	1						1	1	36
V	M		1	5	12	12							1	31
	F		1	4	8	4	1						1	19
VI	M			4	11	12	3	3	2	2				37
	F			4	2	1	2							9
VII	M				2	1		1				1		5
	F			1		1			1					3

life in the second calender year, *i.e.* from April to August, that no rise in the upper limit of measurement is observed. This may be due both to the considerable slowing down of the growth process and the disappearance from the population of the largest individuals. During the maximum life span under field conditions, which in the case of the present

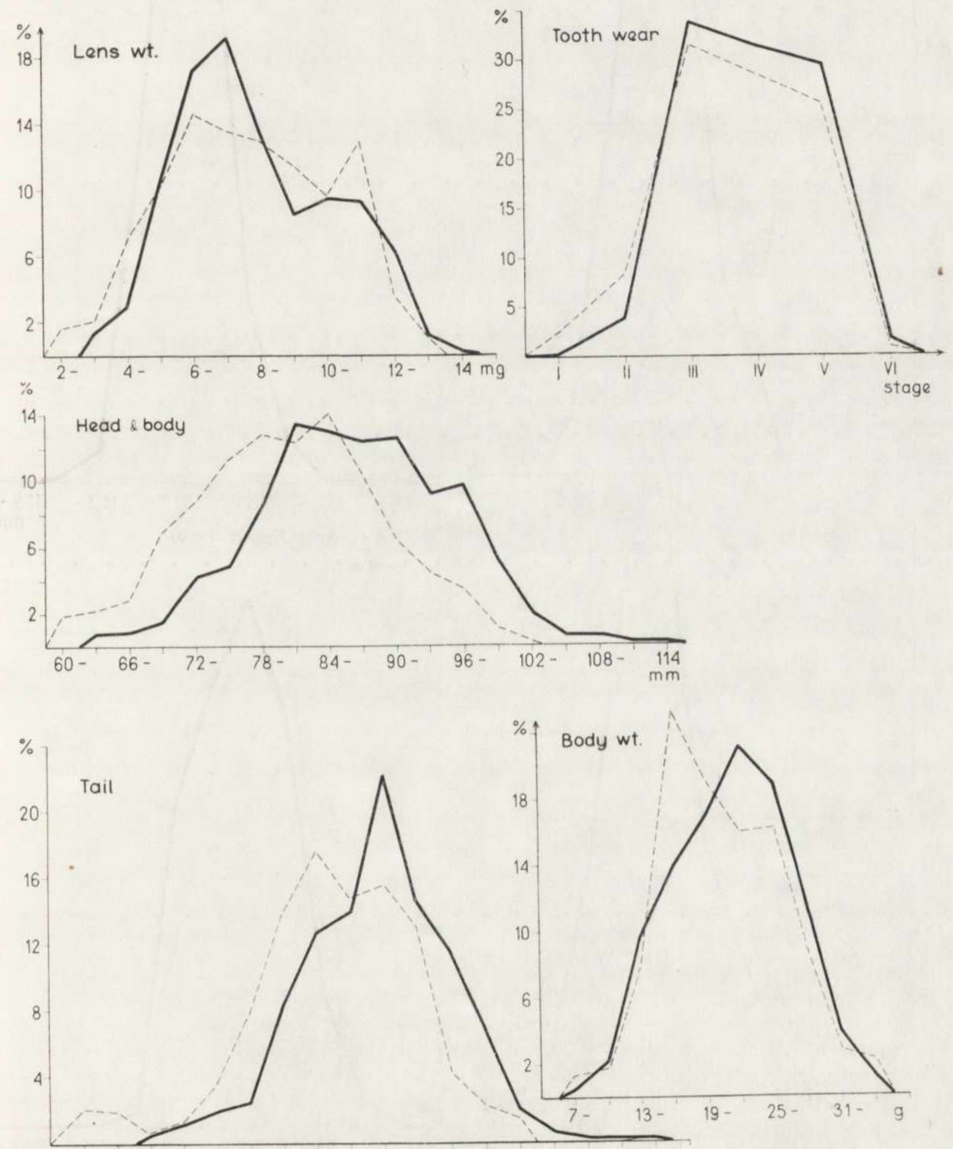

Fig. 2.

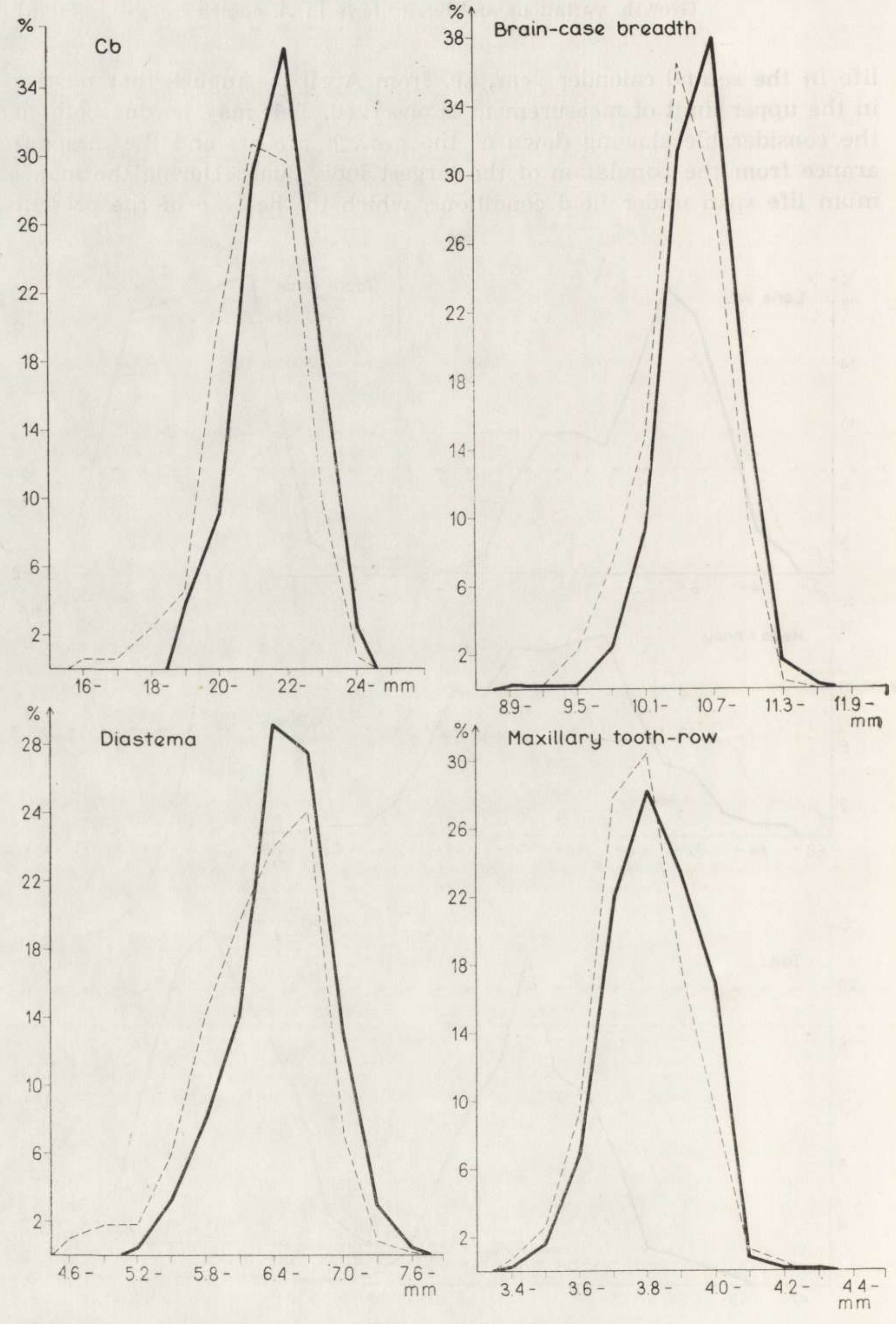

Fig. 2. Continued.

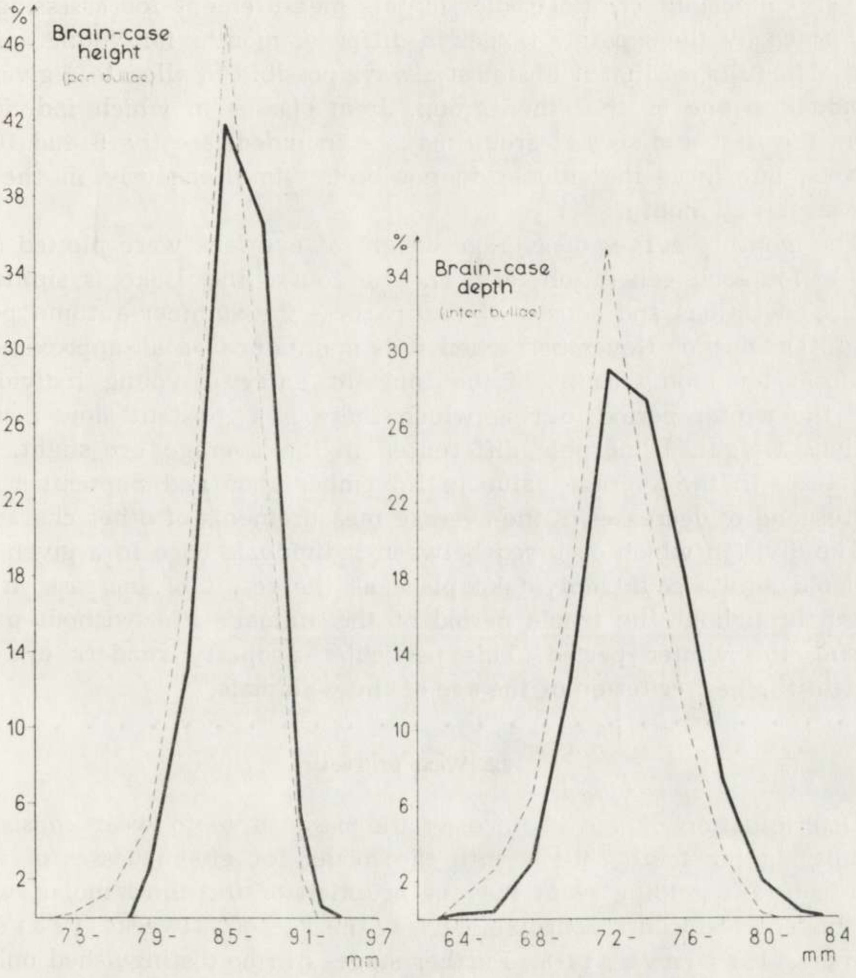

Fig. 2. Distribution of frequencies for successive measurements in percentages.

material was 18 months, the lens increases in weight from 2 to 13 mg, and sporadically to 14 mg, giving an average value of 0.66 mg increase a month. As young individuals join the old adults in the distribution of individuals, it can be gathered from this that the growth rate of the lens decreases with age. Males may remain from 4 months in the 10 mg class to 6 months in the 13 mg class. The slackening of the growth rate of lens weight in the higher ranges of values (over 9 mg) is probably the explanation of the second peak of numbers in the distribution of frequencies.

The greatest range of values for one generation occurs in November. A very important characteristics of this measurement for assessing age is formed by the separate ranges in different months for young animals and old adults, so that it is almost always possible to allocate a given individual to one or the other group. Joint classes in which individuals from the first and second group may be included, are the 9 and 10 mg classes, but these individuals do not occur simultaneously in the two classes in any month.

The monthly curves of average weight of eye lens were plotted separately for each generation (Fig. 1). The course they take is similar in both generations and consist of two parts — the summer-autumn period up to October or November, when it is maintained on an approximately uniform level on account of the constant entry of young individuals, and the winter period, during which there is a constant slow increase in lens weight. Dimorphic differences in the average are slight. Two decreases in the average value in November 1965 and September 1966 correspond to decreases in the average measurements of other characters.

The division which occurred between individuals born in a given year and old adults could only take place as the result of increase in lens mass throughout the whole period of the animal's life, without pauses during the winter period. This particular property renders eye lens weight the best criterion of the age of these animals.

3.2. Wear of Teeth

Determination of age in mice on the basis of tooth wear consists in comparing the teeth chosen with the model for given classes of wear. One constant guiding point may be eruption of the third molar, which in this species occurs approximately at the age off 3 weeks (Varšavskij & Krylova, 1948). Further stages can be distinguished only on the basis of gradual wear of the cusps of molars.

The material was divided into 6 stages of wear according to a model chosen from the whole of the material (Fig. 3).

3.2.1. Stages in Tooth Wear — Model Tooth

Stage 1. M^3 during the period it grows up from gum level to a level almost even with the grinding surface of M^2 and M^1. The apexes of the cusps of M^1 exhibit minimum wear, this being relatively most marked on cusps *t*4, *t*5, *t*6. Wear is almost imperceptible on M^2.

Stage 2. M^3 completely grown. Wear is evident on all molars. The best formed cusps *t*4 and *t*5 on M^3 are most worn, and there is distinct connection with the band of dentine. Residual cusp *t*7 is connected with *t*5 and slightly worn.

Slight wear can be seen on all cusps of M^2. $t1$ is separated from the other cusps, which begin to connect in a closed ring due to the appearance of a more or less broad border of enamel, or even bands of dentine. The greatest wear is evident in the middle row of cusps, in this case $t5$ and $t8$. M^1 exhibits a very similar degree of wear to M^2. The cusps of the 2nd and 3rd row begin to connect in a ring, but dentine does not appear between the cusps in M^2. Cusps $t1$—$t3$ are very weakly connected and relatively the least worn of the whole tooth row.

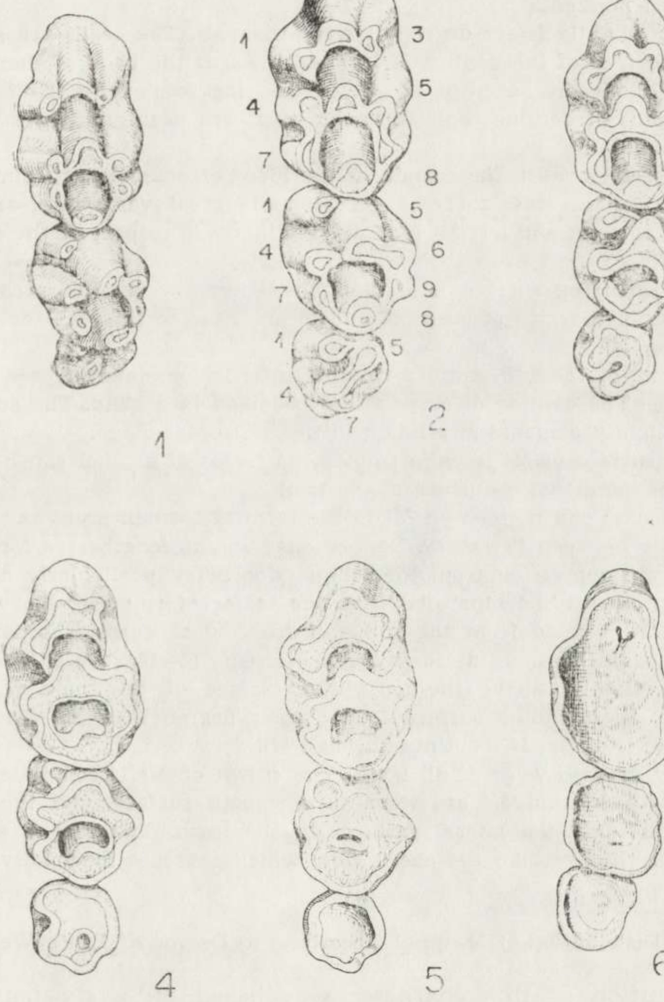

Fig. 3 Model tooth for determining age. Identification of order of cusps accepted after Miller (1912). Explanation of the numbers in the text.

Stage 3. M^3 has completely worn tops of cusps, so that the whole grinding surface of the crown consists of dentine surrounded by an external layer of enamel.

A loop of enamel enters into the middle of the grinding surface as the remains of the once existent space between cusps *t*4 and *t*7.

Wear of *M*² has proceeded very markedly. There is a space between only *t*4 and *t*7 in the ring formed from the 2nd and 3rd row of cusps. The thickness of the layer of dentine connecting the cusps may be the same as the external layer of enamel. *t*5 and *t*8 have lost their shape of inclined cones and their grinding surface is almost horizontal.

*M*¹ exhibits a slightly lesser degree of wear than *M*². The cusps are still conical and the worn surface of the dentine is inclined towards the back of the tooth. This can be seen most clearly on cusps *t*2—*t*5. In the ring formed by the 2nd and 3rd of cusps the bands of dentine connecting the cusps are usually slightly wider than the layer of enamel.

Stage 4. *M*³ greatly worn, the remain of the loops of enamel have almost entirely disappeared. (In this case there is exceptionally great variability, and even in one individual the right and left *M*³ may differ slightly in respect of the distinctness of the loops).

A large flat grinding surface is formed on *M*³ by the marked wear of cusps *t*4—t9. The anterior margins of cusps *t*5 and *t*8 are close to the level of the posterior edge of *t*8 on *M*¹.

On *M*¹ the ring of the 2nd and 3rd row of cusps is completely closed by a wide band of dentine. The dentine of cusps *t*1—*t*3 is joined in a band. The surface of *t*2 and *t*5 is still slightly diagonal in relation to the horizontal plane.

Stage 5. The surface of *M*³ is worn smooth, no traces of enamel can be discerned in the middle of the grinding surface of the tooth.

A trace of enamel can be seen on *M*² in the form of a small arch, as the remains of the depression between *t*5 and *t*8. Depressions running lengthways form between rows of cusps, the depression from the tongue side being particularly clearly visible. Only *t*1 continues to be separated from the surface formed by the worn cusps.

The ring on *M*¹ formed from the 2nd and 3rd row of cusps is separated from the 1st row of cusps by the anterior margin of cusps *t*4—*t*6 covered with enamel, still protruding slightly above the horizontal surface of the tooth row. *t*8 also protrudes above the grinding surface to a greater degree than *M*². The longitudinal depressions visible on *M*² continue through *M*¹.

Stage 6. Very marked wear of all teeth. The crown of *M*³ is completely worn in some places. Both *M*² and *M*¹ are worn to a smooth surface, and the border of enamel surrounds only the lateral surfaces of the teeth. The tongue side of the teeth is generally higher than the cheek side, which causes a diagonally positioned grinding surface.

3.2.2. Distribution of Material According to Degree of Tooth Wear

The distribution of this character was based on a six-degree scale, similary to the distribution of lens weight (Fig. 2). Stages 3 and 4 are similar to each other in the percentages of individuals. With the working division of material into smaller stages of wear two peaks become visible, corresponding to the two generations, analogically to the distribution of frequencies of eye lens weight: A striking phenomenon in the distribution of frequencies of tooth wear is the presence of individuals with very old teeth in almost the whole of the study period, since they are absent in only a few of the autumn-winter months. This shows that the most marked wear of teeth does not always correspond to the greatest dimensions of the animals.

The teeth of animals entering the trappable population in May are more worn than these of the subsequent litters from the middle of summer, but these differences are only slight.

During the 6-month period from October to April the young mice proceed from the 1st and 2nd stage of wear to the 4th, and sporadically to the 5th. This gives increase of 3 stages during a halfyear, and thus the shift from one stage to another would last on an average two months, treating the course taken by wear as a straight line. Assuming this to be so, it is difficult to account for the individuals exhibiting the 4th stage of wear in May or June. This forms evidence of considerable differences in the rate of tooth wear. As in the case of *Apodemus flavicollis* field mice with the later stages of wear live longer than those with the earlier stages (Adamczewska, 1959).

If we assume that an individual born in April lives until September of the following year, then the maximum length of life is 18 months (on the basis of the other criteria and after Haitlinger, 1962). During this period the field mouse passes from stage 1 to 6 of tooth wear, and in this case three months of its life would cover one stage. This is confirmed by the phenomenon of the increasingly less perceptible changes taking place in the degree of wear in increasingly older individuals.

Changes in average tooth wear in months for the two generations exhibit lesser regularity than lens weight, but the general tendency of changes is very similar in both years (Fig. 1).

Tooth wear exhibits a number of characteristic properties: (1) it does not differentiate very young individuals, (2) it progresses in winter also, as a non-growth character, (3) it does not depend on the size of the animal, (4) it exhibits only slight dimorphic differences.

3.3. Body Length

The distribution of frequencies for the measurement for the whole material has one almost symmetrical peak, although it exhibits fluctuations in the middle values (Fig. 2). Sex dimorphism is observed, the curve of distribution of females being shifted far more in the direction of lesser values than the curve of males.

From April to July 1965 large animals over 81 mm long predominate, only ten mice being smaller. Small individuals, up to 75 mm, occur in the population up to December inclusive, but individuals of smaller dimensions are caught in October at the latest. From November 1965, when the smallest individuals no longer appear, up to April 1966, the lower limit of range of measurement shifts from 72 to 78 mm, and the situation is similar in the following winter period. The shifts in the upper ranges of values from November to April is also slight. In spring 1966 the old adults are slightly smaller (72 mm to 99 mm). It is impossible to trace the gradual growth of individuals, as the great variations in the measurements efface the dividing line between generations.

Except for the old adult males in the spring of 1965, the largest individual body measurement are attained by mice in August, when this value may reach 100 mm.

The greatest monthly averages for body length in old adults occur in June and July (Fig. 1). In the case of the young animals the monthly average in spring is higher than in autumn, on account of the entry into the population of new individuals with increasingly slow growth. The systematic increase in the average starts in October, when the entry of young individuals ends. It must be assumed that this cycle is repeated every year, with certain deviations. On an average females are smaller than males, but variations in body length in time are similar in tendency in the two sexes.

3.4. Tail Length

Measurement of tail length may have a relatively high value, as it can be carried out on live animals, and the degree of error is low owing to the ease of measurement. On the other hand an important defect of this measurement is that the skin of the tail tears very easily.

The curve of frequencies of individuals is symmetrical in males, with one peak, whereas in females there is a slight tendency to two peaks (Fig. 2). The range of this measurement in females is narrower than in males, and the position of peaks of numbers differs by 6 mm.

It is not possible to distinguish current year's individuals from old adults in the monthly distribution of tail length. In months when the percentage of young animals entering the population is relatively high, it is impossible to trace a line of demarcation between young and old animals, which is certainly due to the very slow growth of the tail in winter.

Growth of the tail during the spring-summer period from May to November is from 65 to 86 mm, that is, 21 mm during a 6-month period. In winter, on the other hand, the tail almost completely fails to grow in some of the individuals, because there are the individuals in the lowest range of this dimension in December and in March as well, despite the fact that appearance of new individuals in the population ended in November.

Differences between the summer seasons of the two years can be seen on the curve illustrating monthly averages for tail length (Fig. 1). In 1965 the decrease in average monthly length was marked from July to October, whereas in 1966 this was from September to November. Differences between averages for old adults and newcomers to the population are small in summer, reaching up to 16% of the whole range of values.

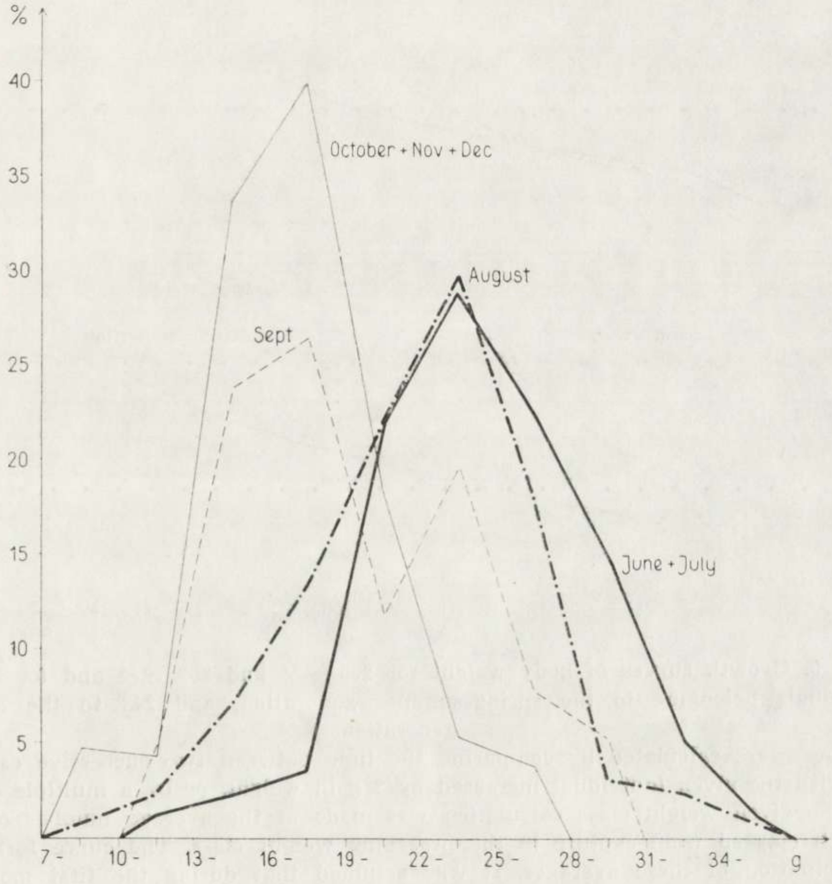

Fig. 4. Distribution of frequencies of body weight in males in months from summer to winter.

Sex dimorphism is marked during the whole period of growth as in the case of body length. All monthly averages for males are higher than for females, although minimum—maximum measurements do not always maintain this regularity.

3.5. Body Weight

3.5.1. Distribution of Material According to Body Weight

Distribution of frequencies of males according to this criterion is very close to symmetrical, females exhibiting a peak in their numbers shifted towards the lower weigths by 6 g (Fig. 2). The range of weight is almost uniform for the two sexes.

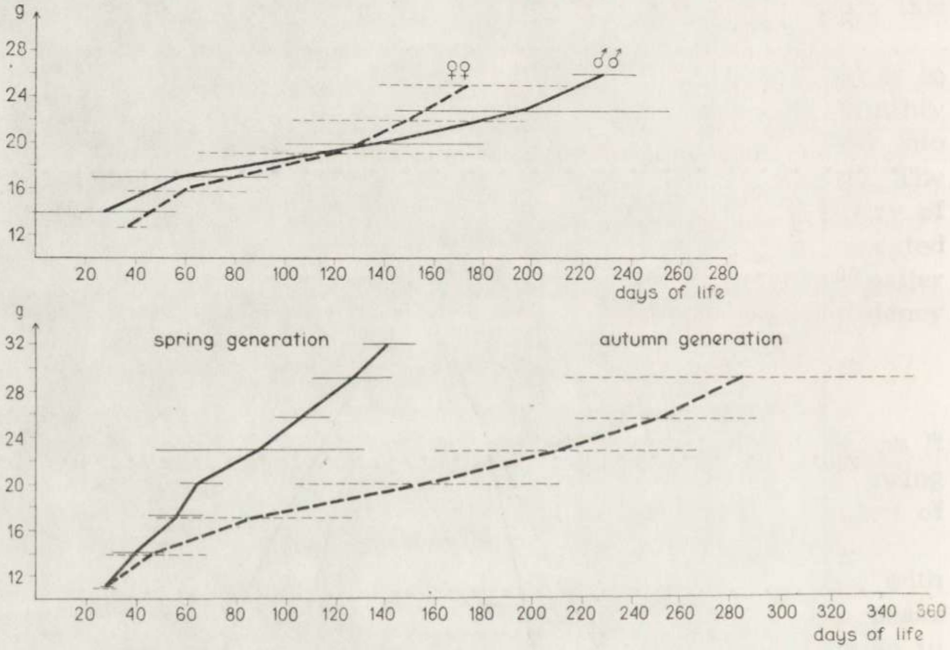

Fig. 5. Growth curves of body weight for 263 ♀♀ and 232 ♂♂ and for 252 individuals belonging to the spring-summer generation, and 243 to the autumn generation.

Curves were calculated by comparing the time between two successive captures, in with the given individual increased by 3 g in weight, or by a multiple of 3 g. In the given weight class calculation was made of the average number of days which elapsed from capture in the preceding weight class. The curve forms the combination of these averages. It was assumed that during the first month of life the field mouse gains at least 10 g, basis this assumption on data from captive animals. Horizontal lines indicate the standard deviations of the means

Single individuals of minimum weight, up to 7 g, are encountered only during the autumn months, and individuals weighing less than 10 g occur during the second half of summer. The heaviest individuals are found throughout summer, but in autumn maximum weights decrease markedly in both the study years in both sexes. Males with body weights within the highest ranges of weight (over 31 g) occur from April to August inclusive. In the case of females the picture of maximum weights is confused by pregnancy, nevertheless from October to spring is minimal in autumn and at the beginning of winter, but rises in March and April. This process can be better illustrated by a more detailed analysis of the distribution of weights of individuals in the summer and autumn months. The distribution of frequencies of weights for males has been presented separately for successive months (Fig. 4). Average weights for June and July were very similar and the material was therefore combined. In August, although a peak of numbers is maintained in this same class, there is a slight shift in the curve in the direction of smaller dimensions. Like the body and tail lengths, body weight also exhibits the greatest range of variations in August. A distinct division of material can be observed in September and the curve takes on the form of two peaks. The new and higher peak occurs at weights of 17.5 g, and the other, lower peak, at 23.5 g. In later months the range of variations decreases, and peak numbers occur at 14.5—17.5 g. In effect of old adult from even the last October litters must be at least 6 months old in April in order to reach a weight of 19 g, but an individual born in spring, in April at the earliest, can reach this same weight in July, that is, at the age of 3 months.

An even slower rate of growth in body weight is observed in females in winter and during the season of 1966—67 body weight did not increase at all.

The curve of monthly average weights is similar to that described earlier on for body measurements (Fig. 1). The greater average weight in summer than in winter in the same population is very distinct.

3.5.2. Growth Curve of Body Weight

A growth curve was plotted for marked individuals, the weights of which were recorded each time they were caught (Fig. 5, Table 4) for (1) males and females (2), for individuals which were captured for the first time before August 15th and for those which were caught for the first time after this date. The two study years were treated jointly.

Field mice grow to a weight of 16—17 g, as shown on the curve plotted, during the first two months of life. After this time growth rate decreases and the animals reach a weight of 20 g in about 3 months. During a period of 6—7 months males reach an average weight of 26 g, and females 28 g, counting pregnancy in this. Up to the time a weight of 20 g is reached, the curve for males exceeds the curve for females, but later the weight of females increases more quickly. Short-lived but high increases in the weight of females during gestation and lactation affect the different shape of growth curves for males and females.

A growth curve calculated in this way is burdened by several errors due to such cases, as *e.g.* treating mice caught in all the periods jointly. Calculation was therefore made of the average error and standard deviations (σ) for each point on the curve determined by the time average for the given weight class. The smallest standard deviations occur on the growth curve for the youngest animals, but even with an average observation time of 122 days for females this error is greatest, being ± 65 days. It follows from this that a female weighting 19 g may be either 55 days of 187 days old. For males the maximum error of 63 days occurs at a weight of 23 g and on an average on the 200th days of life. Analogically it may be said that the youngest males of this weight are 137 days old, and the oldest 263 days. The other weight classes are burdened by slightly smaller errors, reducing their values in the direction of the youngest and oldest individuals. Apart from the above point all standard deviations are greater for males than females.

Table 4

Numerical data for growth curves of body weight for males and females and for the spring-summer and autumn generations.

Males					Females				
Body wt class, g	n	Avg. time, days	± error	σ	Body wt. class, g	n	Avg. time, days	± error	σ
14	49	28	4.76	33.32	13	31	37	1.38	7.68
17	68	57	4.77	39.36	16	69	60	3.36	27.89
20	46	140	6.71	45.49	19	60	122	8.39	65.00
23	35	200	10.69	63.25	22	38	150	8.34	51.40
26	34	230	4.88	28.44	25	39	175	6.69	41.80
—	—	—	—	—	28	26	188	2.91	14.82
Spring and summer, **before August 15.**					Autumn and spring after August 15.				
11	8	28	0.77	2.17	11	7	28	1.38	3.64
14	32	40	2.02	11.42	14	50	46	3.51	24.83
17	27	55	2.42	12.57	17	88	87	4.49	46.80
20	31	66	1.67	9.32	20	45	158	8.95	60.07
23	40	91	7.61	48.15	23	21	214	13.19	60.47
26	43	106	1.98	12.97	26	22	253	9.90	46.46
29	46	127	2.62	17.79	29	10	288	27.02	85.47
32	25	142	2.56	12.78	32	—	—	—	—

Over the weight of 11 g increase in body weight in spring and summer proceeds at a different rate than in autumn, as is shown by both the divergance of curves and the value of standard deviations. Autumn individuals have far greater deviation than spring animals at this time, and this point to greater differences in the growth rate of body weight for the various autumn individuals than in spring mice. Increase in body weight in spring is very rapid: after two months of life the mice attain an average weight of 18 g, and 28 g after four months. Increase is considerable in autumn after the first 6 weeks of life, as weight reaches an average of 14 g (in spring animals up to 15 g). After three months, however, the animals weight only 17 g, and after four 18.5, and therefore on an average almost 10 g less than the spring animals.

The difference between growth curves increases markedly with increasing age. Spring-summer individuals attain the same or even slightly greater body weights during a period more than half as short as that taken by autumn mice. Spring individuals attain maximum weights on an average in 142 days (32 g), but autumn voles in 288 days (29 g). At the same time far more considerable variations in weight occur in autumn individuals and, *e.g.* at a weight of 29 g the standard deviation of the average is five times greater than in the case of spring-summer mice.

All individuals were divided according to the seasons of the year, assuming that the first capture of individuals in the first group took place on April 15th, and the second on August 15th. The average period of life of spring individuals therefore lasted from April to August (4.5 months) and of autumn individuals from August to June (9.5 months). These data, based on observations of live animals, may be taken as the average life span of these generations of field mice under natural conditions and they show that overwintering individuals live on an average twice as long as those born in spring and rapidly growing.

When estimating age on the basis of body weight of mice it is necessary to take into consideration the very great differences in growth rate at different seasons of the year of different generations.

3.6. Condylobasal Length of Skull

The distribution of frequencies of this measurement is almost symmetrical. Over 65% of the males and 59% of the females come within values of 21—22 mm (Fig. 2). There is a relatively great difference in the lower range on this dimension between males and females.

In winter months (from December to March or April) there are no individuals with short skulls (up to 20 mm). The upper limit of the range of variations from December or November is maintained on a constant level, and from March and April the lower range of this measurehent rises by 1—2 mm. The full range of variations in this dimension occurs from July to September.

The curve of monthly averages for Cb measurement exhibits a more regular course of growth than that of body dimensions (Fig. 1). Maximum averages occur at the beginning of summer, and minimum in October or November. There is an exceptionally great decrease in average value in Septembr 1966 in femals, caused by the occurrence of several individuals with very short skulls.

3.7. Length of Diastema

The distribution of frequencies for the two sexes is similar, being very slightly shifted in the direction of smaller measurements in females (Fig. 2).

There is an increase in this dimension during the winter months from December to February in both minimum and maximum values, the upper range of the dimension exhibiting the greatest increases. Like other measurements, individuals with the shortest diastema do not appear until the autumn, in September and October, while young animals from May are characterized by a longer diastema. There is no month with a full range of measurements, and ranges smaller by 0.3 mm occur in July, August and September. The disappearance of individuals with the longest diastema begins in September.

Fluctuations in monthly averages are almost identical with the analogical curve for Cb (Fig. 1). The distribution of frequencies of Cb length and diastema is also very similar, a smaller range of measurements occurring in males and a greater representation of the average values of this dimension. The difference occurring between the monthly distribution of Cb and diastema is also evident in winter. The diastema increases more intensively during this period than Cb, and this confirms the observation made by Wasilewski (1952) that during the animal's life the viscerocranium grows more evenly than the neurocranium, which affects the less even increase in condylobasal length.

3.8. Breadth of Brain-case

Seasonal variations in this dimension are very slight. The distribution of frequencies is very high and regular, 95% males and 89% females coming within the range from 10.10 mm to 11.30 mm (Fig. 2). It is clear from the monthly distribution that increase in the lower range of this measurement from November to June is 0.3 mm, while the upper range of the dimension exhibits almost no increase.

The curve illustrating monthly averages is very irregular, especially for females (Fig. 1), but there is a visible increase in values from August to June of the following year and differences during the summer between young animals and old adults.

3.9 Length of Upper Row of Teeth

The tooth row has the smallest range of measurement and limits of variations of all those described in this study. The distribution of frequencies is very regular (Fig. 2). Sex dimorphism is only faintly evident.

The curve of the monthly average of the dimension takes a very irregular course and does not exhibit growth in time, and therefore successive generations are not differentiated (Fig. 1). The monthly distribution of material does not exhibit any shifts in ranges of measurements in consecutive months.

3.10. Height of Brain-case Measured Per Bullae

The distribution of frequencies of this measurement and the monthly distribution of material are similar to the distributions for length of tooth row. The occurrence of the largest dimensions does not coincide in time with the presence of the oldest individuals (Fig. 2). The monthly averages for successive generations overlap and continue through the whole time on an unvarying level (Fig. 1).

3.11. Height of Brain-case Measured Inter Bullae

The distribution of frequencies is analogical to that of height of brain-case measured *per bullae* (Fig. 1). It is impossible to indicate the entrance of young animals or disappearance of old animals from the population on the basis of the monthly distribution.

The monthly averages on this dimension make it possible to differentiate between individuals from different generations during the summer (Fig. 2).

It can be seen from the material described above that the greatest age variations are exhibited by the weight of dry mass of eye lens, and also the degree of wear of the teeth, which is an objective, even though insufficiently accurate, criterion for determining age. Measurements of body length, body weight and tail length, and also Cb length and diastema, exhibit considerable variations due to growth, but with seasonal variations in growth rate co-occurring with them, hence young individuals entering the population in spring are larger than individuals entering in autumn.

The other skull measurements rapidly end their period of growth and individual variations are masked to a considerable degree by age variations. Even so, young animals fail to differ from old adults in respect of monthly averages only in relation to length of tooth row and height of brain-case measured *per bullae*.

Almost all measurements exhibit sex dimorphism. The greater irregularity of increase in monthly averages for females is due primarily to the smaller amount of material in the different months.

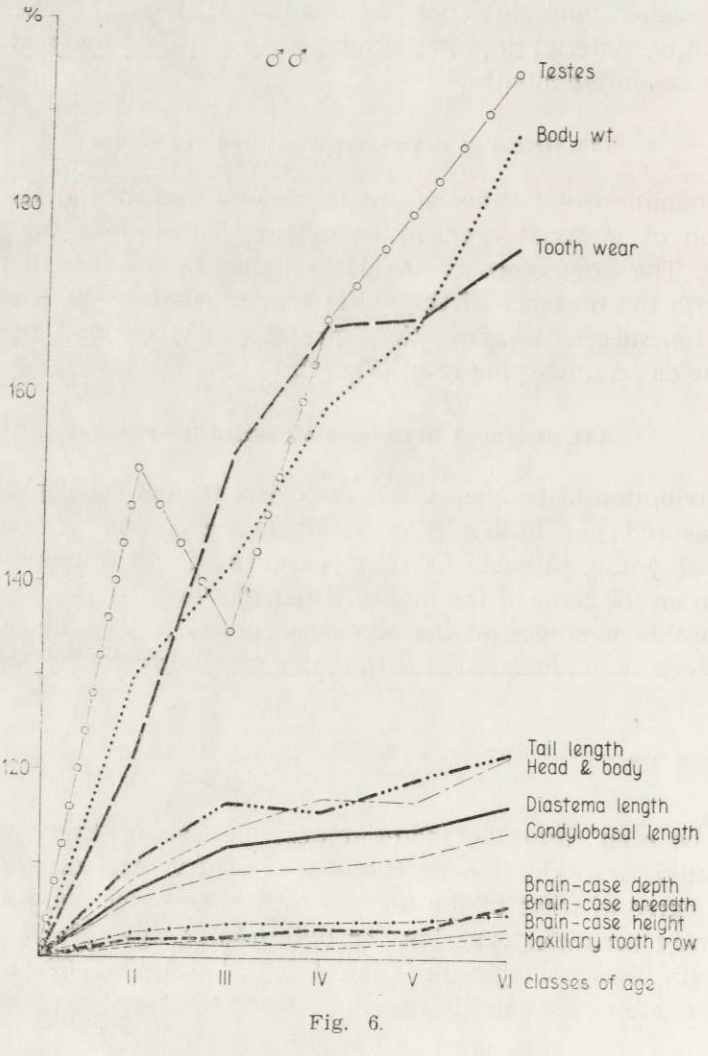

Fig. 6.

4. AGE VARIATIONS OF MEASUREMENTS

All individuals were segregated into seven age classes established on the basis of weight of the dry mass of eye lens. Minimum and maximum values, averages, standard deviations and coefficient of variation were determined in each age class for all measurements, separately for the two sexes (Table 5). Curves of increase in measurements in successive classes were plotted (Fig. 6). It was found that wear of teeth, body weight and size of testes (area of longitudinal section of the testis

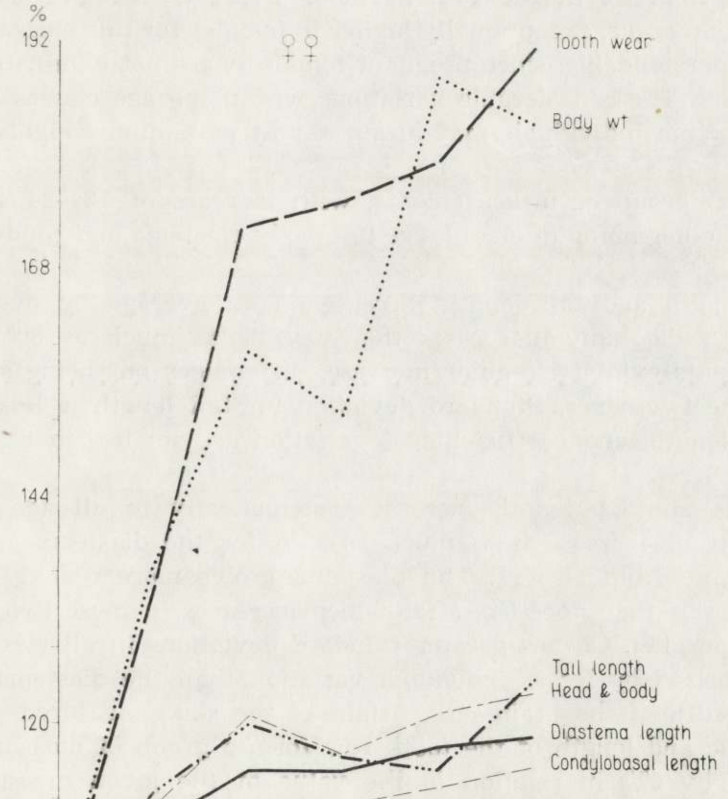

Fig. 6. Increase in average values of measurements in successive age classes determined on basis of eye lens weight.

calculated by means of the equation *abΠ/2*) form a group which exceeds by almost 100% in value the measurements for age class I.

Tooth wear is most intensive in classes I and II, but in class III the rate of wear slows down to some degree, this being particularly distinct in females. Later wear progresses with similar intensity to that found in the first classes. The coefficient of variation (*C.V*) of tooth wear in successive age classes is very high, possible due to individual variations in wear of teeth.

Body weight increases very regularly in males, but in females there is a decline between classes III and IV probably caused by the end of reproduction, which on an average occurs at this age for the generation born in spring. As in the case of tooth wear, very high coefficients of correlation occur, exceptionally higher in females for this measurement. This is understandable, since pregnant females were not eliminated from the material. The considerable variations within the age classes are due to the fact that individuals may attain almost maximum weights in age class II.

The next group of measurements, with increase of 13—24% in relation to the beginning of class I, are tail, body diastema and condylobasal length.

Body length and tail length increase on an average by over 20%, and in sporadic individual cases this may be as much as 80%. Both measurements exhibit irregular increase, differences not being synchronous in the two sexes. Standard deviation for tail length is lesser than for body length, and coefficients of variation are smaller in all classes except the first.

Diastema and Cb length increase systematically in all age classes. On an average increase is as much as 18% for the diastema and 13% for Cb value from class I. The diastema grows more quickly to the end of class II than does Cb, after which increases in these two dimensions are parallel. Cb has greater standard deviations in all classes, but is characterized by lesser individual variation than the diastema.

The breadth of the brain-case, height of the skull measured *per* and ***inter bullae*** and length of the tooth row form a group of measurements increasing by 6% in relation to the value of the given measurement for class I, length of the tooth row not exceeding on an average 3% of increase. Growth takes place chiefly in the youngest classes, as from class II there are fluctuations in growth, or even decreases in this value. Standard deviation is slight in all four measurements, and individual variations are maintained on a similar level.

Minimum and maximum measurement indicate that the field mouse may attain maximum size as early as age class III, that is, halfway is also connected with calendar time, in which rapid growth takes place. The decline in growth rate usually occurring after age class III or IV can be explained by the fact that it takes place in autumn or winter, that is, during a period of slower or even inhibited growth.

5. CORRELATION BETWEEN MEASUREMENTS

Each of the criteria discussed is distinguished by positive and negative characters, on account of the accuracy of measurement and also the ease with which the measurement can be made for use in determining age. It would appear important to establish allomorphic groups in order to estimate the proportions of the body and skull of the field mouse as a whole, also the relations between the various criteria and their groups, and also for defining the degree to which one measurement can replace a second. Correlations between all the measurements made were used for this purpose.

5.1. Analysis of Correlation Coefficients by the Dendrite Method

Coefficients of correlation were calculated separately for 570 males and 352 females. The various measurements were arranged in order by Perkal's dendrite method (1963), from the most correlated (situated in the centre of the distribution) to the least correlated (situated in the most eccentric position (Fig. 7). The significance of the coefficients of correlation were checked by means of the Student's test, with $P \leqslant 0.01$. All the coefficients, except for the degree of tooth wear with the length of the tooth row, proved to by significant in both sexes.

Condylobasal length occupies the central place in the diagram in the case of both males and females, on account of the greatest number of highest coefficients of correlation with other measurements. In males the following are directly connected with Cb: diastema ($r = .88$), body weight ($r = .83$), tail length ($r = .76$), body length $r = .73$) and breadth of brain-case ($r = .63$).

In the case of females the degree of wear of teeth ($r = .75$), which in males is separated from Cb by diastema and lens weight, is also well correlated with Cb (Fig. 7).

The remainder of the measurements correlate in the same way in both sexes, except for the reversed order of measurements of skull height.

The degree of tooth wear and eye lens weight correlate well with each other (♀♀ $r = .77$, ♂♂ $r = .68$), but they do not belong to the central group of measurements with the highest coefficients with Cb. The reverse order of tooth wear and eye lens weight in relation to Cb in

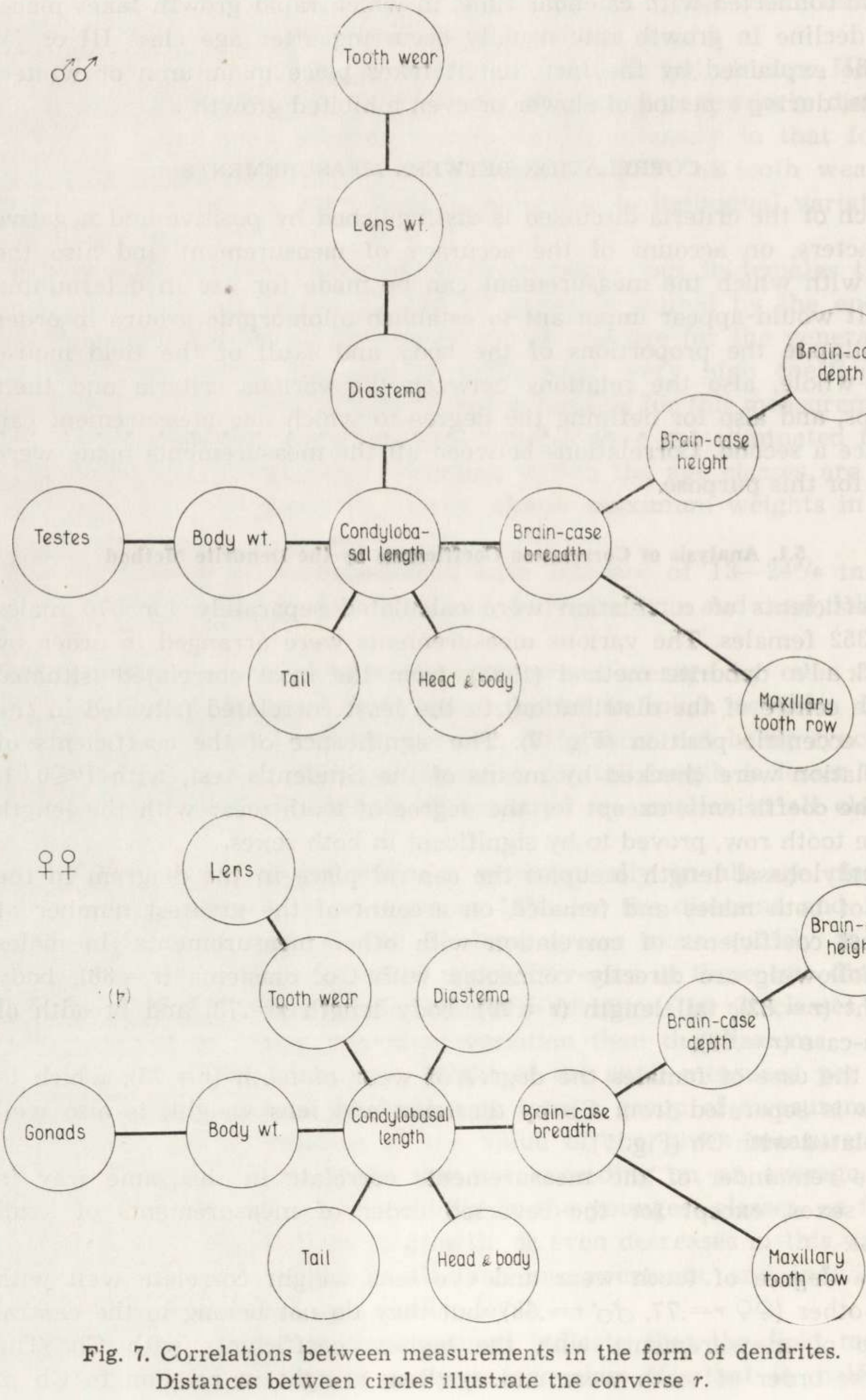

Fig. 7. Correlations between measurements in the form of dendrites. Distances between circles illustrate the converse r.

the two sexes is not significant. In females measurements most closely connected with age correlate better with Cb than with diastema, whereas in males the reverse is the case, but the differences are very slight.

The third group, well internally correlated, are formed by the three skull measurements: breadth of brain-case and height of skull measured per and *inter bullae*. Heights are particularly well correlated (♂♂ $r=.76$, ♀♀ $r=.67$). Breadth of brain-case is most closely correlated with Cb of all the measurements made of the neurocranium (♂♂ $r=.63$, ♀♀ $r=.75$).

A high degree of correlation occurs between body weight and Cb. The coefficient of correlation for males is higher than for females (♂♂ $r=.83$), ♀♀ $r=.79$). Coefficients between weight and length of body are similarly distributed. In males this correlation is higher ($r=.73$) than in females ($r=.68$). Sex dimorphism is most clearly reflected in these two measurements.

The three groups of measurements most closely correlated with each other exhibit certain characters typical of age variation. Degree of tooth wear and eye lens weight are closest to changes directly dependent on age. Measurements of the neurocranium are the farthest from them and are characterized by shortlived increase. Finally the control group of measurements surrounding Cb would appear to combine the phenomenon of constant increase with more or less strong influence of other processes, making this increase to differing degrees.

Reciprocal correlation between measurements also points to the morphological connections occurring in the whole organisms. It is possible to establish the order of characters which will occupy the central place on the dendrite diagram after gradual rejection of the most closely correlated. When considering data for males, the measurement connecting with the greatest number of measurements will, after rejecting Cb, be body weight, and in females diastema length. In males the diastema occupies third place, then come in the following order: body length, tail length and breadth of brain-case, with eye lens weight only seventh. In females, after rejecting the diastema, the central place is occupied by tail length, then body weight, body length and tooth wear, finally eye lens weight (which, as in males, comes seventh).

The arrangement of coefficients of correlation in order by the dendrite method makes it possible to realize how development mechanisms, and even some external factors, act in the organisms and which characters are reciprocally connected and what the cause of this connection may be.

5.2. Calculation of the Value of One Measurement on the Basis of Another

When examining the relations occurring between measurements it is possible to find the approximate value of one measurement on the basis of another. This method may prove useful for elaborating incomplete material, *e.g.* obtained from owl pellets or fossils.

The relation between two measurements laid off on axes of coordinates is expressed in the form of straight line determined by the regression coefficient. If the accuracy of a measurement laid off on axis y is calculated on the basis of a measurement laid off on axis x, then the equation for the regression coefficient will be as follows:

$$\rho_y^x = \sqrt{\frac{S_y}{n}} \tag{1}$$

and conversely in the opposite situation

$$\rho_x^y = \sqrt{\frac{S_x}{n}} \tag{2}$$

The distribution of each measurement is expressed by the dispersion which can be imagined as two lines of an arched shape lying symmetrically on each side of a straight line determined by the coefficient of regression. As the difference in value of dispersion between the point situated in the middle of the straight line of regression and its ends is close to 1, the minimum value was omitted, taking only maximum dispersion into account in this discussion.

The following equation was used for calculating the dispersion of the value of measurement y on the basis of measurement x.

$$d_x = t_{0,05}\, \rho_x^y \sqrt{1 + \frac{x^2}{n\, \sigma^2 xx}} \tag{3}$$

and for the reverse distribution, analogically

$$d_y = t_{0,05}\, \rho_y^x \sqrt{1 + \frac{y^2}{n \cdot \sigma^2 yy}} \tag{4}$$

Values of dispersion for all measurements are given in the table six. If the left vertical space is considered as axis y, and the lower horizontal space as axis x, then it is possible to read from the intersection of these spaces the accuracy with which the measurement referred to on axis y can be calculated on the basis of the measurement referred to on axis x. It can be seen from the table that there are no basic differences in dispersions of measurements between males and females.

The accuracy with which it is possible to calculate one measurement on the basis of the other depends on the coefficient of correlation, the ranges of data for measurements and the dispersion of material. For instance: the coefficient of correlation of Cb length and diastema in males is high $r = .879$. The range of Cb varies from 19 to 24.90 mm, the diastema from 5.40 to 7.80 mm. Dispersion calculated for the diastema according to Cb is .37, for Cb calculated according to diastema .97 mm. Correspondingly, this forms 14.8% of the whole range of the diastema measurement and 16.44% of the range of Cb length.

When calculating Cb according to length to tooth row, with which the coefficient of correlation is .226, the value of dispersion is 2.034, or 33.84% of the whole range of Cb length. The error committed in this case is twice as great.

6. CORRELATION BETWEEN ABSOLUTE AGE AND MEASUREMENTS

On the basis of marked material consisting of 65 mice of known age calculation was made of the correlation between different characters and time of life in months.

Correlation of age (w) with the measurement of a certain character (x) was calculated in accordance with the equation for η. The value is contained within limits from 0 to 1 and is interpreted in the same way as for coefficient of correlation

$$\eta^2 = 1 \frac{\sum_{i=1}^{k} \left(\sum_{j=1}^{n_i} x_{ij}^2 - \bar{x}_i \sum_{j=1}^{n_i} x_{ij} \right)}{\sum_i \left(\sum_j x_{ij}^2 \right) - \bar{\bar{x}} \sum_i \left(\sum_j x_{ij} \right)} \qquad (5)$$

1 — number of age group
j — current number in age group
n_i — number of mice in age group
k — number of age groups
$\bar{x}_i$ — average for age group
$\bar{x}$ — average for whole

Standard deviations were calculated for each age group in accordance

$$\bar{x}_i = \frac{1}{n_i} \sum_{j=1}^{n_i} x_{ij} \quad ; \quad \bar{\bar{x}} = \frac{1}{\sum_{i=1}^{k} n_i} \sum_{i=1}^{k} \sum_{j=1}^{n_i} x_{ij} \qquad (6)$$

with the equation:

$$S_{xw} = \sqrt{\frac{1}{n-k} \sum_{i=1}^{k} \left[\sum_{j=1}^{n_i} x_{ij}^2 - \bar{x}_i \sum_{j=1}^{n_i} x_{ij} \right]} \tag{7}$$

and average age:

$$\bar{w} = \frac{1}{n} \sum_{i=1}^{k} n_i w_i \tag{8}$$

and finally dispersion was calculated for each age in each measurement.

$$d = \pm 2 S_{xw} \sqrt{1 + \frac{1}{n_i}} \tag{9}$$

The measurements were arranged in order of value of intercorrelation η, which shifted the weight of dry mass of eye lens to the leading place among measurement correlated with age (Table 7, Fig. 8). The growth curve of average weights of eye lens from the first to the ninth month of life rose very evenly, dispersion not being great, slinghtly exceeding 1.6 mg. This forms 14.5% of the range of lens weight. Rate of increase falls markedly with age. During two months of life the average is 5.60 ± 1.86 and by adding value of dispersion a weight is obtained similar to the average eye lens weight at the age of 3 months (7.233 ± 1.60), that is, an error of one month is made. This error increases with a shift in the direction of greater weights, for instance the

Table 7

Coefficient of intercorrelation (η) with absolute age of marked individuals.

Measurement	S_{xw}	η	$\bar{x}$
Eye lens weight	0.959	0.759	9.480
Cb. length	0.903	0.700	21.717
Tail length	0.900	4.510	68.745
Diastema length	0.877	0.276	6.429
Head & body length	0.824	5.589	81.555
Tooth wear	0.797	1.690	7.219
Body weight	0.745	4.395	18.828
Brain-case height *(per bullae)*	0.729	0.230	8.587
Brain-case breadth	0.716	0.244	10.613

average for 6 months of life is 10.54 ± 1.60 mg which after substracting dispersion gives a value coming within the 4th or 5th month of life, and after adding dispersion exceeds the average values for 9 months. The error made may thus total even as much as 5 months. Further months will be burdened with even greater error.

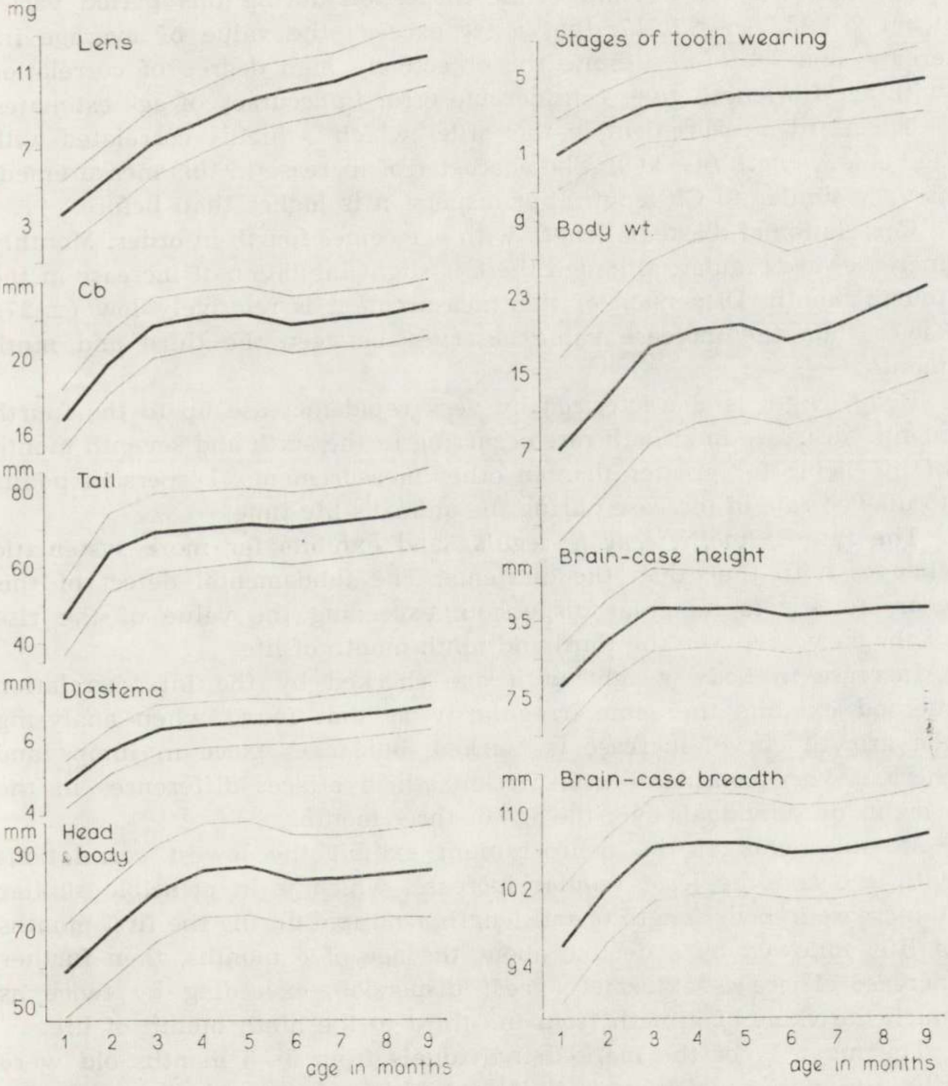

Fig. 8. Growth curves for body and skull measurements calculated on the basis of intercorrelations with absolute age in 68 marked individuals. Thin lines indicate dispersion of the measurement values.

Average values for other measurements and their dispersion were calculated in an analogical way.

Cb length comes second in respect of value. The growth up to the age of three months rises very rapidly and as in the case of eye lens weight, the error made in determining age is one month. Over the age of three months average increase in Cb length is slight, since up to 9 months it is only 1 mm, while dispersion during this period varies from ±1.453 to ±1.617, that is, it exceeds the value of average increase, and therefore despite the objectively high degree of correlation with age Cb length gives considerable error in accuracy of age estimates.

The third measurement in this order which is highly correlated with age is tail length ($\eta = .900$). The character of increase in this measurement is very similar to Cb length, but dispersion is higher than before.

Correlation of diastema length with age comes fourth in order. Monthly increases are regular, although there is slight inhibition of increase in the fourth month. Dispersion of this measurement is relatively low (±.27), lower than the increase value observed between the third and ninth month.

Body length is characterized by very rapid increase up to the fourth month, decrease in growth rate occurring in the sixth and seventh month of life being far greater than in other measurements. Dispersion points to uneven rate of increase during the animal's life time.

The rate of tooth wear is regular and exhibits far more systematic changes with time than the diastema. The fundamental defect of this characteristic is its great dispersion, exceeding the value of the rise of the curve between the third and ninth month of life.

Increase in body weight with age checked by the intercorrelation method exhibits the same irregularity as that found when analysing the growth curve. Increase is marked, but takes place in jumps and there is very considerable dispersion which effaces differences in the weights of individuals over the age of three months.

Measurements of the neurocranium exhibit the lowest correlations with age and the least regular increase, which is in principle similar to increase in body length or tail length, *i.e.* rapid during the first months of life, followed by a decline about the age of 6 months, then further increase. There is extremely great dispersion, exceeding by twice as much the value of growth from the third to the ninth month of life.

The majority of the marked individuals from 5—8 months old were killed in winter, which explains the inhibition of growth reflected in the deflection of grows curves at this particular period. The relatively small amount of material collected for this study was not capable of »smoothing out« irregularities in the course taken by curves.

7. DISCUSSION

The main purpose of this study was to divide body measurements in such a way as to be able to ascertain which of them vary strictly in accordance with age, which with growth, which are subject almost entirely to individual variations and which are modified by growth and age to a slight degree only.

Among the measurements which give the best picture of age changes are tooth wear and weight of the dry mass of eye lens. This maesurement, in relation to other species, has both supporters and opponents as a criterion for determining age. Matschke (1963) states that food conditions exert an important influence of variations in eye lens weight in wild boar. This is an objection made in respect of almost all the other criteria, but in the case of the eye lens is relatively less important to mice. Rongstad (1966) found considerable dispersion of eye lens weight, particularly in captive and free-living rabbits, but considers the eye lens as the best criterion for segregating young from old individuals. Friend (1967 a, b) considers that diet not affect eye lens weight and that this method is satisfactory for a very large number of species. The course taken by variations in eye lens weight and its growth curve point to minimum dependence on external conditions, and consequently there is a distinct division of material into individuals born the current year and old overwintered adults, throughout all the months in the year (Table 3). No such clear distinction between young and old individuals was observed in any other measurement. Tanaka (1968) considers that individual variations in the eye lens are so great that they make it impossible to determine age exactly and therefore proposes the method based on tooth wear, in the form of the ratio of worn surface to an area marked out by the quotient of length and breadth of the tooth row.

Askaner & Hansson (1967) checked the eye lens weight method for three species of *Clethrionomys* on material obtained from field conditions, and considered it better than that hitherto used for voles, *i.e.*, the method of measuring pseudo tooth roots. In *Sylvilagus floridanus* Wight & Conoway (1962) held this method to be better than radiograms. Martinet (1966) found a close relation between age and eye lens weight in captive *Microtus arvalis*. Mead (1967) who studied 5 age indexes in the skunk: ossification of sutures and epiphyses, body weight and weight of baculum and eye lens, considered eye lens to be the most exact. Generally studies on eye lens weight were made on species living longer than one year, but accuracy of age estimates is greater during the first period of the animals' life, while later it is possible to estimate only yearly intervals of age (Lord, 1959; Rongstad, 1966; Sanderson, 1961). For small mammals, whose life span under natural conditions rarely exceeds one year, and some of whose measurements continue to increase even during this period, this method is exceptionally useful. The curve of increase of the eye lens in *A. agrarius* exhibits lesser dispersion than other measurements. Dispersion of individuals round this curve is, however, far greater than shown by other authors who had individuals of known absolute age at their disposal (*e.g.* Lord, 1959 in *Sylvilagus floridanus,* Tiemeier & Plenert 1964 in *Lepus californicus*). It is probable that the parallel character of dispersion, the same for the youngest as the oldest marked mice, depends on inexact determination of age at the time of marking.

Tooth wear was given by Varšavskij & Krylova (1948) as an age criterion in four species of *Murinae,* including *A. agrarius.* The model used by these authors agrees in general outline with that given in the present study, althought no stage was observed corresponding to the 2.5—3 year old individuals defined as «vetus». Haitlinger's division (1962) would not appear to be sufficiently accurate, since the whole of middle age, from eruption of M^3 to complete wear of the teeth, is in his opinion separated by only three stages. The final stage — V, in which individuals with completely worn teeth occur, he counts as from the 10th month of life, which is not in complete agreement with the data discussed, in which this stage occurs in individuals over one year old. It is of course obvious that there are great individual variations in tooth wear and considerable deviations from this time may take place.

It is difficult to interpret the occurrence in the study material of individuals with considerable degree of tooth wear as early as age class II, determined on the basis of eye lens weight. Maximum wear is high in all age classes and wear does not coincide exactly with the age trend according to eye lens weight. This shows how great individual variations in rate of water of the molars may be. Schwarz & Smirnoff (1959) drew attention to this property in the musk rat. Varying hardness of teeth may occur in shrews in different years, which results in their not wearing uniformly, and thus affects the estimate of wear (Adamczewska-Andrzejewska, (1966). Felten (1952), for *A. flavicollis* and *A. sylvaticus,* gives age in classes of teeth wear and draws attention to the »different age« of animals from meadows and forests. The data given by these authors confirm the occurrence of great variations which made it difficult to classify mice in age groups. Ommiting these disturbances, the rise in the curve of average tooth wear for marked individuals is very similar to the course taken by the curve of increase in eye lens weight.

Body weight is a measurement very often used as an approximate guide to age, but it is simultaneously a measurement which is exceptionally sensative to any physiological and habitat changes, it must therefore be treated with considerable caution as a criterion of age.

The growth curves exhibit constant and intensive increase in body weight with age and this increase is fairly regular. A very important disturbance here is due to seasonal variations, causing differentiation of growth rate of the spring and autumn generation. This phenomenon was observed earlier in *A. flavicollis* (Adamczewska, 1961) and other species of small mammals (Haitlinger, 1962, Reichstein, 1964, Schwarz *et al.*, 1964, Pelikan, 1967). Differences in increase may be as much as almost 100%, as is shown by the data given in section 4. Zejda (1965) found that in voles there is a relation between body weight of adult individuals and their sexual activity only, and consequently rejects it as a criterion for ascertaining age.

Differences due to sex dimorphism are most clearly seen in body weight. The growth curve for females exceeds values for males in the second half of its course, but when the material is divided into age classes females are heavier than males in class V only. In all other classes, whether average, minimum or maximum, the weights of males are greater.

Females react somewhat differently to changes connected with sexual maturation. The rapid jump in growth of males in spring does not coincide with the growth of females, which takes place about two months later, as shown by average monthly measurements. Similar results were obtained by Ilenko & Zubčaninova (1963), who plotted curves of increase in body weight for voles and forest mice.

The materials presented show that young individuals entering the population in spring and at the beginning of summer are larger than the late summer and autumn mice. This would appear to provide evidence of the influence of habitat conditions, or population conditions during the early period of the individual's development, or even during the prenatal period. Christian (1961) has recorded the effect exerted through the mother on the degree of development of an individual in a mice population. The influence which this phenomenon exerts on the possibilities of estimating age fails to be reflected only in the method based on tooth wear.

Use of the measurement of tail length to assess age is justified by the high correlation with eye lens weight and tooth wear and the high coefficient of correlation with age. It must, however, be very limited on account of the considerable degree of dispersion, the slowing down of growth rate in winter and relatively small differences between old adults and the current years animals in summer. The period of rapid growth ends after 3 months (*cf.* also Haitlinger, 1962).

Cb length of the skull was held by Prychodko (1951) to be a dimension which constantly increases. Wasilewski (1952) refused this opinion, maintaining that Cb in *Clethrionomys glareolus* unevenly and more slowly increases in autumn than in spring. The material presented here provides support for Wasilewski's view (1952), since the autumn-winter increase in Cb length is significantly slower.

Cb plays a specific role among other measurements, as it has the greatest number of highest coefficients of correlation with the other measurements, and is as it were the link between measurements systematically changing with age, the group of measurements proving the individual's growth and also measurements which quickly end their increase and are completely unconnected with age. It is thus a measurement best representing the growth of the field mouse together with all the other factors affecting it, such as seasonal variation and slowing of growth with age. The high coefficient η is evidence of the considerable values of this measurement for determining age, and also dispersion is lesser than that of tooth wear. It is therefore primarily the slower rate of growth in adult individuals during the autumn-winter period which makes it difficult to determine age on the basis of Cb length.

Diastema length is considered as a characteristic measurement of the viscerocranium, which exhibits more intensive growth than Cb. In *A. flavicollis* the diastema exibits growth throughout the animal's whole life (Adamczewska, 1959). The present results agree with those published earlier. Of the skull measurements it is only the diastema which grows in winter months, although this growth is slower than at other times of the year. The diastema is characterized by relatively slight individual variation. Increase in Cb is the result of increase in diastema to a considerable degree, hence the diastema is more suitable for determining age than Cb.

The other skull measurements grow quickly only during the first period of the animal's life, after which they either fail to increase or, as in the case of the breadth of the brain-case, increase is very slight. The great dispersion of individuals round the growth curves completely effaces differences in values after the second month of life.

Rossolimo (1962), using Terientiev's pleiad method, divided the skull measurements in *Clethrionomys glareolus* into groups correlating with each other either well or badly. These skull measurements, which are subject to great and fairly long-lasting growth, may be allocated to the group represented according to Rossolimo (1962) by zygomatic breadth, to which both Cb and diastema belong. The second group is represented by breadth of brain-case, and includes other closely-correlated measurements of the neurocranium of the short-lived growth type in the first age classes.

If body measurements are added to skull measurements after arranging them in the same order then tail length, body length and body weight will belong to the first group. Characters changing primarily with age will form a separate group.

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WZROST, ZMIENNOŚĆ I KRYTERIA WIEKOWE U *APODEMUS AGRARIUS* (PALLAS, 1771)

Streszczenie

Na materiale 1210 osobników myszy polnej *Apodemus agrarius* złowionych w ciągu dwóch lat na terenie parku miejskiego w Warszawie, zbadano wzrost i starzenie się osobników na podstawie 9 pomiarów ciała i czaszki oraz starcia zębów i ciężaru suchej masy soczewki oka. Stwierdzono, że najbardziej równolegle z wiekiem myszy i najmniej zależnie od warunków środowiska i fizjologii osobnika zmienia się stopień starcia zębów i ciężar suchej masy soczewki. Dla oceny wieku wygodniejsza i dokładniejsza jest metoda ciężaru soczewki od stopnia starcia zębów (Tabela 7, Fig. 8). Obliczono interkorelację z wiekiem dla wszystkich pomiarów w grupie 65 osobników o znanym wieku. Najwyższy współczynnik interkorelacji ($\eta = 0.959$) wykazuje ciężar soczewki.

Najintensywniej wzrasta ciężar ciała, następnie długość ciała i ogona oraz długość kondylobazalna. Pozostałe pomiary rosną nieznacznie i przez bardzo krótki okres życia zwierzęcia (Tabela 5, Fig. 6 i 8). Wszystkie pomiary wykazują znaczną zmienność indywidualną, maskującą zmienność wzrostową, szczególnie w pomiarach mało wzrastających.

Z obliczenia korelacji między wszystkimi pomiarami dla 922 osobników wynikło, że Cb jest najwyżej skorelowana ze wszystkimi pozostałymi pomiarami. Współczynniki korelacji analizowane metodą dendrytów wskazują na istnienie trzech grup pomiarów silnie wewnątrz skorelowanych zgodnych z typem wzrostu i starzenia zwierząt (Fig. 7).

Wykreślono krzywe wzrostu ciężaru ciała i stwierdzono znacznie szybszy wzrost ciężaru osobników urodzonych na wiosnę i w pierwszej połowie lata, niż w drugiej połowie lata i na jesieni (Tabela 4, Fig. 5). Zmiana tempa wzrostu u różnych pokoleń występuje z różną intensywnością w poszczególnych pomiarach.