AGE DETERMINATION OF THE BANK VOLE, *CLETHRIONOMYS GLAREOLUS*, SCHREBER, 1780

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Abstract

Many methods of age determination have been devised for use on large mammals. An attempt was made to discover whether they were applicable to a small species, how accurate the methods could be and whether the age determination criteria were influenced by environmental factors.

This study was based on 199 known-age specimens of the mainland bank vole, Clethrionomys glareolus britannicus (Miller), and 169 specimens of the Skomer vole, C. g. skomerensis (Barrett-Hamilton).

These two laboratory-raised samples were used to assess the relative accuracy and reliability of different age determination criteria.

Morphological characters which were used for ageing included: body weight, body measurements, skull measurements, molar root development, tooth wear, fusion of epiphyses, baculum, pelage, and dry weight of the eye lenses.

Changes in these characters were studied through 18 months of age. Laboratory study showed that the dry weight of the eye lens gave the best results for ageing. Development of the molar roots found to be highly correlated with age, as was tooth wear. Fusion of ten sets of epiphyses combine to give a high degree of accuracy in age-determination up to the age of 14 months. The correlation of skull measurements, moult, body measurements, and body weight with age was also studied.

Tables were prepared for estimating the age of the two subspecies from every character used and 95% confidence limits were attached to the results.

A low-calcium diet was given to 60 known-age mainland bank voles but there was no measurable effect even on bones and teeth.

Seventy three known-age mainland bank voles were released in outdoor enclosures. Growth data of 18 of them were analysed and compared with data from laboratory-raised animals. The results were in agreement with the latter, except in regard to tooth wear and to some extent in root growth.

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CHAPTER I. Introduction

1.1. Acknowledgements

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I.2. General Introduction

Reliable criteria for estimating the age of mammals, in order to study different phases of their life, are still needed. Unless the ages of individuals are known with accuracy, it is not possible to make critical studies on population dynamics, growth rates, longevity, sexual maturity, and other aspects of the life of mammals. With the continuous increase in the study of mammalian populations, the need for reliable criteria to determine their age must be fulfilled.

The use of different criteria for ageing in wildlife studies has been reviewed by Alexander (1958). Literature (up to 1967) on ageing of wildlife was listed by Madsen (1967). Ageing in mammals has been reviewed briefly by Gandal (1954), and most extensively by Morris (1972) and by Pucek & Lowe (1975). Certain groups have been reviewed separately, e.g. Pinnipedia (Laws, 1962); and Cetacea and Pinnipedia (Jonsgård, 1969). Most other ageing studies have been mentioned by Morris (loc.cit.) and Pucek & Lowe (loc. cit.).

The degree of accuracy needed for estimating the age of mammals differs according to the life span of the different species. For example, yearly divisions for big mammals, which reach maturity after the first year of their life, are probably adequate. But in the case of small rodents, which mostly breed during their first year of life, and may only live for a few months, criteria of shorter time span are needed for estimating their age.

Some work has been carried out for ageing small mammals e.g. Schofield (1955) on *Ondatra zibethicus* ;

Bujalska *et al* (1965) on *Lepus europaeus* ; Skoczen (1966) on *Talpa europaea* ; and Adamczewska-Andrzejewska (1971 & 1973b) on *Apodemus agrarius* . In such studies, the sample under investigation was divided into age-related groups because known-age animals were not available and the ages assigned to each group were only educated guesses. Division like this gives only a rough approximation of age for these species.

Because it is difficult to get large numbers of exactly known-age wild animals, various methods of age determination have been calibrated using animals of known age raised in captivity. Three problems arise from this procedure. The first pertains to the reliability of the techniques used, the second involves the influence of external factors that are independent of age, and finally there is the question whether the extrapolation from captive data to the wild is a valid procedure.

The bank vole, *Clethrionomys glareolus*, Schreber 1780, was chosen in the present study to answer these questions and to see how it fits in with previous work and with methods mainly applied to large mammals.

The purpose of the present study was to:

1. Apply age determination methods (used successfully on large mammals) to the bank vole to assess the possibility of using these methods on small mammals. (Attempts have been made previously, with equivocal results).
2. Assess the relative accuracy and reliability of the methods employed.
3. Determine whether or not the fundamental principles upon

which these methods are based are liable to be affected by factors (e.g. environmental ones) which are independent of age.

4. Discuss whether extrapolation from captive animals to the wild is valid, bearing in mind that this has been done in the past.

The species Clethrionomys glareolus is one of the commonest mammalian species in Britain. Its world distribution is from Great Britain through Europe, Asia, Asia Minor, to Japan (Walker, 1968). In Britain, it occurs in deciduous woods, hedge rows, scrub, and parkland all over the country (Barrett-Hamilton & Hinton, 1910-21 ; Matthews, 1952 ; Southern, 1964 ; and Van Den Brink, 1967) .

Five subspecies occur in Great Britain (Southern,1964). C. g. britannicus (Miller) lives on the mainland. The other four subspecies are island forms. One of these is C. g. skomerensis (Barrett-Hamilton) found on Skomer Island, Pembrokeshire.

The mainland bank vole and the Skomer vole, were the subject of the present study.

C. g. britannicus is generally distributed over the British mainland (Southern, loc.cit.). A full description of it has been given by Barrett-Hamilton & Hinton (loc.cit.). Other authors have published work on the species which was mostly taxonomic (e.g. Hinton, 1926; and Steven, 1953 & 1957).

Habits, habitat, behaviour and breeding in captivity and some other aspects of its life were studied by Baker (1930); Miller (1954 & 1955); Delany & Bishop (1960); Bishop

& Delany (1963); and Tanton (1969).

Other aspects of the life of Clethrionomys such as population dynamics, age structure, and morphological studies have been studied by many investigators. Zejda made the largest contribution in these studies (1959, 1961, 1964, 1966, 1968, and 1971), in addition to many other authors such as Wasilewski (1952); Manning (1956); Haitlinger (1965); and Kubik (1965).

Reproduction and growth of reproductive organs of C. glareolus in Britain have been studied by Rowlands (1936), Brambell & Rowlands (1936), and Coutts & Rowlands (1969).

Pucek et al (1969) estimated the maximum life span of C. glareolus in Poland and Czhechoslovakia to be between 17 and 21 months. While Lowe (1971) found that the mainland bank vole in Britain may live up to 24 or 25 months.

Ageing of C. g. britannicus was studied by Lowe (loc. cit.). He used root length of the first lower molar for this purpose. Before him, Delany & Bishop (1960) found the anterior root of the third upper molar a useful guide to determine the age of C. g. britannicus and two other sub-species.

The Skomer vole is confined to Skomer Island. It is believed to be derived from ordinary mainland stock , introdused accidently by man (Corbet, 1961), and a historical review of its taxonomic status was given by Jewell (1965). Saunders (1961) recorded some notes on its habits. Fullagar et al (1963) estimated the population size, and Jewell (1965 & 1966) worked on population, breeding, and some other aspects of the life of this subspecies.

Information concerning age determination in the Skomer vole is lacking.

Molar root development has mainly been used for determining the age of the bank vole. Molars in Clethrionomys have one open root which at a definite age becomes divided into two roots (Southern, 1964). These roots grow throughout the vole's life, and their length corresponds to the vole's age. Many investigators have used this character as an age indicator in this genus. The first lower molar has usually been emplyoed, but the second and third upper molars have also sometimes been used (Zimmerman, 1937; Wrangle, 1939; Prychodko, 1951; Wasilewski, 1952; Koshkina, 1955; Zejda, 1961; Shaw, 1959; Mazak, 1963; Haitlinger, 1965; Tupikova et al, 1968; Pucek & Zejda, 1968; and Viitala,1971)

Few attempts have been made to find other techniques to determine the age of Clethrionomys.

Askaner & Hansson (1967) examined the dry weight of the eye lenses in Clethrionomys rufocanus and C. rutilus in Norway, Finland, and Sweden as age indicator. Le louarn (1971) studied the monthly increase in the dry weight of the eye lenses of C. glareolus in France.

Fedyk (1974 c) used the water contents of the body of C. glareolus to determine the age of voles during the first 3 months of their life with an accuracy of ± 14 days.

Linear measurements, fusion of epiphyses, moult, the baculum, and tooth wear have not previously been used as precise age criteria in Clethrionomys .

I.3. Materials

A. Laboratory populations:

a. The mainland bank vole, *Clethrionomys glareolus britannicus* (Miller):

A breeding colony of wild mainland bank voles, collected in the vicinity of the Botany Department, Zoology Dept., and the grounds of Royal Holloway College , Surrey, was established during November and December 1972, and January to May 1973. Offspring of these wild voles were also used as breeders. Bisexual pairs were maintained in plastic cages covered by mesh lids and provided with small doors to enable the voles to be handled. These cages were 40 cm by 25 cm by 20 cm deep. Peat and hay were used for bedding and nesting. Each cage was provided with commercial rat food (Formula 86 of Cooper Nutrition Products Ltd.), and water.

Fifteen breeding pairs formed the foundation stock, followed by 30 others which were all, the offspring of the first breeding group.

Not all the females were fecund, many of them did not breed. The breeding females were weighed weekly. The pregnant ones were checked daily until they gave birth. Because the male did not harm the young, he was left in the cage in order to gave the pair another chance to copulate soon after parturition.

The laboratory-born voles, which were used as breeders, were kept in pairs when they were 5 to 6 weeks old.

Usually the juveniles were removed from the cage of their parents, when they were 3 weeks old. But if their mother gave birth to another litter before that time, they were removed immediatly. Even when they have been left with their parents and the new young, however, they have not harmed them.

All the voles were sexed and marked when they were 2 to 3 weeks old. The toe-clipping method was used for this purpose (Fig. 1).

Bank voles are docile animals and it is easy to handle them. They are not aggressive; sometimes they bite but this is usually in defence.

All the voles were kept in an air-conditioned room with a temperature of 55° to 70° F and a photoperiod of 12 hours per day. The cages were cleaned every 1 to 3 weeks.

Studying the age of the mainland bank vole was based on a sample of 199 known-age animals, (94 females and 105 males). A schedule was made for killing the voles (Table 1). Additional voles have not been included in the schedule. They were kept to substitute for the voles which died prior to attaining the desired age.

The sample was composed of 33 age-group samples extending in age from 5 days to 18 months. Each age-group sample was planned to be derived from mixed parentage and composed of a maximum of 17 voles including males and females. In some later ages it was composed of 4 or 3 voles only.

A record was prepared for each vole onto which the data were put (Fig. 2). The record bore the identity of the parents, litter number, and litter size, in addition to all the other data which were taken for each vole.

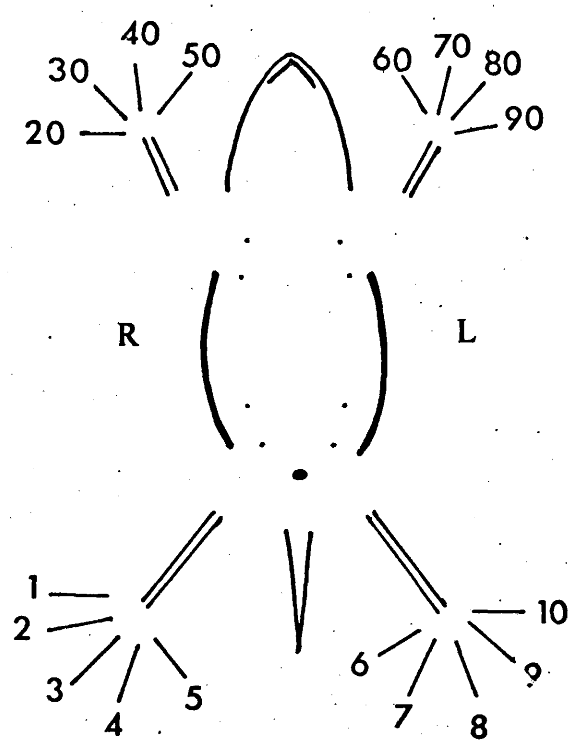


Fig. 1. A diagram for the ventral side of a vole, showing the toe-clipping system, used in the present study.

Table 1. Schedule for killing the mainland bank voles and Skomer voles:

Age/ days	Mainland bank vole		Skomer vole		Experimental mainland vole		Released mainland vole	
	M	F	M	F	M	F	M	F
5	2	2	1	1	-	-	-	-
7	3	2	3	1	-	-	-	-
10	2	2	3	2	-	-	-	-
14	2	2	2	2	-	-	-	-
17	3	4	2	2	-	-	-	-
21	7	2	2	2	1	-	-	-
24	3	3	2	2	-	-	-	-
30	4	4	4	2	2	-	-	-
35	2	3	2	2	2	1	-	-
42	3	2	3	5	-	2	-	1
49	8	2	2	2	1	1	-	-
60	7	10	7	6	2	2	1	1
72	3	4	2	2	2	1	-	1
80	3	2	3	2	3	2	1	-
90	2	2	2	3	2	2	1	1
100	5	3	5	2	-	-	1	-
120	4	3	2	2	1	2	-	1
135	3	3	2	3	-	-	-	-
150	2	3	3	2	2	2	-	2
165	3	2	2	3	-	-	-	-
180	3	5	3	2	2	1	1	2
210	5	1	4	2	2	2	2	1
240	3	4	3	2	2	3	-	-
270	4	2	3	2	2	2	-	-
300	2	2	3	4	2	1	-	-
330	3	4	3	2	3	-	-	-
360	2	1	2	3	1	1	-	-
390	2	2	3	2	2	-	-	-
420	1	2	2	2	1	-	-	-
450	3	2	3	1	-	-	-	-
480	1	2	2	2	-	-	-	-
510	1	2	2	2	-	-	-	-
540	2	1	3	1	-	-	-	-

M: male

F: female

Parents' No   Litter size   Litter No

<u>Species</u>:   <u>No</u>:

Date of birth: Date of death: Known age:

Manner of death:

<u>Sex</u>:

<u>Body weight</u>: 1. Whole   2. Eviscerated:

<u>Lens weight</u>: 1.   2.   Total:

HB l.   T   E   HF

<u>Skull</u>:

Skull l.   Zyg. breadth   L. jaw l.

<u>Molar teeth</u>:

	Lower molars			Upper molars		
	1	2	3	1	2	3
Crown height:						
neck & root length :						

Fig. 2. A record onto which the data of every vole were included.

Bank voles were killed with chloroform when they reached the required age in days. Each vole was then weighed. The eyeballs were removed and preserved in 5% formalin for hardening. The standard body measurements were recorded in mm. These were: head-body length, tail length, ear pinna length, and hind foot length.

The abdomen was then opened and the alimentary canal with the liver were removed, and then the vole was weighed. This weight was the eviscerated weight.

The body was skinned, the pelt was pinned out on a cork board for drying.

The skull was separated from the whole body and cleaned. The whole body was then presevéd in 70% Alcohol for further studies.

b. The Skomer vole, Clethrionomys glareolus skomerensis (Barrett-Hamilton):

Thirty three Skomer voles (8 females and 25 males) were trapped by me on Skomer Island, Pembrokeshire, during the period 13 to 16 May 1973. Another 16 females were collected during 25 to 27 August of the same year and provided by T. D. Healing.

Fifteen breeding pairs were established and their offspring were also used to supplement the breeding colony. All were kept in the same room and under the same conditions as the mainland bank vole.

The Skomer vole was used for a parallel study of the same age-related characters under investigation in the mainland bank vole.

Studying the age of the Skomer vole was based on a sample of 169 known-age specimens (77 females and 92 males). This sample was composed of 33 age-group samples extending in age from 5 days to 18 months (Table 1).

B. Experimental laboratory population:

Food was assumed to be a factor which might affect the criteria of age determination. A low-calcium diet was selected to study its effect on growth of teeth and bones, as these two criteria are most likely to be affected by this diet. It contained less than half the amount of calcium (0.45% gm Ca) that was used in the usual food (1.10% gm Ca).

Thirty bank voles (12 females and 18 males) were given the low-calcium food when they were 19 to 22 days old. They were kept in cages which contained only peat. Hay was not provided in order to be sure that they would not chew it. Bisexual pairs were put together for breeding and were kept under the same conditions as the other bank voles.

A schedule was prepared to kill these voles when they reached the desired age (Table 1). The sample comprised 60 voles (25 females and 35 males). It was divided into 20 age-group samples extending in age from 21 days to 14 months.

C. Field population:

To field-test the techniques, a total number of 73 laboratory-born mainland bank voles were released subsequently in two enclosures which were build in the gardens of the Zoology Department. The first enclosure was 4 m long, 3 m wide; with sides 1 m high, and 0.9 m deep under the ground surface. The second enclosure was 6 m by 3 m by (1 m + 0.9 m), (Fig. 3).

Not more than 10 voles in the first enclosure, and 16 voles in the second, were released at the same time. The voles were 21 to 28 days old when they were first released.

Water and extra food pellets were provided in the two enclosures. Eight open longworth small mammal traps (Chitty and Kempson, 1949), were put in the first enclosure, and 15 in the second. All were filled with hay and food in order to get the voles used to entering them, so that recapturing the voles would be easy. All the traps were cleaned and refilled every fortnight. A schedule for killing the voles was prepared and the traps were set to capture and sacrifice any vole that reached the required age (Table 1).

Fig. 3. The two enclosures into which the laboratory-born mainland bank voles were released.

D. Treatment of the data:

Numerical data were treated the same way for every measurable character. Student's t test was applied to compare the means of males and females, to see if any difference existed.

For each age-group sample, the mean of the measurement under investigation, standard deviation (S.D.), and standard error (S.E.) were taken. Variability of the measurement within each group sample was computed and represented by the coefficient of variation (V), and 95% confidence limits were attached to the mean of the measurement of every group sample. The correlation coefficient (r) between age and growth of every measurable character was computed. Bishop (1966), Jarman (1970), and Parker (1973) were used as statistical references.

Numerical data are presented in appendices. Graphs have been drawn based upon the data mentioned above.

The data afterwards treated in a different way in order to estimate the age by giving numerical results.

To estimate the age according to a certain measurable character (e.g. body weight), the whole sample was divided into groups, each containing animals of the same weight. Thus, animals weighing 14 to 15.9 gm, irrespective of their age, formed one group. All other characters were treated in a similar way.

The mean age for each size-group sample was obtained from the known ages of the voles comprising each group. Standard deviation, standard error, and coefficient of variation were computed and 95% confidence limits were attached to the mean age. Therefore, results were accurate with a probability of 0.05. Data are presented in tables, one table for each measurable character including: body weight, body measurements, skull measurements, molar root length, molar crown height, and dry weight of the eye lens for the mainland bank vole and the Skomer vole.

CHAPTER II. ageing techniques

II. 1. The body weight

A. Introduction and methods:

a. The whole body weight:

The body weight is the most obvious indication of size. If increase in size is directly correlated with increasing age, then size may be taken as an age index.

Body weight has long been used to discriminate between age groups in a population of mammals.

To examine with what accuracy this method may be applied to the genus *Clethrionomys*, it has been employed throughout the present study. A torsion balance was used to weigh the voles, to the nearest 0.05 gm, immediatly after they were killed (pregnant females were excluded). To supplement the data, weights of live voles were taken to the nearest o.5 gm, at intervals through the first two months of their life. The graphs include both live weights and fresh dead weights.

b. The eviscerated weight:

The whole body weight may fluctuate according to the amount of food eaten by the animal. So removal of the alimentary canal may reduce the variability in the body weights. Thus, animals were eviscerated and weighed on the same torsion balance to see if:

1. The eviscerated weights were less variable than the whole weights.
2. The eviscerated weights were equally closely related to age as were the whole weights.

B. Results:

a. Mainland bank vole:

a.1. Growth curve of the body weight:

Data for the weights of the laboratory-born bank voles are presented in Fig. 4 and Appendix 1. The differences between the sexes for this character were not significant, (t_{64}= 1.2, $P \geq 0.2$), and therefore, the values were combined.

Bank voles grew very quickly and the growth curve rose steeply during the first month of life. The average weight at birth was 1.64 gm, and it increased to a mean weight of 13.9 gm at the age of one month. The body weight up to the age of 35 days was highly correlated with age (r=0.95). The standard deviation of the mean and the coefficient of variation, of each age-group sample, within the range of this age, were not high (Appendix 1).

After the age of 35 days, growth slowed down, and the voles reached an average weight of 17 gm at 2 months, 18 gm at 3 months, and 20.5 gm at 4 months. The weight after this age was more variable, but the means remained fairly constant, and on the graph, 20.5 gm was the average weight of 8 months old voles, the same as for 4 months old.

The body weight increased faster above the age of 8 months. The heaviest weights were usually found between voles ageing 9 to 15 months. The average weight was 24.88 gm for 10 months old voles, 25.74 gm for one year old voles.

Over this age, the voles started to lose some weight, suggesting that they had reached senility. The subjective impression was gained that activity became much reduced above this age. The mean body weight for the 16 months old voles was 22.73 gm. It was 26.03 gm for 17 months old, and 21.98 gm for 18 months old voles.

The correlation coefficient for the body weight starting at the age of 5 days up to 18 months of life was 0.74.

The variability within each age-group sample was high. The highest (v being 24.3) was among the 100 days old voles, and also among the 7 and 9 months old voles (v=22.5 and 22.4 respectively).

The variability was lower among the young, and the very old voles, (e.g. v=10.29 for 14 days old voles; 12.54 for 21 days old; 11.84 for one year old; and 10.29 for 16 months old voles). This might be because the young were all growing at the same rate, and because the old animals had already attained adult size and were less active. Therefore, the low variability in both groups was the result of individual variations only.

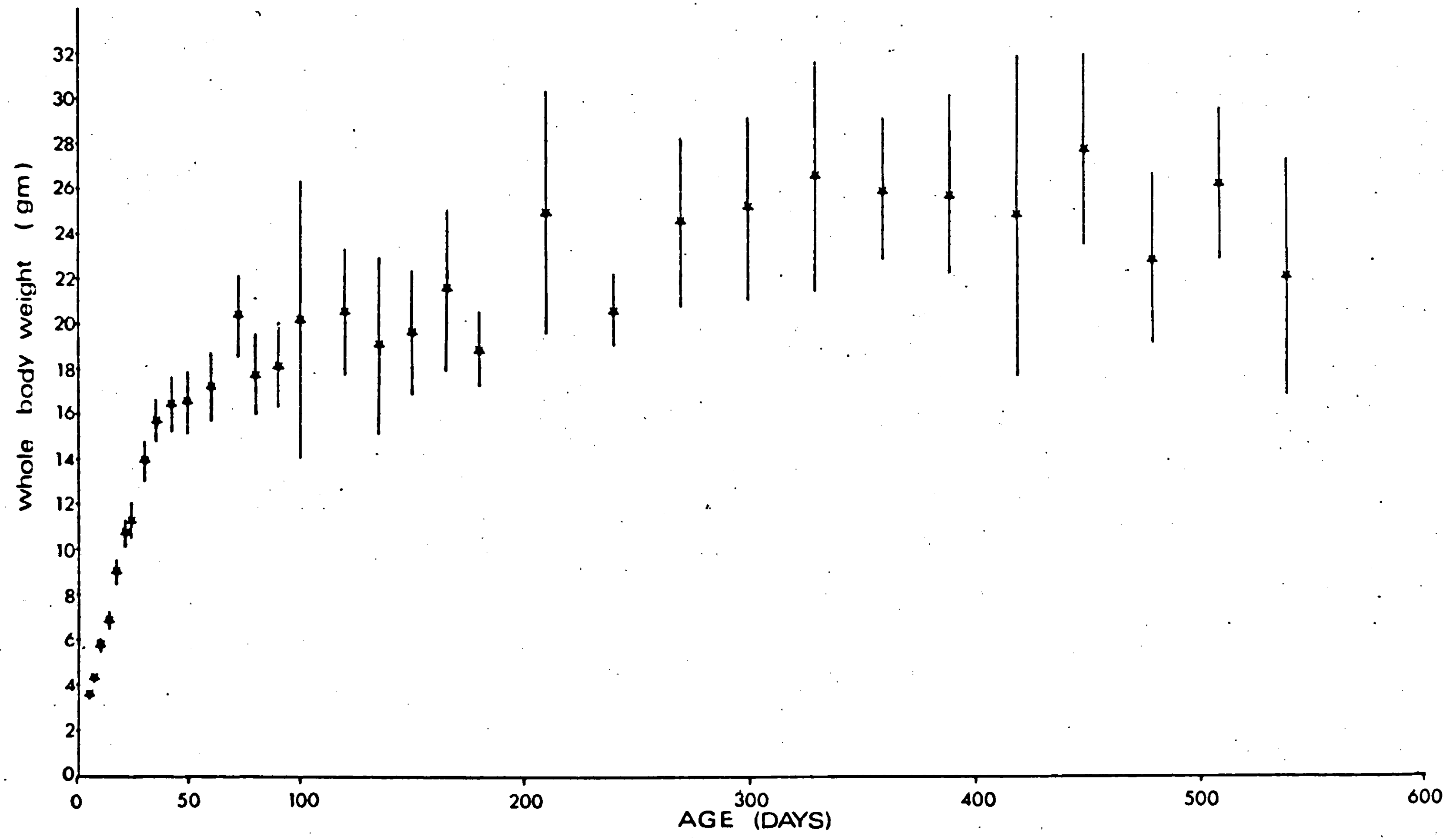


Fig. 4. Growth curve for the mainland bank vole. The star represents the mean, and the vertical line represents one 95% confidence limits on each side of the mean.

a.2. Estimating the age from the body weight:

In an attempt to find how reliable the body weight is, as a character for determining the age of the mainland bank vole, the whole sample was arranged into 17 groups according to their body weight.

In this case, the body weight was assumed to be the independent variable (x axis), and the dependent age was calculated from the known-age voles comprising each group and having the same body weight.

Standard deviation, standard error of the mean, and the coefficient of variation were taken for each size-group and, are presented in table 2.

Because individual variations were low during the first month of life, voles having this age were arranged into 12 groups according to their body weight. These groups included 46% of the whole sample. They contained voles weighing less than 14 gm. The accuracy for estimating their age was high. The remaining 54% of the sample included voles above the age of 35 days, and weighing more than 14 gm. They were divided into 5 groups only, because the overlap of data was very high.

The highest variability, occurred between the weights 14 to 23.9 gm (groups 13 to 16). The highest coefficient of variation (70.8) occurred between voles weighing 18 to 19.9 gm (group 15) representing a range of age 30 to 540 days and an estimated age range of 106 to 182 days, with a probability of 0.05.

The accuracy for estimating the age of voles weighing more than 14 gm was low because of the high variability that occurred above this weight. This result rendered the body

Table 2. Numerical data for estimating the age of the mainland bank vole from the body weight:

G. No	Body W./ gm.	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1- 1.9	9	at birth	- -	-	-	-
	2- 2.9*	-					
2	3- 3.9	13	5 day old	5.0± -	-	-	5 day old
3	4- 4.9	18	5- 7	7.0+ 0.10	0.46	6.54	6.8- 7.2
4	5- 5.9	26	7- 10	10.0± 0.18	0.96	9.62	9.6- 10.4
5	6- 6.9	12	10- 14	12.6± 0.54	1.89	15.00	11.4- 13.8
6	7- 7.9	7	10- 17	12.7± 0.96	2.55	20.00	10.4- 15.1
7	8- 8.9	12	14- 21	16.8± 0.48	1.68	10.00	15.8- 17.9
8	9- 9.9	12	17- 24	19.8± 0.75	2.61	13.18	18.2- 21.5
9	10-10.9	17	17- 30	21.8± 0.93	3.83	17.57	19.8- 23.8
10	11-11.9	8	21- 24	22.5± 0.53	1.50	6.60	21.3- 23.8
11	12-12.9	14	17- 60	31.0± 3.38	12.60	40.64	23.7- 38.3
12	13-13.9	11	21- 60	35.9± 4.09	13.56	37.77	26.8- 45.0
13	14-15.9	31	24-180	59.0± 7.36	41.00	69.49	44.0- 74.0
14	16-17.9	39	30-270	74.9± 7.98	49.80	66.48	58.8- 91.0
15	18-19.9	30	30-540	144.0±18.60	101.96	70.80	106.1-181.9
16	20-23.9	50	42-540	215.5±17.67	124.95	57.97	180.0-251.0
17	24-35.9	37	100-540	367.9±25.00	109.60	29.79	317.4-418.4

G.No: Group Number
O.range: Observed range
F. : Frequency
S.E.: Standard error
S.D.: Standard deviation
V. : Coefficient of variation
* : Data for this weight were not available

weight useless as an age criterion in voles heavier than 14 gm and therefore older than 36 days (Table 2).

b. Skomer vole:

b.1. Growth curve of the body weight:

Data for the body weight of the laboratory-born Skomer voles are presented in Figs. 5 & 6, and Appendices 2 & 3. The differences between the sexes up to the age of 35 days, were not significant (t_{16}=0.86, $P > 0.3$), and the data were combined for both of them. Above the age of 35 days, the differences were found to be significant, (t_{46}=5.06, $P < 0.001$) , and the data were treated separately for each.

Skomer voles, as the mainland bank voles, grew very quickly during the first month. They started their life with an average weight of 2.2 gm, and grew to an average weight of nearly 20 gm at the age of 35 days. Age, during this phase, was highly correlated with the body weight, (r=0.98), and the sex differences were not obvious.

In voles above this age, there was some body weight vaiation, depending upon the sex. This was obvious starting at the age of 2 months onward which is also the time at which they attained sexual maturity. The males over 2 months gained weight faster than the females.

Until the age of 10 months, growth in the females was very slow. The average weight throughout this period ranged between 19.5 and 23 gm only. A sick abnormally heavy female (which had one of her uterine horns enlarged) raised the mean weight for 7 months old animals to 25.7 gm. The females, at and above the age of 10 months started again to gain some weight. They reached an average weight of 24.72 gm when they were one year old, 24.45 gm at 14 months and 26.75 gm when they were 17 months old.

The increase of body weight in the males was faster than in the females. To make it easier to understand, the growth in the body weight of the males was divided into four stages.

The first stage ended at the age of 35 days with an average weight of 20 gm. The second stage ended at age 165 days. All the mean weight in this stage ranged between 22 to 26 gm with one exception at age 90 days. The third stage included voles up to 330 days old. Their mean weight ranged from 28 to 31 gm. The heaviest male voles were found at the age of one year onward. All the male voles of this fourth stage weighed more than 30 gm.

In spite of the body weight increase being regular and highly correlated with age (r=0.75 in females and 0.74 in males, 5 days to 18 months old), a high variability could still be found within each age-group sample.

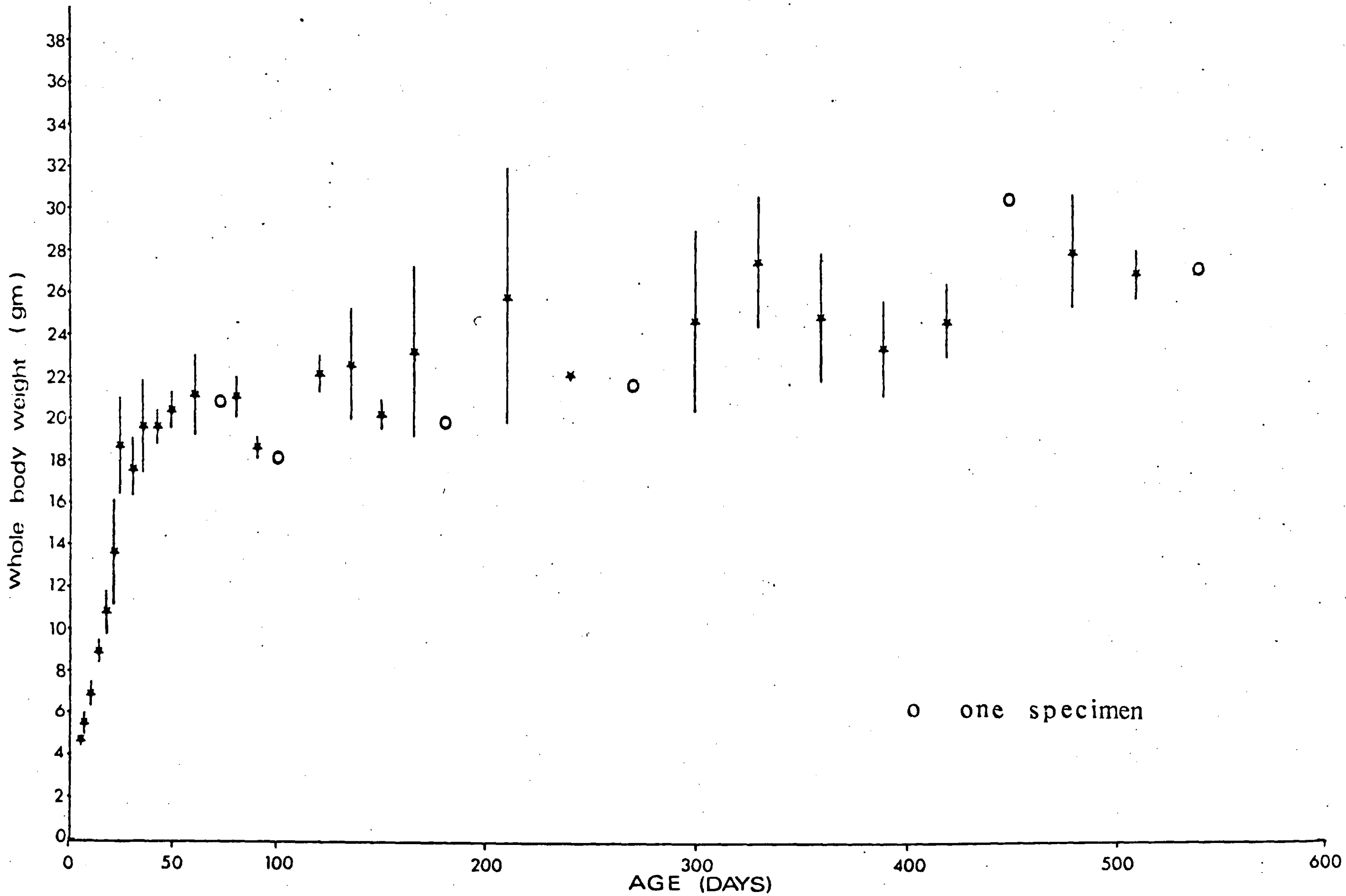


Fig. 5. Growth curve for the female Skomer vole. (see Fig. 4 for explanation).

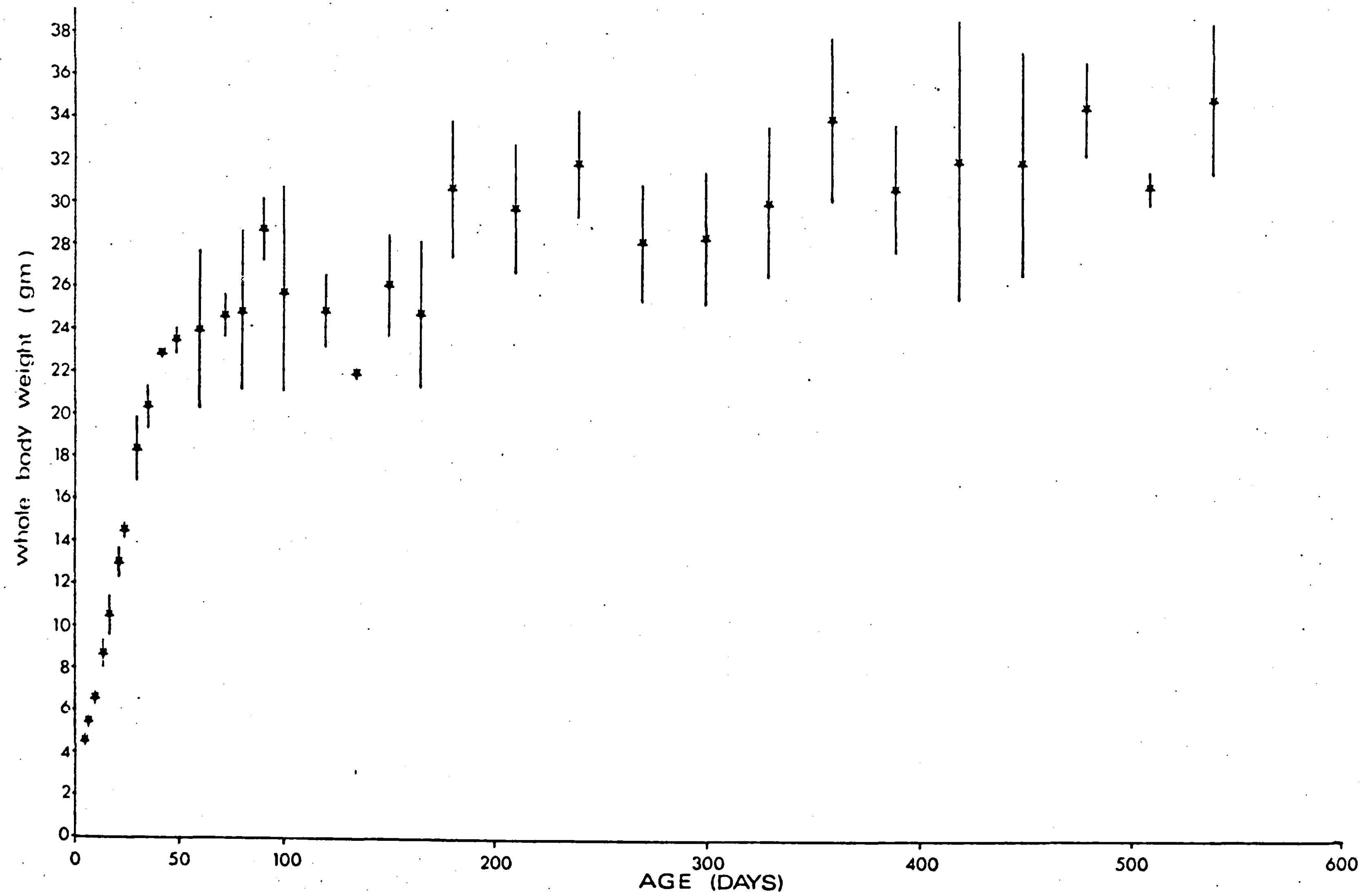


Fig. 6. Growth curve for the male Skomer vole . (see Fig. 4 for explanation).

b.2. Estimating the age from the body weight:

The whole sample was divided into two main groups according to the body weight. The first main group included all the voles up to 17.9 gm weight. Data for the sexes were combined as no sex variation in weight were found. This group was divided into 8 groups (Table 3, groups 1 to 8), according to the body weight of the voles.

The second main group included all the voles above the weight of 18 gm. Males and females were separated as differences between the sexes started to appear at this weight. Females belonging to this main group were divided into 5 groups and the males into 6 groups, all according to their body weight. Data were treated as before (Table 3).

Variability in the dispersion of the males and females according to their body weight was not high within the first main group (groups 1 to 8), ($\bar{v}$=7.88). The highest variable weight value (v being 13.09) was 16 to 17.9 gm, corresponding to an average age of 29.8 days with an accuracy of $\pm$4.8 days (group 8).

Variability was higher in the second main group (groups 9 to 14), ($\bar{v}$=48.95). Moreover, body weight was more variable in females than in males. This is probably due to the females being smaller in size, and therefore growing more slowly, so that overlap of the data can be expected. There were only two females (10 & 15 months old) out of the whole sample, which weighed more than 30 gm (30.3 gm), while 12 males were found to exceed this weight, extending in age from 180 to 540 days.

The most variable weight value which gave the lowest accuracy for estimating the age of female Skomer voles

Table 3. Numerical data for estimating the age of male and female Skomer vole from the body weight:

G. No	Body W/ gm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	4- 4.9	9	5- 7	5.2± 0.22	0.67	12.88	4.7- 5.7
2	5- 5.9	8	5- 7	6.8± 0.25	0.71	10.52	6.2- 7.3
3	6- 7.9	8	10 days	10.0± -	-	-	10 days
4	8- 9.9	9	14- 17	14.7± 0.44	1.32	9.00	13.7- 15.7
5	10-11.9	6	17 days	17.0± -	-	-	17 days
6	12-13.9	4	17- 21	20.0± 1.00	2.00	10.00	16.8- 23.2
7	14-15.9	3	21- 24	23.0± 1.00	1.73	7.52	18.7- 27.0
8	16-17.9	5	24- 35	29.8± 1.74	3.90	13.09	25.0- 34.6
				Female			
9	18-18.9	6	30-100	66.7±12.82	31.41	47.11	33.7- 99.6
10	19-20.9	14	35-180	92.5±14.15	52.93	57.22	61.9-123.1
11	21-22.9	17	35-390	192.3±27.88	114.96	59.78	133.2-251.4
12	23-24.9	7	60-420	257.1±54.62	144.51	56.20	123.3-391.0
13	25-30.3	12	165-540	406.3±32.06	111.05	27.34	335.7-476.8
				Male			
9b	18-19.9	5	30- 60	37.0± 5.83	13.00	35.14	20.8- 53.2
10b	20-20.9	4	35-100	68.0±13.90	27.80	40.88	23.8-112.2
11b	21-23.9	13	35-165	88.8±13.03	46.97	52.91	60.4-117.2
12b	25-27.9	19	60-450	194.0±28.57	124.55	64.20	134.0-254.0
13b	28-29.9	11	80-510	221.8±44.12	146.34	65.97	123.4-320.2
14b	30-37.9	22	180-540	379.1±25.63	120.19	31.70	325.8-432.4

was 23 to 24.9 gm (group 12). It had a mean age of 257.1 days and its accuracy was ±133.9 days under the probability of 0.05. This low accuracy was mainly due to the small sample size, as the coefficient of variation for this group was as high as for groups 10, 11, and 13.

The most variable value in the body weight of the males was 28 to 29.9 gm. Because of this variability males having this weight would have a minimum age of 123.4 days, a maximum age of 320.2 days, and a mean age of 221.8 days. Variability was also high in male voles weighing 21 to 29.9 gm (groups 11b, 12b, and 13b).

The variability in body weight of voles older than one year was low (v being 27.34 for the females -group 13-, and 31.7 for the males -group 14-).

Accuracy for estimating the age of voles weighing more than 18 gm, and less than, 25 gm in females and 30 gm in males, was low. This result rendered the body weight useless as an age criterion in voles locating within this weight range.

c. <u>Eviscerated weight:</u>

Data for the eviscerated weight of the mainland bank vole and the Skomer vole were plotted against the data for the whole body weight. The correlation between the two values was very high (r=0.997 for the mainland bank vole, and 0.93 for the Skomer vole). Therefore, using either of them as an age criterion would give the same result.

C. Discussion:

Using the body weight as a means for age determination has been discussed by many authors working on different species of mammals. Most of these studies were on wild populations. Most authors say the body weight is no good as an age criterion, for different reasons. In the muskrat (Ondatra zibethicus), for instance, the body weight is indicative of age, but the high level of individual variation severely reduces its value for accurate age determination (Alexander, 1951, and Schofield, 1955). Variations occur according to season, for example in the body weight of Apodemus flavicollis and A. agrarius (Adamczewska-; 1961, and Adamczewska-Andrzejewska, 1973 respectively), and in Lepus timidus (Flux, 1970).

Some other authors recommended the use of body weight to determine the age of several species of mammals. Lueth (1963), for instance, used the body weight to determine the age of different species of deer in Alabama, in preference to using the eye lens weights, for both gave equally useful results.

The body weight of laboratory-raised small mammals has also been discussed but not recommended as an age criterion by several investigators. Chipman (1965), for instance, recorded that the body weight of the cotton rat (Sigmodon hispidus) was the factor least related to age and the most variable measurement. Lidicker &MacLean (1969) used a variety of criteria in their formulae for estimating the age of laboratory-raised California voles (Microtus californicus), but, avoided the body weight.

The growth and body weight of the bank vole have been discussed by many authors. Most of their studies dealt with field populations, e.g. Wasilewski (1952); Koshkina (1955); Kubik (1965); Haitlinger (1965); and Zejda (1961, 1964, 1966, & 1971). All agreed on the presence of individual, seasonal, and sexual variations. Moreover, Zejda (1971) rejected the idea of using the body weight as an age criterion. He showed a closer correlation between growth and sexual activity than between growth and age.

The body weight and growth of wild populations of British bank voles have also been discussed by many authors, e.g. Brambell & Rowlands (1936); Steven (1957); Delany & Bishop (1960); Fullagar et al (1963); Southern (1964); Jewell (1965 & 1966); and Tanton (1969). Most of them gave discriptive data and also average weights of young and adult specimens, while others, such as Southern (loc.cit), considered the weight as a factor subject to seasonal variations. Voles caught in summer were said to be heavier than those trapped in winter.

The results obtained in the present study, for body weight, can be used to determine the age of bank voles with an accuracy which differs according to the weight of the animal (Tables 2 & 3). Accuracy is high if the vole's weight is less than 14 gm in the mainland bank vole and less than 18 gm in the Skomer vole, representing a maximum age of 60 days for the former and 35 days for the latter. Once voles reached a weight of 14 and 18 gm respectively, variability started to increase and accuracy for estimating their age diminished. The accuracy for the mainland bank vole was ± 37.9 days at the weight 18 to 19.9 gm; ± 36.5 days at the weight 20 to 23.9 gm; and ± 50.5 days at the weight 24 gm and more. In Skomer voles, accuracy was ± 33 days for females and ± 16.2 days for males at the weight 18 to 19.9 gm. It reached ± 133.9 days in females weighing 23 to 24.9 gm. The less accurate results for the Skomer vole were most likely due to the small sample size, especially, after the females were treated separately from males, since, in general the growth of the Skomer vole was found to be more regular than the mainland bank vole.

Environmental factors, including seasons, have been excluded under laboratory conditions. Food was the only external factor which affected body weight. But in spite of controlling the environmental conditions, i.e. food and temperature, through the whole year, the variations between individuals of the same age were still high.

Jewell (1966) in his study on the age structure of a population of the Skomer vole, divided the sample into 3 age categories namely, juveniles, immatures, and adults. His division was based on the sexual status of each individual. His results on correlating the body weight to these age categories showed that all the juveniles had a body weight range of 8 to 19 gm, though some weighed up to 24 gm. The immature voles had a weight range of 18 to 28 gm, and some weighed 24 to 43 gm (excluding pregnant females).

The laboratory-raised Skomer voles have limited, juvenile and immature stages, ended during the third month of life, the time when they became sexually mature and started to breed. This took place regardless of the date of birth. Their weight when they reached this stage ranged from 18.6 to 23 gm in females and from 19.4 to 29.6 gm in males (age 60 to 90). This weight is similar to the weight of field immature voles recorded by Jewell (loc.cit.).

It seems that since the seasonal factors were excluded under the laboratory conditions, voles breed soon after reaching sexual maturity at a definite age with no environmental stress. While field voles, in contrast, are always at the mercy of environmental conditions, and even if they reach the age of sexual maturity they may not breed because of the external environmental conditions. Therefore, the immature voles in Jewell's sample are the new sexually mature voles in my sample. Both of them have similar body weight. They have not started breeding, mainly because that they have not reached the age of maturity.

The body weight of the juveniles was similar in both samples and therefore results of the present study can be applied on wild voles having the juvenile weights.

The adult voles in Jewell's sample (the sexually mature) included all voles above a body weight of 28 gm, though some of them weighed down to 23 gm. The values overlapped with those of the immature voles, which in turn reflect the variability of the body weight as an age criterion.

The results of comparing the two samples showed that the body weight is a useful age criterion in juvenile voles. Variability was high in the body weight of voles above that stage.

II. 2. General body measurements

A. Introduction:

Generally speaking, body size in animals is directly correlated with age, but often only up to adulthood.

In mammals, certain linear measurements are usually taken in order to study the increase in their size. These are: head-body length (HB); tail length (T); ear pinna length (E); and hind foot length (HF).

These classical measurements have mainly been used for taxonomic purposes. They were also used for the ageing of different species of mammals, (e.g. the cotton rat (*Sigmodon hispidus*), Chipman, 1965; the California vole (*Microtus californicus*), Lidicker & McLean, 1969; and the striped field-mouse (*Apodemus agrarius*), Adamczewska-Andrzejewska, 1973 b.

I investigate the validity of this method for determining age in *Clethrionomys*.

B. Methods:

Jewell & Fullagar (1966) reviewed the different methods which are used for taking the standard measurements of small rodents.

The method which was used in the present study was partly similar to that of the British Museum (Natural History) mentioned by the above authors. The measurements were taken immediatly after the voles had been killed. In order to measure the length of the head & body, the vole was laid prone on a ruler which was accurate to 1mm. The base of the tail was held with a pair of forceps to detect the end of the body. Fingers of the other hand were placed over the head pressing it gently in order to hold the animal firmly in position. In this way the body was straightened out without being streched. The length was taken from the tip of the snout until the base of the tail (Fig.7).

The tail length was taken from its base to its free end, excluding the free tip hairs.

The ear pinna length was taken from the base of its notch to the highest point of its free edge.

The hind foot length was the distance between the calcaneum and the end of the longest toe, excluding the claw.

C. Results:

a. The mainland bank vole:

Results on the growth of the head and body, tail, ear pinna, and hind foot of the mainland bank vole were analysed. Data for the two sexes were combined, because no significant differences were found, (HB: $t_{64}=0.41$, $P > 0.6$; T: $t_{64}=0.35$, $P > 0.7$; E: $t_{64}=0.25$, $P > 0.7$; HF: $t_{64}=0.89$, $P > 0.3$).

a.1. The head-body length:

a.1.a. Growth curve of the head and body:

Data for the growth of the head and body of the mainland bank vole are presented in Fig. 8 and appendix 4.

It is obvious that the head-body length increased very quickly during the first two months of the vole's life. Its length averaged 45 mm at the age of 5 days, 61.75 mm

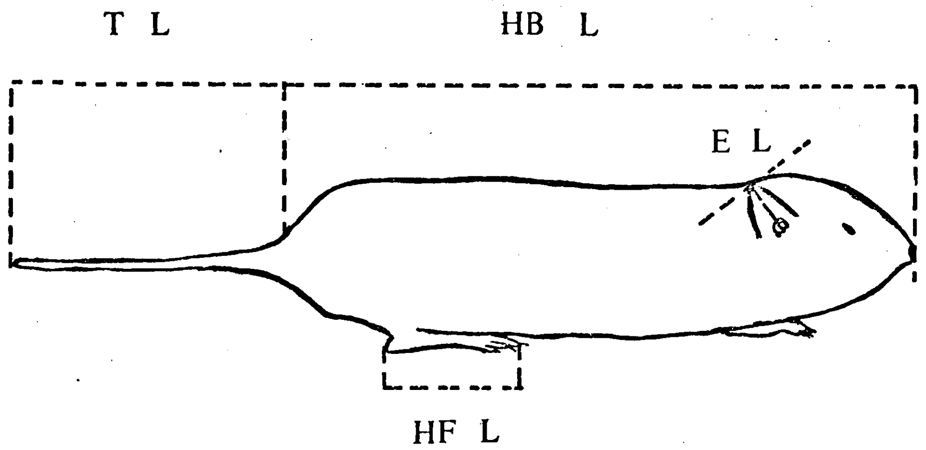


Fig. 7. A diagram for a vole showing the body measurements which were studied.

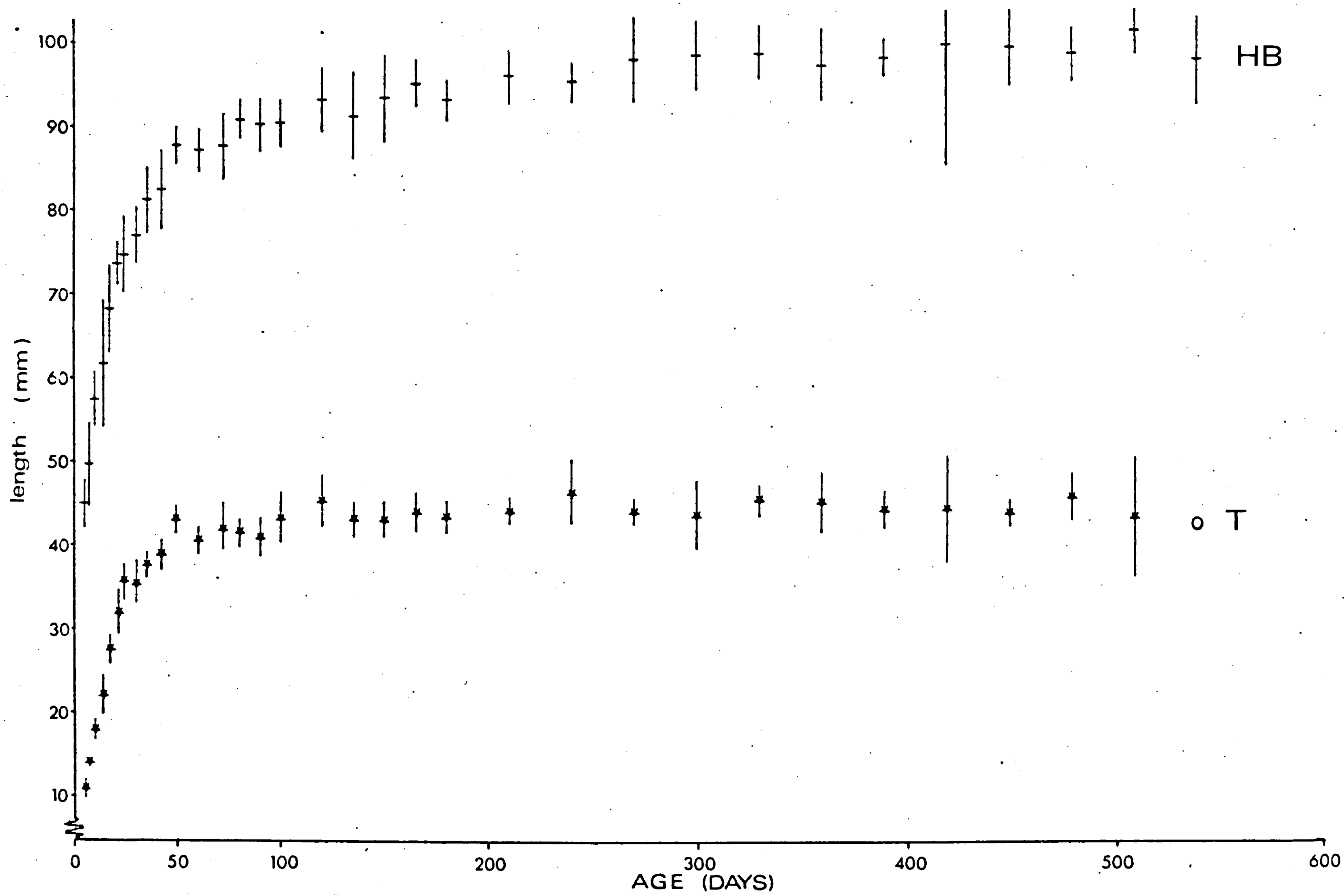


Fig. 8. Growth curves for the head-body and tail lengths of the mainland bank vole. The star and the horizontal line represent the mean, and the vertical line represent one 95% confidence limits on each side of the mean.

at two weeks, 77 mm at one month and 82.5 mm at 42 days. The correlation coefficient up to the age of 42 days was 0.91.

Above this age the growth of the head and body slowed down. Its average length was 87 mm at the age of 2 months, 90 mm at 3 months, 93 mm at an age extending from 4 to 6 months, 95 mm at 7 to 8 months, and above 97 mm at the age of 9 months onward.

The correlation coefficient for the whole sample was 0.66. The standard deviations and coefficients of variation were found not to be high (Appendix 4).

a.1.b. Estimating the age from the head-body length:

To test the accuracy of head-body length as an age indicator, and the variability of this criterion, the whole sample was arranged into 13 groups according to the length of the head and body (Table 4).

Variability within the first 8 groups and until a head-body length of 87.9 mm was reached, was not very high representing a maximum age of 110.1 days (group 8) with a probability of 0.05. Accuracy for estimating the age in voles having a head-body length of up to 87.9 mm was high, extending from ±11 day for voles with a mean age of 35.7 days (group 1), to ± 18 days for voles with a mean age of 87.1 days (group 8). Variability increased in voles having a head-body length above 87.9 mm. The highest variability (v=59.05) was in voles with head-body length of 88 to 89.9 mm (group 9). The accuracy for estimating their age was ± 30.6 days. Because of this variability, voles with this head-body length would have a maximum age of 124.3 days,

Table 4. Numerical data for estimating the age of the mainland bank vole from the head-body length:

G. No	HB 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	40-49.9	6	5- 7	5.7± 0.42	1.03	18.17	4.6- 6.8
2	50-59.9	6	7- 14	9.7± 1.05	2.58	26.68	7.0- 12.4
3	60-69.9	7	10- 17	14.7± 0.97	2.56	17.40	12.3- 17.1
4	70-74.9	9	17- 30	23.6± 1.43	4.28	18.17	20.3- 26.9
5	75-79.9	12	21- 60	34.1± 3.96	13.73	40.29	25.4- 42.8
6	80-82.9	9	24- 72	41.3± 5.37	16.10	38.95	28.9- 53.7
7	83-85.9	12	35-120	59.5± 7.81	27.07	45.50	42.3- 76.7
8	86-87.9	10	60-150	87.1±10.17	32.17	36.93	64.1-110.1
9	88-89.9	15	42-210	93.7±14.29	55.35	59.05	63.2-124.3
10	90-91.9	26	49-270	111.5±11.78	60.09	53.91	87.2-135.7
11	92-95.9	39	60-420	174.7±14.97	93.49	53.52	144.4-204.9
12	96-99.9	35	120-540	303.4±20.82	123.16	40.59	261.2-345.7
13	100-109.0	27	180-540	347.8±22.20	115.37	33.17	302.1-393.5

a minimum of 63.2 days and a mean age of 93.7 days.

Variability decreased in old age voles. The accuracy was ± 45.7 days for a mean age of 347.8 days (group 13).

The average variability for the distribution of voles within each size-group was not very high ($\bar{v}$=37.1).

a.2. The tail length:

a.2.a. Growth curve of the tail:

Data for the growth of the tail are presented in Fig. 8 and Appendix 5.

There was a slight sex difference in the tail length, with the males' tail being longer, between the ages 21 to 120 days. This difference was statistically not significant, and the data for the sexes were combined.

The growth of the tail occurred mainly during the first six weeks of the vole's life. The tail increased by 28 mm during a period extending from 5 days up to 42 days, (r=0.92). Since then and up to the age of 150 days, no more than 4 mm were added to the tail length. The maximum average tail length occurred at the age of 240 days. All the tail measurements, starting from the age of 49 days, have got more or less the same means, with a range of 40.5 to 45.7 mm.

The correlation coefficient for the whole sample was 0.56.

a.2.b. Estimating the age from the tail length:

To find out how valuable the tail length is as an age indicator, the whole sample was arranged into 13 groups according to the tail length of the voles (Table 5).

Variability within the first 7 groups was not very high representing a maximum mean age of 30.3 days, a maximum age of 40.3 days, and a maximum tail length of 35.9 mm (group 7). The accuracy for estimating the age of voles with a tail length of less than 35.9 mm is high, extending from ± 0.5 day for a mean age of 5.2 days (group 1), to ± 10 days for a mean age of 30.3 days (group 7).

Variability was very high in the distribution of voles with a tail length of more than 36 mm. The most variable size group (v being 107.79) was 39 to 40.9 mm (group 9) representing a mean age of 132.5 days, an observed age range of 30 to 540 days and an estimated age of 69.1 to 195.8 days. Data for the estimated age in groups 9 to 13 overlapped. The high variability, along with the overlap of the data indicate that it is of no value to use tail length as an age indicator above the age of 6 weeks, and above a tail length of 36 mm.

a.3. The ear pinna length:

a.3.a. Growth curve of the ear pinna:

Data on the growth of the ear pinna are presented in Fig. 9 and Appendix 6.

The growth of the ear pinna of the mainland bank vole was found to be very fast while the vole was still in the nest. It slowed down afterwards but continued to grow until old age.

The correlation coefficient for the whole sample was 0.57. It was 0.85 in voles 42 days and younger.

a.3.b. Estimating the age from the ear pinna length:

The whole sample was divided into 13 ear-size groups and the data treated as before (Table 6).

Variability in the distribution of the voles within the first 7 groups was not high. The 95% confidence limits were not attached to the mean age of groups 4 and 6 because the sample size was very small. Data on the estimated age for the first seven groups were not overlapped and therefore, accuracy for estimating the age of voles locating within these groups, i.e. having an ear pinna length of up to 10.9 mm, was high. The accuracy for estimating their age extended from ± 0.0 (groups 2 & 3) to ± 7.7 days (group 7) with a maximum age of 40 days.

Variability in the distribution of voles with ear pinna length of 11 to 13 mm, was high (groups 8 to 11), and accuracy for estimating their age was less than the first 7 groups. The lowest being ± 72.4 days for a mean age of 255.6 days (group 11).

Table 5. Numerical data for estimating the age of the mainland bank vole from the tail length:

G. No	T 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	10-13.9	9	5- 7	5.2± 0.22	0.67	12.84	4.7- 5.7
2	14-15.9	10	7- 10	7.6± 0.40	1.26	16.58	6.7- 8.5
3	16-20.9	16	10- 14	10.8± 0.40	1.61	14.98	9.9- 11.6
4	21-25.9	10	10- 17	14.4± 0.86	2.72	18.89	12.5- 16.3
5	26-30.9	11	14- 21	17.8± 0.67	2.23	12.51	16.3- 19.3
6	31-32.9	5	17- 30	23.0± 2.95	6.60	28.70	14.8- 31.2
7	33-35.9	9	21- 60	30.3± 4.34	13.03	42.96	20.3- 40.3
8	36-38.9	31	21-240	55.7± 7.59	42.28	75.89	40.2- 71.2
9	39-40.9	22	30-540	132.5±30.44	142.77	107.79	69.1-195.8
10	41-42.9	44	35-420	142.4±14.98	99.35	69.79	112.1-172.6
11	43-43.9	24	49-450	185.7±25.57	125.29	67.47	132.8-238.6
12	44-44.9	19	60-480	197.4±30.73	133.95	67.87	132.8-261.9
13	45-54.0	60	49-540	251.2±17.54	135.89	54.11	216.1-286.2

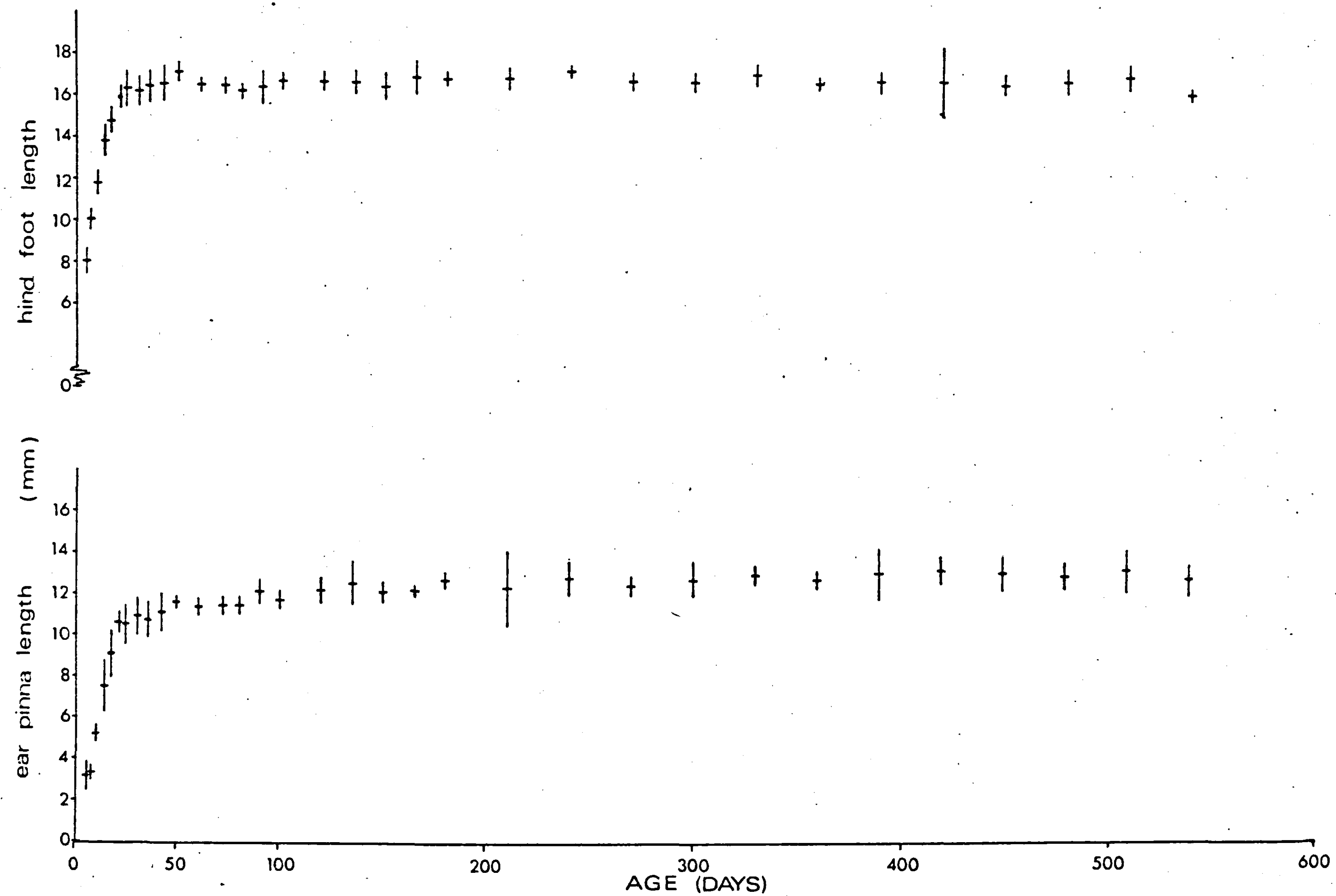


Fig. 9.Growth curves for the ear pinna and hind foot lengths of the mainland bank vole. The horizontal line represents the mean, and the vertical line represents one 95% confidence limits on each side of the mean.

Table 6. Numerical data for estimating the age of the mainland bank vole from the ear pinna length:

G. No	EP 1/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	3- 3.9	10	5- 7	6.2± 0.33	1.03	16.61	5.5- 7.0
2	4- 4.9	1	10 days	10.0± -	-	-	10.0 days
3	5- 5.9	6	10 days	10.0± -	-	-	10.0 days
4	6- 6.9	2	10- 14	12.0± 2.00	2.83	23.58	*
5	7- 8.9	6	14- 17	15.5± 0.67	1.64	10.58	13.8- 17.2
6	9- 9.9	3	17- 30	23.7± 3.76	6.51	27.50	*
7	10-10.9	15	17- 60	32.3± 3.57	13.82	42.75	24.7- 40.0
8	11-11.4	35	21-270	68.7± 8.48	50.18	73.08	51.5- 85.9
9	11.5-11.9	16	30-240	86.7±15.52	62.09	71.62	53.6-119.8
10	12-12.4	55	30-480	150.5±13.29	98.54	65.48	123.8-177.2
11	12.5-12.9	18	60-540	255.6±34.28	145.42	56.90	183.2-327.9
12	13-13.4	36	90-540	323.3±20.77	124.65	38.55	281.2-365.5
13	13.5-14.0	10	135-510	331.5±38.11	120.51	36.35	245.4-417.6

* The 95% confidence limits were not attached to the mean age because the sample size was small.

Variability started to decrease again in voles with ear pinna length of more than 13 mm (groups 12 & 13) and therefore, accuracy for estimating their age was higher, being ± 42.2 days for a mean age of 323.3 days (group 12), and ± 86.1 days for a mean age of 331.5 days (group 13).

The results show that ear pinna length is a reliable indicator of age throughout life, but voles can only be assigned to wide range age groups because ear pinna growth is very slow.

a.4. The hind foot length:

a.4.a. Growth curve of the hind foot:

Data for the growth of the hind foot are presented in Fig. 9 and Appendix 7.

It was found that the growth of the hind foot was completed when the voles were one month old. The correlation coefficient until the age of 30 days was 0.82. Above this age, no correlation was found between the age and the hind foot length, (r being 0.04). The correlation coefficient for the whole sample was 0.43.

a.4.b. Estimating the age from the hind foot length:

It was rather difficult to arrange the voles into groups according to their hind feet length as the latter ceased to grow after the first month of life. The high variability started to appear at a hind foot length of 15 to 15.9 mm (Table 7), and continued to increase onward

Table 7. Numerical data for estimating the age of the mainland bank vole from the hind foot length:

G. No	HF 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	7- 8.9	6	5 days	5.0± -	-	-	5 days
2	9-10.9	8	5- 7	6.8± 0.25	0.71	10.52	6.2- 7.3
3	11-12.9	13	7- 10	9.8± 0.23	0.83	8.50	9.3- 10.3
4	13-14.9	15	10- 17	13.9± 0.72	2.79	20.03	12.4- 15.5
5	15-15.9	19	14- 90	31.0± 5.09	22.20	71.73	20.4- 41.6
6	16-16.4	49	24-540	170.7±21.75	152.24	89.17	127.5-214.5
7	16.5-18.0	126	17-510	186.1±12.46	139.80	75.14	161.6-210.5

(groups 5, 6, & 7). These size-groups represented a very wide range of age extending from 14 days to 540 days. It included 82.2% of the whole sample (194 voles out of 236). The high variability and the overlap of the data indicate that using the hind foot length as an age indicator, above the age of 3 weeks, is of no value.

b. The Skomer vole:

Results on the growth of the head & body, tail, ear pinna, and hind foot of the Skomer vole were analysed. Data for the sexes were combined, because no significant differences were found, (HB: $t_{64}=0.53$, $P \geq 0.6$; T: $t_{64}=0.22$, $P > 0.8$; E: $t_{64}=0.04$, $P > 0.9$; HF: $t_{64}=0.13$, $P > 0.8$).

b.1. The head-body length:

b.1.a. Growth curve of the head & body:

Data for the growth of the head and body of the Skomer vole are presented in Fig. 10 and Appendix 8.

The value for males was slightly greater than that for females between the ages 72 days and 9 months. It was not noticeable beyond the age of 9 months and not existing throughout the first two months of the vole's life, i.e. before sexual maturity.

Skomer voles grew very fast in length in the first two months of their life. An increase of 20 mm was added during a period extending between the ages 5 to 17 days (an increase in average length of 48.5 mm to 68.88 mm), another increase of 14 mm was recorded up to the age of 30 days, (average length was 82.44 mm), and 12 mm up to the age of 2 months, (94.23 mm). The growth slowed down afterwards, and no more than another 4 mm were added up to the age of 5 months (98.4 mm), and a further 7 mm, up to the age of 13 months (105.4 mm). The head and body, above the age of 15 months, ceased to grow. The highest average length reached by the voles was 110.25 mm, at the age of 15 months.

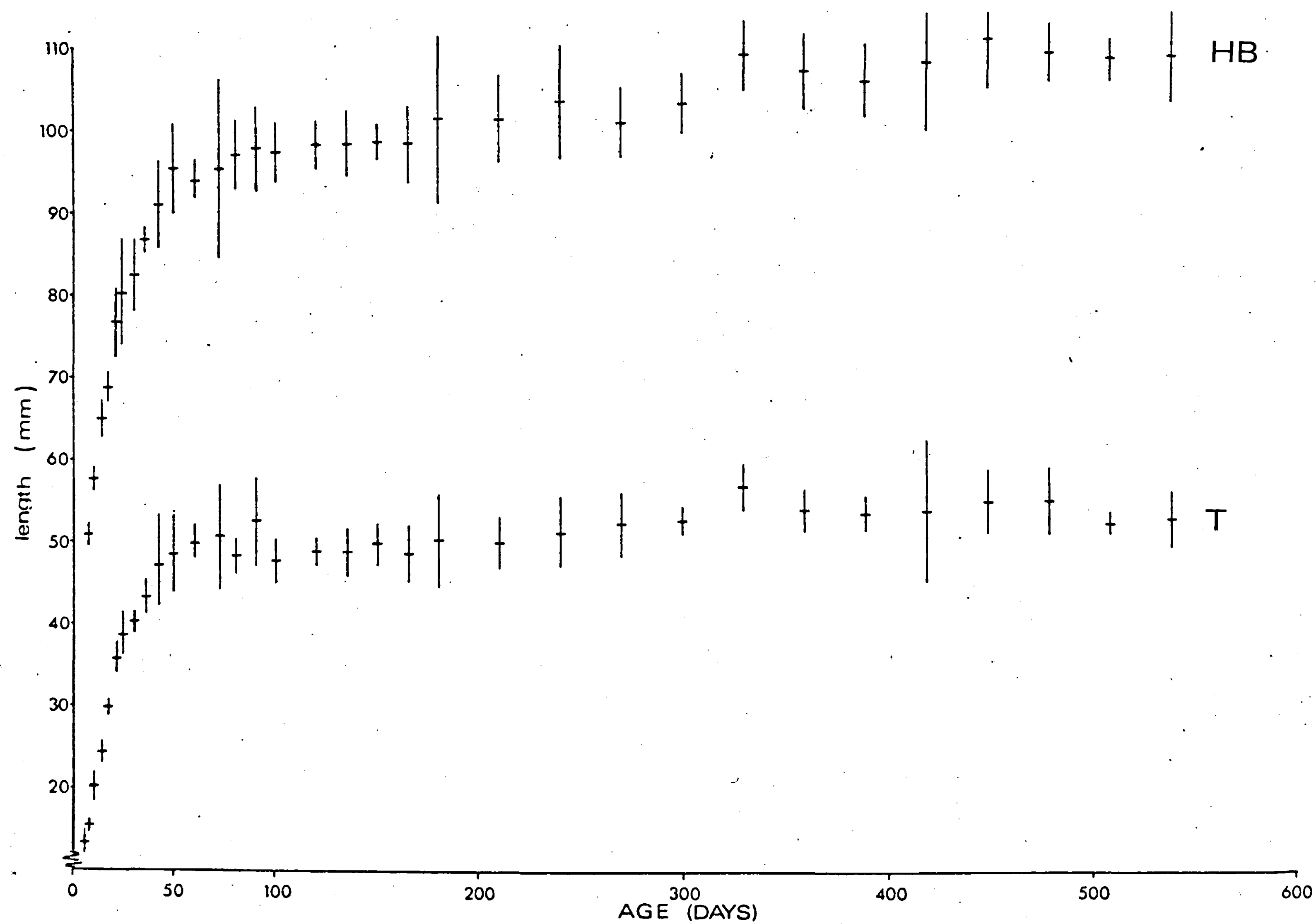


Fig. 10. Growth curves for the head-body and tail lengths of the Skomer vole. (see Fig. 9 for explanation).

The correlation coefficient for the whole sample was 0.71. It was 0.95 for voles 42 days and younger.

b.1.b. Estimating the age from the head-body length:

The whole sample was arranged into 14 size-groups (Table 8). The values for the sexes were combined in the first eight groups as no differences were found between them. These groups included all the young voles and most of the immatures. Their average age ranged between 5.7 to 38.5 days, and their head-body length, ranged between 45 to 89.9 mm.

The values of the two sexes were arranged separately in the last six groups (9 to 14), as slight differences were found between them. These groups included all the adult voles and very few of the immatures. Their average age ranged from 95.5 to 442.5 days for the females, and from 68.4 to 390 days for the males. Their head-body length ranged from 90 to 115 mm. More than half of the females (60.78%) in these groups fell into the first three groups (9 to 11), (31 females out of 51 individuals), while 68.57% of the males were in the last three groups (12 to 14), (48 males out of 70 voles). This is due to the males being bigger than the females, and therefore resulting in females always being older than males within each size-group.

Accuracy for estimating the age in the first 8 groups was high, extending from ± 0.0 (groups 2, 3, & 4) to ± 10 days (group 7), and representing a mean age of up to 38.5 days, a maximum age of 45.6 days, and a head-body length of up to 89.9 mm.

The accuracy was lower in voles with a head-body

Table 8. Numerical data for estimating the age of male and female Skomer vole from the head-body length:

G. No	HB 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	45- 50.9	3	5- 7	5.7± 0.66	1.15	20.37	2.8- 8.5
2	51- 55.9	3	7 days	7.0± -	-	-	7.0 days
3	56- 59.9	3	10 days	10.0± -	-	-	10.0 days
4	60- 65.9	3	14 days	14.0± -	-	-	14.0 days
5	66- 70.9	5	14- 17	16.4± 0.60	1.34	8.18	14.7- 18.1
6	71- 79.9	7	21- 30	24.0± 1.60	4.24	17.68	20.1- 27.9
7	80- 85.9	8	24- 60	32.1± 4.22	11.93	37.14	22.1- 42.1
8	86- 89.9	14	30- 72	38.5± 3.29	12.31	31.99	31.4- 45.6
9	90- 94.9	F 9	42-210	95.6±20.07	60.20	62.99	49.2-141.9
		M 5	42-100	68.4± 9.91	22.20	32.45	40.9- 96.0
10	95- 98.9	F 19	60-300	135.9±16.62	72.46	53.32	101.0-170.8
		M 13	42-165	89.4±11.60	41.87	46.84	64.1-114.7
11	99- 99.9	F 3	100-210	143.3±33.87	58.59	40.88	*
		M 2	60-165	112.5±52.66	74.25	66.00	*
12	100-104.9	F 11	135-420	302.7±28.20	93.63	30.93	239.8-365.6
		M 18	72-300	161.5±18.86	79.97	49.52	121.7-201.3
13	105-109.9	F 7	300-540	420.0±35.20	93.27	22.21	333.8-506.2
		M 17	180-540	363.5±31.09	128.11	35.24	297.6-429.5
14	110-115.0	F 4	330-510	442.5±39.42	78.90	17.83	317.1-567.9
		M 13	180-540	390.0±27.77	100.25	25.71	329.5-450.5

F : Female
M : Male
* : The 95% confidence limits were not attached to the mean age because the sample size was small.

length of more than 90 mm (groups 9 to 14). Moreover, it was lower in the females than in the males. This is probably due to most of the females having a limited growth above the length of 90 mm. Only 30% of them, within the groups 9 to 14, had a length greater than 100 mm, while the growth of males was uniform throughout life.

The lowest accuracy, being ± 125.4 days (group 14), was in females with a mean age of 442.5 days. This low accuracy was mainly due to the small sample size (only 4 females), as the variability for this group was low (v being 17.83). The accuracy for estimating the age of males of the same group was ± 60.5 days, corresponding to a mean age of 390 days, a maximum age of 450.5 days, and a minimum age of 329.5 days.

b.2. The tail length:

b.2.a. Growth curve of the tail:

Data for the growth of the tail of the Skomer vole are presented in Fig. 10 and Appendix 9.

The tail in the Skomer vole grew very quickly and reached the adult length at the age of 60 to 90 days. Further growth was not detectable beyond that age, and the overlap of the values was apparant. The variability and standard deviation within each age-group sample was not high. The correlation coefficient for the whole sample was 0.60. It was 0.96 up to the age of 42 days.

b.2.b. Estimating the age from the tail length:

The whole sample was divided into 14 tail-length categories (Table 9).

Variability in the distribution of the material was not high up to a tail length of 40.9 mm (groups 1 to 7), corresponding to a maximum mean age of 28.5 days, a minimum estimated age of 33.3 days. The lowest accuracy for estimating the age of voles with a tail length of less than 41 mm was ± 4.8 days (group 7).

The variability increased in the distribution of voles with a tail length of more than 41 mm (groups 8 to 14). The highest variability (v=74.22, group 12) was in voles with a tail length of 50 to 51.9 mm. Their mean age was 236.6 days and the accuracy for estimating their age was ± 66.8 days.

Adult voles have a fully grown tail of length varying between 44 and 61 mm, and this variability of adult tail length rules out its use beyond 40 days, as an age criterion.

Table 9. Numerical data for estimating the age of the Skomer vole from the tail length:

G. No	T 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c. l.
1	13-14.9	4	5 days	5.0± -	-	-	5.0 days
2	15-16.9	6	7- 10	7.5± 0.50	1.22	16.33	6.2- 8.8
	17-19.9*						
3	20-22.9	7	10 days	10.0± -	-	-	10 days
4	23-26.9	7	14 days	14.0± -	-	-	14 days
	27-27.9*						
5	28-31.9	8	17 days	17.0± -	-	-	17 days
	32-33.9*						
6	34-38.9	11	21- 30	23.2± 1.08	3.57	15.41	20.8- 25.6
7	39-40.9	4	24- 30	28.5± 1.50	3.00	10.53	23.7- 33.3
8	41-43.9	12	24-100	37.4± 5.75	20.00	53.45	24.8- 50.1
9	44-45.9	6	35-180	85.5±24.04	58.89	68.87	23.7-147.3
10	46-47.9	17	35-240	107.9±15.74	64.84	60.11	74.5-141.3
11	48-49.9	25	49-420	144.3±18.05	90.25	62.54	107.1-181.5
12	50-51.9	29	60-540	236.6±32.58	175.62	74.22	169.8-303.4
13	52-53.9	21	42-510	268.5±32.74	149.97	55.86	200.1-336.9
14	54-61.0	29	60-540	329.4±24.42	137.00	41.59	279.3-379.4

* Voles with this measurement were not available in the sample.

b.3. The ear pinna length:

b.3.a. Growth curve of the ear pinna:

Data for the growth of the ear pinna are presented in Fig. 11 and Appendix 10.

The ear pinna grew very quickly while the voles were still in the nest. They reached the adult length when the vole was 2 to 3 months old. The growth rate slowed down, through time, but it never ceased.

The correlation coefficient for the whole sample was 0.52. It was 0.90 in voles 5 to 42 days old.

b.3.b. Estimating the age from the ear pinna length:

The whole sample was divided into 10 ear-length groups (Table 10). The first 6 of them included all young voles under 30 days old (except for one vole, 42 days old) with ear pinna length of up to 10.9 mm and a maximum mean age of 25.2 days. The accuracy for estimating their age was high, extending from ± 0.0 (groups 1, 3, & 4) to ± 5.8 days for a mean age of 20.7 days (group 5).

Variability in the distribution of voles with ear pinna length of more than 11 mm, was high. Only two ear-length groups were identified above an ear pinna length of 12 mm and above a mean age of 60.8 days. The first group (9) with an ear pinna length of 12 to 12.5 mm, had a mean age of 143.2 days, and a standard deviation of 93.1 days. The second group (10) had an ear pinna length of 12.6 to 13.8 mm, a mean age of 341.3 days and a standard deviation of 142.7 days. The accuracy for estimating the age of voles belonging to these two groups was, ± 23.5 and ± 39.2 days respectively.

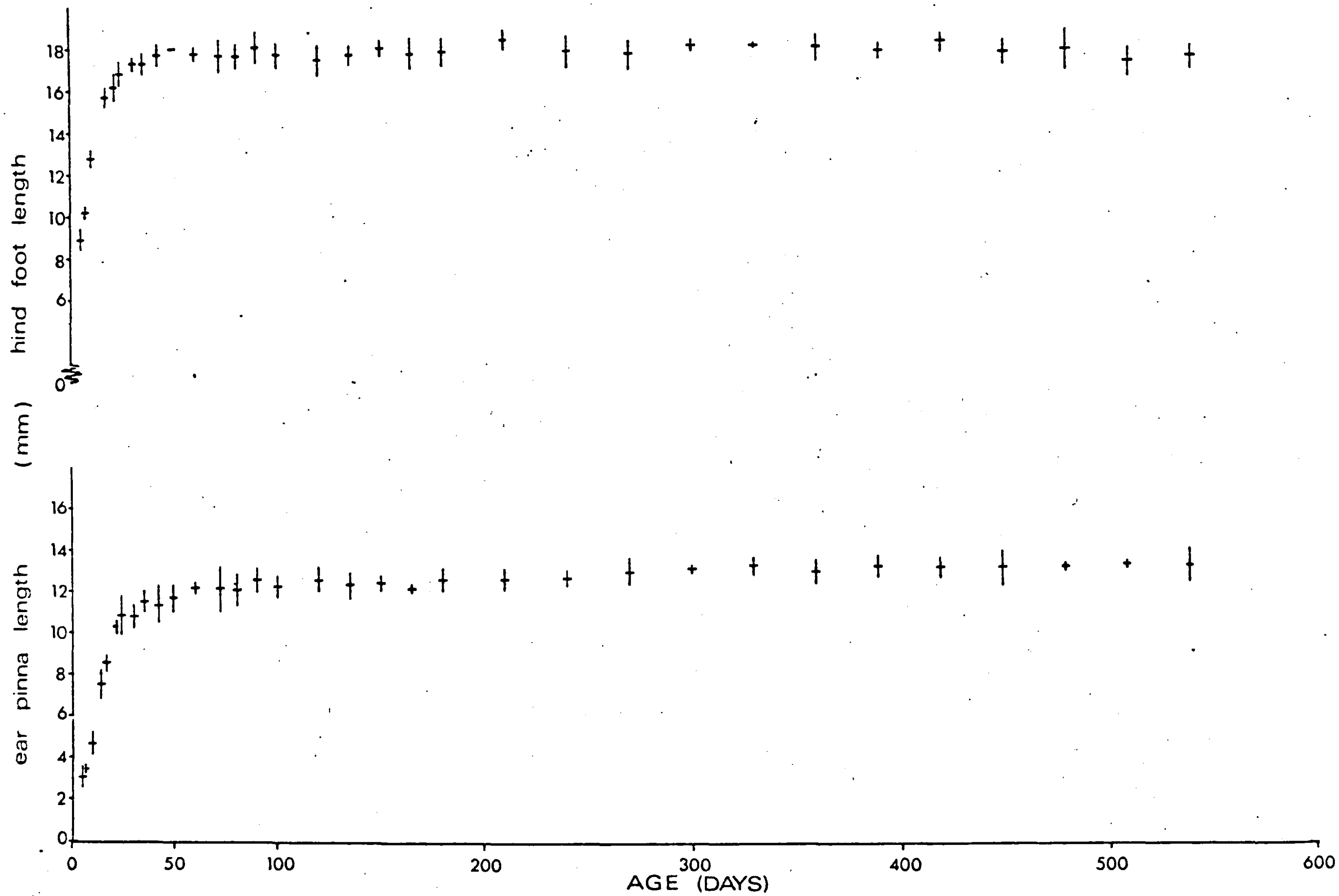


Fig. 11. Growth curves for the ear pinna and hind foot lengths of the Skomer vole. (see Fig. 9 for explanation).

Table 10. Numerical data for estimating the age of the Skomer vole from the ear pinna length:

G. No	EP 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	v.	Estimated age range/95%c.l.
1	2.5-3.0	4	5 days	5.0± -	-	-	5.0 days
2	3.1-3.9	6	5-10	7.2± 0.65	1.60	22.34	5.5- 8.8
3	4-5.9	8	10 days	10.0± -	-	-	10.0 days
4	6-8.0	7	14 days	14.0± -	-	-	14.0 days
5	8.1-9.9	7	17-30	20.7± 2.39	6.34	30.63	14.9- 26.6
6	10-10.9	10	21-42	25.2± 2.20	6.96	27.61	20.2- 30.2
7	11-11.4	15	21-100	39.5± 5.62	21.76	55.13	27.0- 51.1
8	11.5-11.9	8	30-135	60.8±12.68	35.89	59.07	30.7- 90.8
9	12-12.5	63	30-450	143.2±11.73	93.10	65.00	119.8-166.7
10	12.6-13.8	53	60-540	341.3±19.60	142.66	41.81	302.1-380.5

Although not many groups could be identified from the length of ear pinna because of its very slow growth in later life, the few groups which were identified are distinct, and data for estimating the age did not overlap and can be used for ageing the Skomer vole.

b.4. The hind foot length:

b.4.a. Growth curve of the hind foot:

Data for the growth of the hind foot are presented in Fig. 11 and Appendix 11.

The hind foot in the Skomer vole, as in the mainland bank vole, grew very quickly and attained the adult length at the age of one month. The correlation coefficient for the whole sample was 0.42. It was 0.90 up to the age of 30 days, and -0.15 over the age of 42 days.

b.4.b. Estimating the age from the hind foot length:

The whole sample was divided into 8 hind foot-length groups. Data were treated as before and presented in table 11.

As in the mainland bank vole, the high variability in the distribution of Skomer voles according to their hind foot length rendered using the latter as an age indicator of no value above the age of 3 weeks, and above a length of 16.5 mm.

Table 11. Numerical data for estimating the age of the Skomer vole from the hind foot length:

G. No	HF 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	8- 9.9	6	5 days	5.0± -	-	-	5.0 days
2	10-11.9	5	7 days	7.0± -	-	-	7.0 days
3	12-13.9	10	10 days	10.0± -	-	-	10.0 days
4	14-15.9	12	14- 17	15.3± 0.45	1.54	10.13	14.3- 16.2
5	16-16.5	11	17- 35	21.9± 1.76	5.84	26.65	18.0- 25.8
6	16.6-16.9	5	21-510	151.0±93.53	209.50	138.74	00.0-411.0
7	17-17.9	69	21-540	188.5±20.33	168.92	89.61	147.9-229.2
8	18-19.0	72	30-540	206.0±16.80	142.64	69.24	172.4-239.6

D. Discussion:

Of the linear measurements used as age characters, the head-body length showed the best correlation with age, in the mainland bank vole and the Skomer vole, r=0.66 & 0.71 respectively. In the mainland bank vole, the ear pinna length was next in value, r=0.57. The tail and hind foot lengths were of no value in assessing the age, r=0.56 & 0.43, respectively. They ceased to grow during the third month in the case of the tail, and above the age of 3 weeks in the hind foot.

In the Skomer vole, the tail length was next in value to the head-body length, r=0.60. Although its growth was more regular than in the mainland bank vole, as it is longer and needs longer time to attained the adult size, but it is still not useful as an age criterion above the age of 2 months as it grows very fast and reaches adult size very quickly. The ear pinna length was less correlated with age, r=0.52, but it is more useful for ageing than the tail length as it continues growing throughout life. The hind foot length is of no value in assessing the age of voles over the age of 3 weeks, r=0.42. The results for the hind foot length of the bank vole, in the present study, are in agreement with that given by Uhlig (1955) in his work on age determination of the gray squirrel (Sciurus carolinensis), in West Virginia. He concluded that the hind feet offered a good indication of age during the first three weeks only.

Body measurements of C.glareolus have been discussed by many authors, some of whom dealt with their variabilities, while others used them as taxonomic characters.

Kubik (1965) in Bialowieza (in Poland) analysed the variability in the body length of a field population of C. glareolus and their seasonal variation. He mentioned that body length is an indicator of growth in relation to age, and this growth is greater in juveniles and subadults. He added that the body length might serve as an indicator in defining the age-structure of the population.

Haitlinger (1965), in Wroclaw (in Poland), discussed the growth and seasonal variations of the head-body, and tail lengths of C. glareolus. His results were similar to those of Kubik (loc.cit.). Both of them showed that the bank voles grew much quicker in spring and summer; their growth slowed down in winter. They added that the rate of body growth was at its maximum during the second month of the vole's life. Therefore, body growth, in their opinion, is connected with age during the first two months. Afterwards it becomes a subject of seasonal variations.

The results of the present study agree with what the above authors have mentioned regarding the maximum body growth which was reached during the first two months of the vole's life.

Environmental factors have been excluded under laboratory conditions, as the bank voles were kept under a constant temperature and light regime, and uniform food throughout life. Therefore, variability in body measurements were mainly products of individual variation, and not of seasonal variations.

Zejda (1971) studied body growth in a field population of C. glareolus in Moravia (in Czechoslovakia). He linked the growth of juveniles and subadults, which lasts about 2 months, with age, regardless of the date of the vole's birth. And, he again concluded that the growth curve of body length in adult voles, is subject to seasonal variation, and that there is a closer correlation between growth, sexual maturation, and sexual activity, than between growth and age.

The results of the present study showed that maturation of the male and female bank vole occurred at the end of the second month, or during the third month, regardless the date of birth. Because neither seasonal, nor sexual variations were found to exist under the laboratory conditions, as the voles continued to breed throughout the year, age remained the main factor which influenced body growth.

In the British bank voles, body measurements have been used as taxonomic characters only, Southern (1964).

Body measurements have also been used as age criteria in some other rodents. Different results were obtained. Chipman (1965), for instance, considered the use of body measurements as age criteria, of limited value in the cotton rat (<u>Sigmodon hispidus</u>). He gave priority to the body length, and then to the hind foot and ear pinna length. The body and tail lengths of <u>Apodemus agrarius</u> were also claimed by Adamczewska-Andrzejewska (1973 b) to give satisfactory results as age indicators.

II. 3. Linear skull measurements

A. Introduction:

Skull measurements have always been considered as useful features in mammalian studies. They have mainley been used in systematic work, but in recent years have also been used for age determination.

Different skull measurements have been used for the ageing of several species of mammals, such as, the Michigan otter (*Lutra canadensis*), Hooper & Ostenson (1949); the muskrat (*Ondatra zibethicus*), Alexander (1951); the cotton rat (*Sigmodon hispidus*), Chipman (1965); the cottontail (*Silvilagus floridanus*), Hoffmeister & Zimmerman (1967); the California vole (*Microtus californicus*), Lidicker &MacLean (1969); and the striped field mouse (*Apodemus agrarius*), Adamczewska-Andrzejewska (1973 b).

Skull measurements derived from wild populations of *Clethrionomys* have been discussed by many authors, such as Razorenova (1952) in Russia; Manning (1956) in Canada; Wasilewski (1952), & Haitlinger (1965) in Poland; and Delany & Bishop (1960) in Britain.

All these studies mainly dealt with the morphology, growth, and seasonal variations.

The measurements which were used in the present study to correlate with age in *Clethrionomys* were:

1. Skull length.
2. Zygomatic breadth.
3. Lower jaw length.

Skull depth and molar row length were also examined, but after a preliminary study, they were discarded, as they were found to be of no value in estimating the age.

B. Methods:

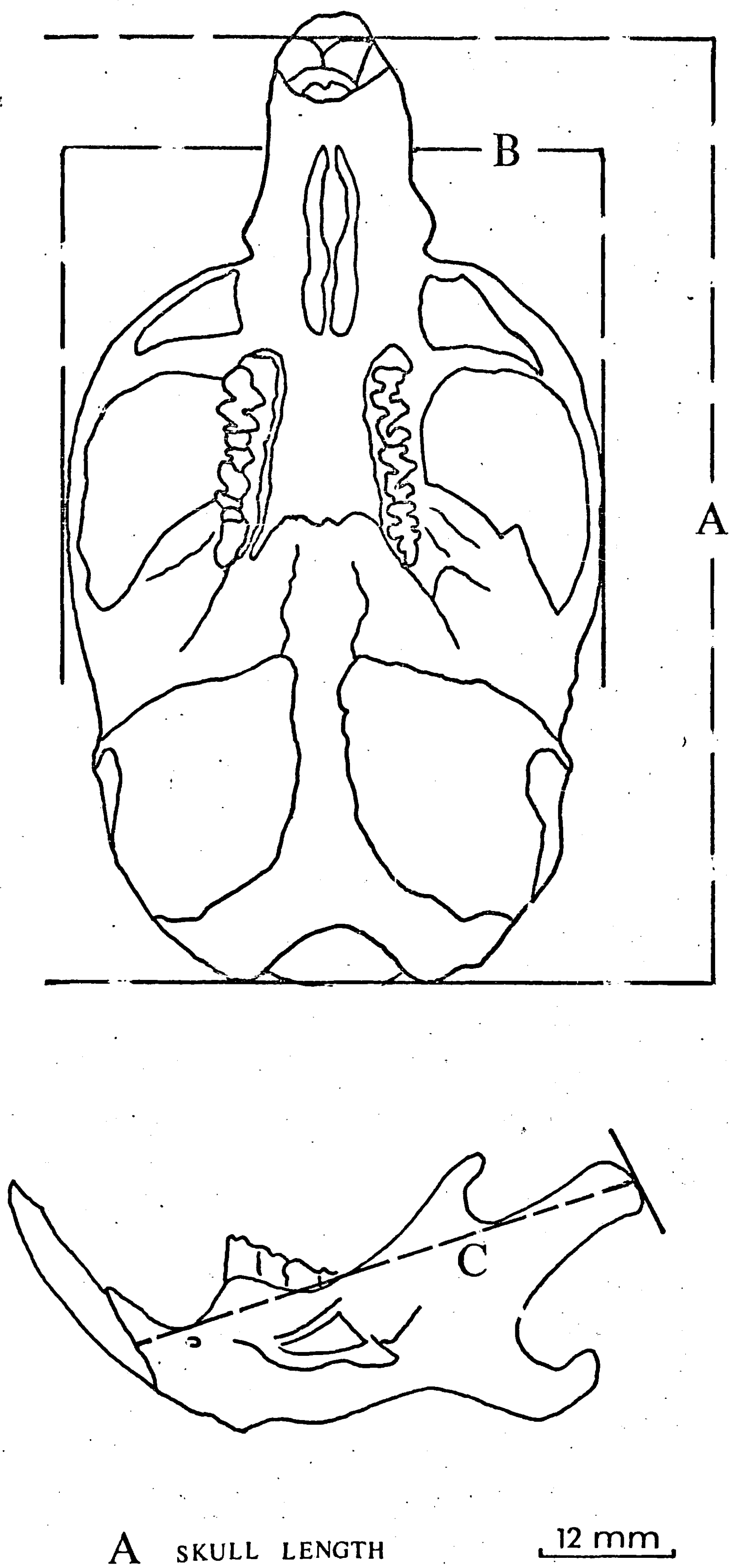
The skull of every sacrificed vole was removed from the carcass, boiled for 5 minutes in water, and cleaned. It was left for one week to dry and then, the measurements were made. In order to avoid the errors in measurement resulting from shrinkage of the skull, (Alexander, 1960), measurements were made soon after the skull had dried. Vernier calipers, accurate to 0.05 mm, were used for taking these measurements.

Skull length was recorded as the distance, in the midline of the skull, from a line across the most anterior point of the curvature of the incisors to the most posterior points of the occipital condyles.

Zygomatic breadth was the greatest distance between the exterior surfaces of the zygomatic arches.

Lower jaw length was the greatest length of the ramus, extending from the posterior surface of the condyle to the midpoint of the alveolus at its attachment with the incisor. The left ramus was usually measured (Fig. 12).

Fig 12. A diagram for the skull and the lower jaw of a mainland bank vole showing the measurements which were studied.



A SKULL LENGTH

B ZYGOMATIC BREADTH

C LOWER JAW LENGTH

C. Results:

a. The mainland bank vole:

Data for the sexes were combined, regarding the three skull measurements, as differences between them were not significant, (skull length: $t_{64}=0.16$, $P > 0.8$; zygomatic breadth: $t_{64}=0.24$, $P > 0.8$; lower jaw length: $t_{64}=0.28$, $P > 0.7$).

a.1. The skull length:

a.1.a. Growth curve of the skull:

Data for the growth of the skull of the mainland bank vole are presented in Fig.13 and Appendix 12.

The skull of the mainland bank vole grew very quickly during the first month of the vole's life, ($r=0.86$ up to the age of 42 days). While its length averaged 13.56 mm at the age of 5 days, it soon reached an average length of 20.24 mm at one month. The growth then slowed down, and the skull attained an average length of 21.89 mm at 2 months, 22.53 mm at 3 months, 22,98 mm at 4 months, and 23.19 mm at 7 months. The average length of the skull, beyond the age of 7 months, was always above 23 mm, with a minimum skull length of 22.1 mm. The correlation coefficient for the whole sample was 0.62.

a.1.b. Estimating the age from the skull length:

The whole sample was divided into 14 groups according to the skull length (Table 12).

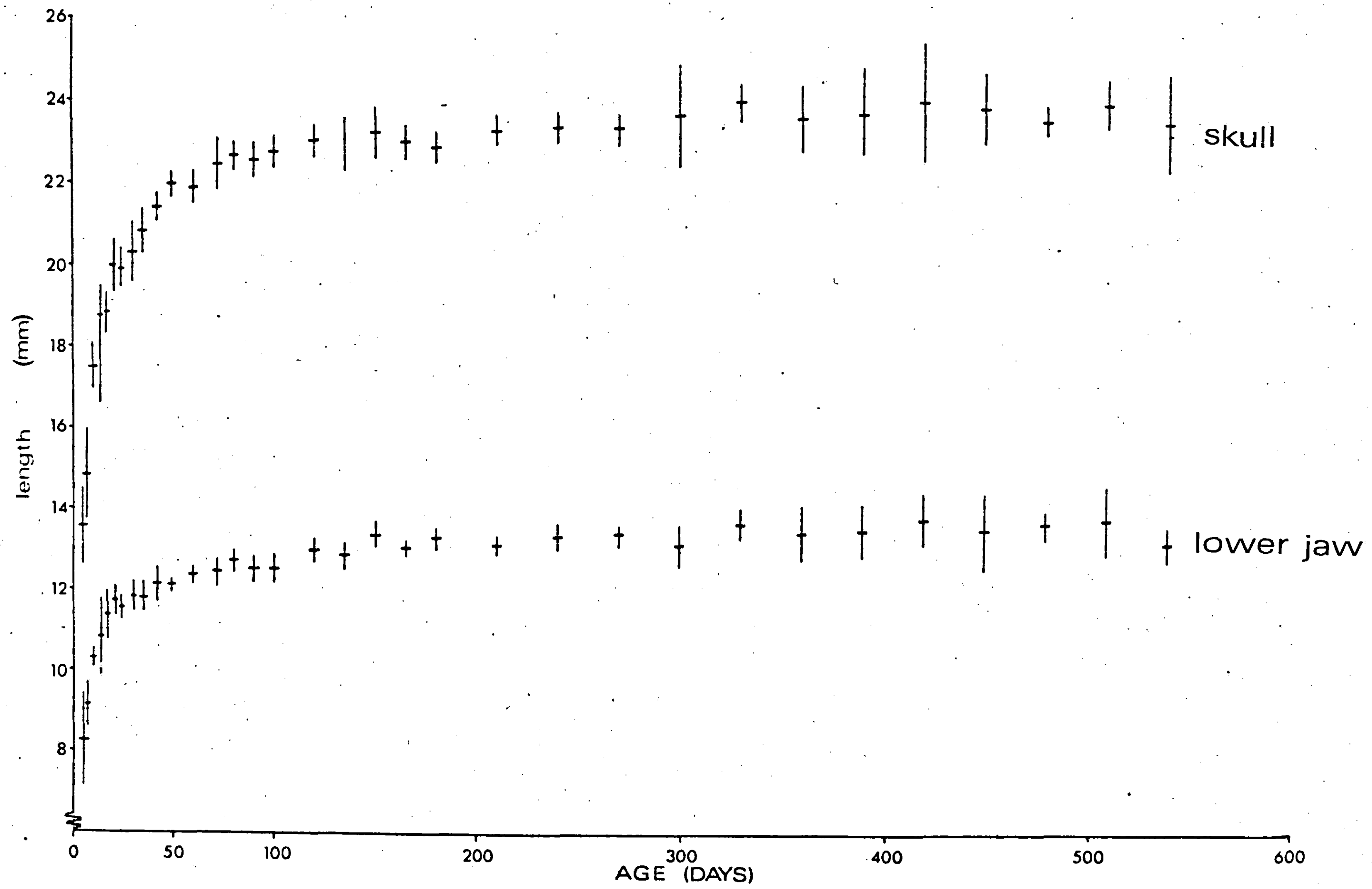


Fig. 13. Growth curves for the skull and the lower jaw lengths of the mainland bank vole. The horizontal line represents the mean, and the vertical line represents one 95% confidence limits on each side of the mean.

Accuracy for estimating the age of the mainland bank vole with a skull length of up to 21.9 mm (groups 1 to 9), was high, as the variability in the distribution of the material within each group was low. The lowest accuracy among the first 9 groups was ± 14.1 days for a mean age of 56.7 days, and a skull length of 21.6 to 21.9 mm (group 9).

Accuracy was lower in groups 10 to 13 which included voles with a skull length of 22 to 23.9 mm. The lowest was ± 41.4 days for a mean age of 185.9 days and a skull length of 22.6 to 22.9 mm (group 11).

Accuracy for estimating the age was higher in voles with a skull length of 24 mm and more, because variability was lower (v=18.84) after the skulls attained this length, which meant that their growth was completed. The accuracy for this group was ± 41 days for a mean age of 342.5 days (group 14).

Table 12. Numerical data for estimating the age of the mainland bank vole from the skull length:

G. No	SK 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	13-13.9	3	5 days	5.0± -	-	-	5.0 days
2	14-14.9	4	5- 7	6.5± 0.50	1.00	15.38	4.9- 8.1
3	15-15.9	1	7 days	7.0± -	-	-	7.0 days
4	16-17.9	5	10- 14	10.8± 0.80	1.79	16.56	8.6- 13.0
5	18-18.9	9	14- 30	17.4± 1.64	4.93	28.25	13.7- 21.2
6	19-19.9	10	17- 30	23.5± 1.60	5.06	21.54	19.9- 27.1
7	20-20.9	14	21- 60	30.1± 2.85	10.67	35.49	23.9- 36.2
8	21-21.5	17	21- 72	46.0± 3.44	14.19	30.85	38.7- 53.3
9	21.6-21.9	6	42- 80	56.7± 5.47	13.41	23.67	42.6- 70.7
10	22-22.5	32	49-270	110.8±10.88	61.54	55.55	86.6-133.0
11	22.6-22.9	34	60-540	185.9±20.28	118.23	63.60	144.5-227.3
12	23-23.4	48	72-540	218.9±16.97	117.54	53.70	184.8-253.0
13	23.5-23.9	25	120-540	330.0±28.25	141.24	42.80	271.8-388.2
14	24-24.64	12	240-450	342.5±18.63	64.54	18.84	301.5-383.5

a.2. <u>The zygomatic breadth:</u>

a.2.a. <u>Growth curve of the zygomatic breadth:</u>

The relevant data are presented in Fig. 14 and Appendix 13.

The zygomatic breadth was found to increase slowly and regularly throughout the vole's life: 10.52 mm was the average zygomatic breadth of 14 days old voles; 11.97 mm for the one month old voles. All the voles above this age and up to the age of 3 months had a mean value extending from 12.19 mm to 12.8 mm. The average zygomatic breadth for all the voles beyond the age of 100 days was over 13 mm.

The correlation coefficient for the whole sample was 0.62. It was 0.84 for voles 42 days and younger.

a.2.b. <u>Estimating the age from the zygomatic breadth:</u>

The whole sample was divided into 11 groups according to the zygomatic breadth. Data were treated as before and are presented in table 13.

Variability in this character was found to be less than the variability in the skull length, and therefore accuracy for estimating the age from the zygomatic breadth is higher. All the coefficients of variation were less than 50% except in group 9 (v=62.16). This group had a zygomatic breadth of 13 to 13.4 mm. It is most likely that this was due to three voles aged 540 days each. Their skulls appeared to have shrunk after reaching this old age. Although the correlation coefficient for the whole sample was not high (r=0.62), due to the slow growth, the lower

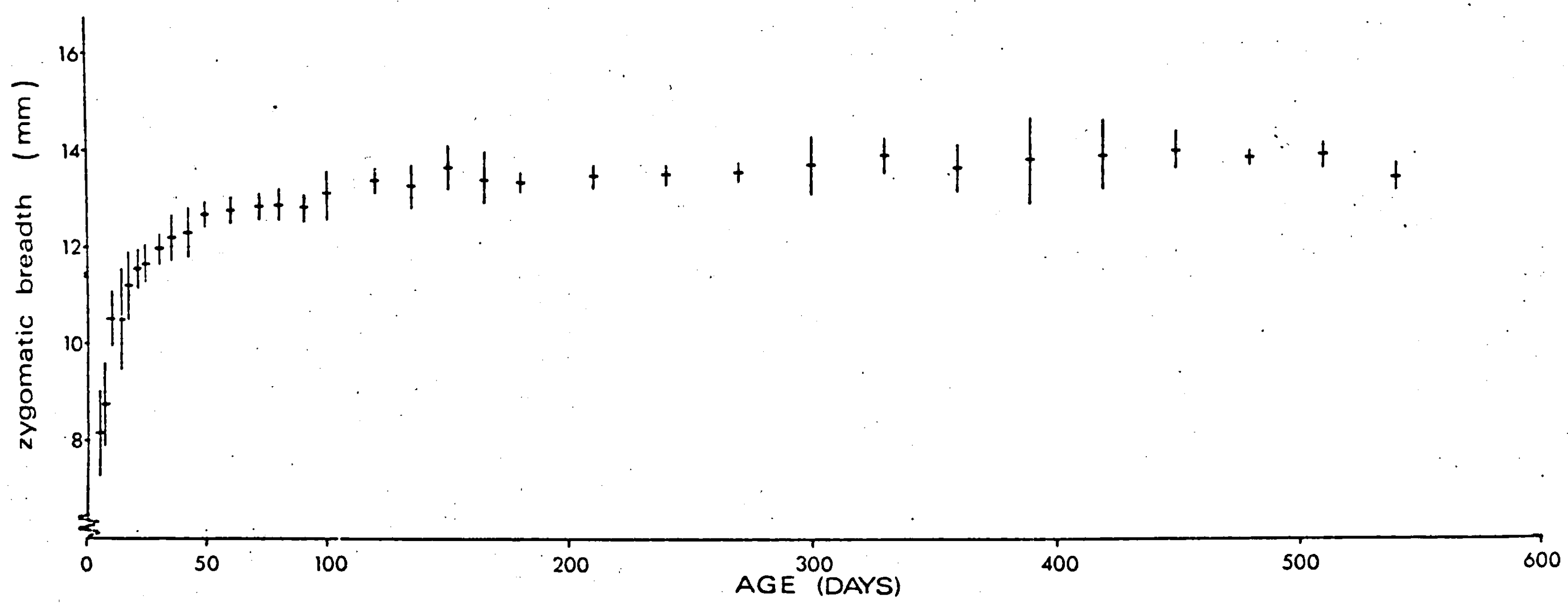


Fig. 14. Growth curve for the zygomatic breadth of the mainland bank vole. (see Fig. 13 for explanation).

Table 13. Numerical data for estimating the age of the mainland bank vole from the zygomatic breadth:

G. No	ZB / mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	7- 7.9	3	5 days	5.0± -	-	-	5.0 days
2	8- 8.9	4	5- 7	6.5± 0.50	1.00	15.38	4.9- 8.1
3	9- 9.9	2	7- 14	10.5± 3.48	4.95	47.14	*
4	10-10.9	7	10-117	12.1± 1.08	2.85	23.51	9.5- 14.8
5	11-11.5	9	14- 42	23.0± 2.83	8.49	36.89	16.5- 29.5
6	11.6-11.9	10	17- 35	25.0± 1.67	5.27	21.08	21.2- 28.8
7	12-12.4	20	21- 90	46.8± 4.09	18.31	39.17	38.2- 55.3
8	12.5-12.9	39	35-210	81.3± 6.09	38.06	46.84	68.9- 93.6
9	13-13.4	57	49-540	202.0±16.63	125.59	62.16	168.6-235.5
10	13.5-13.9	50	60-510	278.7±18.64	131.77	47.28	241.2-316.2
11	14-14.42	11	150-480	330.0±32.86	109.00	33.03	256.7-403.3

* The 95% confidence limits were not attached to the mean age because the sample size was small.

variability and the regular growth gave the zygomatic breadth objective value as an age indicator.

a.3. The lower jaw length:

a.3.a. Growth curve of the lower jaw:

Data for the growth of the lower jaw of the mainland bank vole are presented in Fig. 13 and Appendix 14.

Three age groups could be identified on the basis of the average length of the lower jaw, these were:

1. Voles 35 days and younger. They had a mean lower jaw length less than 12 mm. The average lower jaw length of 35 days old voles was 11.81 mm.
2. Voles aged 42 to 135 days. They had a mean lower jaw length less than 13 mm and more than 12 mm. The average lower jaw length was 12.12 mm for 42 days old voles and 12.97 mm for 120 days old voles.
3. Voles 5 months and older. The mean lower jaw length for this group was more than 13 mm. Only 4 voles out of the whole sample (1.8%), had their lower jaws 14 mm and longer. Their ages were 11, 12, 15, & 17 months.

The correlation coefficient for the whole sample was 0.64. It was 0.80 for voles 42 days and younger.

a.3.b. Estimating the age from the lower jaw length:

The whole sample was divided into 12 groups according to the length of the lower jaw (Table 14).

Variability in the distribution of the material within each group was higher than in the skull length and the zygomatic breadth.

Accuracy for estimating the age was high in voles with a lower jaw length of up to 12.4 mm (groups 1 to 6) representing a maximum mean age of 66.9 days (group 6). The lowest accuracy among these 6 groups was ± 8.8 days for a mean age of 37.8 days, and a maximum lower jaw length of 11.9 mm (group 5).

The accuracy decreased in voles with a lower jaw length of 12.5 to 13.5 mm (groups 7 to 10), being ± 43.4 days for a mean age of 231.8 days and a lower jaw length of 13 to 13.2 mm (group 9), and ± 60.5 days for a mean age of 278.4 days and a lower jaw length of 13.3 to 13.5 mm.

The accuracy increased for estimating the age of voles with a lower jaw length of 13.6 mm and more (groups 11 & 12). The low accuracy in group 12, being ± 131.3 days, was mainly due to the small size of the sample (only 4 voles). In such cases, the standard deviation, and coefficicnt of variation should be referred to.

Table 14. Numerical data for estimating the age of the mainland bank vole from the lower jaw length:

G. No	LJ 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	7.0- 8.9	4	5- 7	5.5± 0.50	1.00	18.18	3.9- 7.1
2	9.0- 9.9	4	5- 7	6.5± 0.50	1.00	15.38	4.9- 8.1
3	10.0-10.9	8	10- 14	11.0± 0.65	1.85	16.83	9.5- 12.5
4	11.0-11.5	19	14- 42	24.6± 1.70	7.39	29.99	21.1- 28.2
5	11.6-11.9	17	17- 72	37.8± 4.16	17.15	45.34	29.0- 46.6
6	12.0-12.4	42	21-120	60.9± 3.45	22.36	36.75	53.9- 67.8
7	12.5-12.7	27	30-360	116.8±15.18	78.90	67.56	85.5-148.1
8	12.8-12.9	28	60-540	196.5±21.58	114.17	58.11	152.2-240.7
9	13.0-13.2	42	60-540	231.8±21.47	139.14	60.03	188.4-275.2
10	13.3-13.5	19	100-510	278.4±28.82	125.62	45.12	217.9-338.9
11	13.6-13.9	22	120-480	301.4±24.61	115.44	38.31	250.2-352.5
12	14.0-14.27	4	330-510	412.5±41.30	82.61	20.03	281.2-543.8

b. The Skomer vole:

Data for skull measurements of the two sexes of Skomer vole were combined, as no significant differences were found between them, (skull length: t_{64}=0.25, P = 0.8 ; zygomatic breadth, t_{64}=0.41: $P > 0.61$; lower jaw length: t_{64}=0.12, $P \geqslant 0.9$).

Growth data for the three skull measurements are presented in Figs. 15, & 16, and Appendices 15, 16, & 17.

b.1. The skull length:

b.1.a. Growth curve of the skull length:

A slight preponderance in the length of the males' skulls upon those of the females, was noticed starting above the age of 6 months. This difference was not evident above the age of 10 months.

The skull of the Skomer vole grew very quickly in the first month (r=0.93 up to the age of 42 days). Afterwards the rate slowed down but growth never stopped. A slight shrinkage was noticed in the two last groups which contained 17 and 18 months old voles. Three age groups could be identified on the basis of the skull average length, these are:

1. Voles 42 days and younger: 95.6% of them had their skulls less than 22.55 mm long.

2. Voles 49 to 180 days old. The average length of their skulls was more than 23 mm and less than 24 mm.

3. Voles 210 days and older. The average length of their skulls was 24 mm and longer, but less than 25 mm.

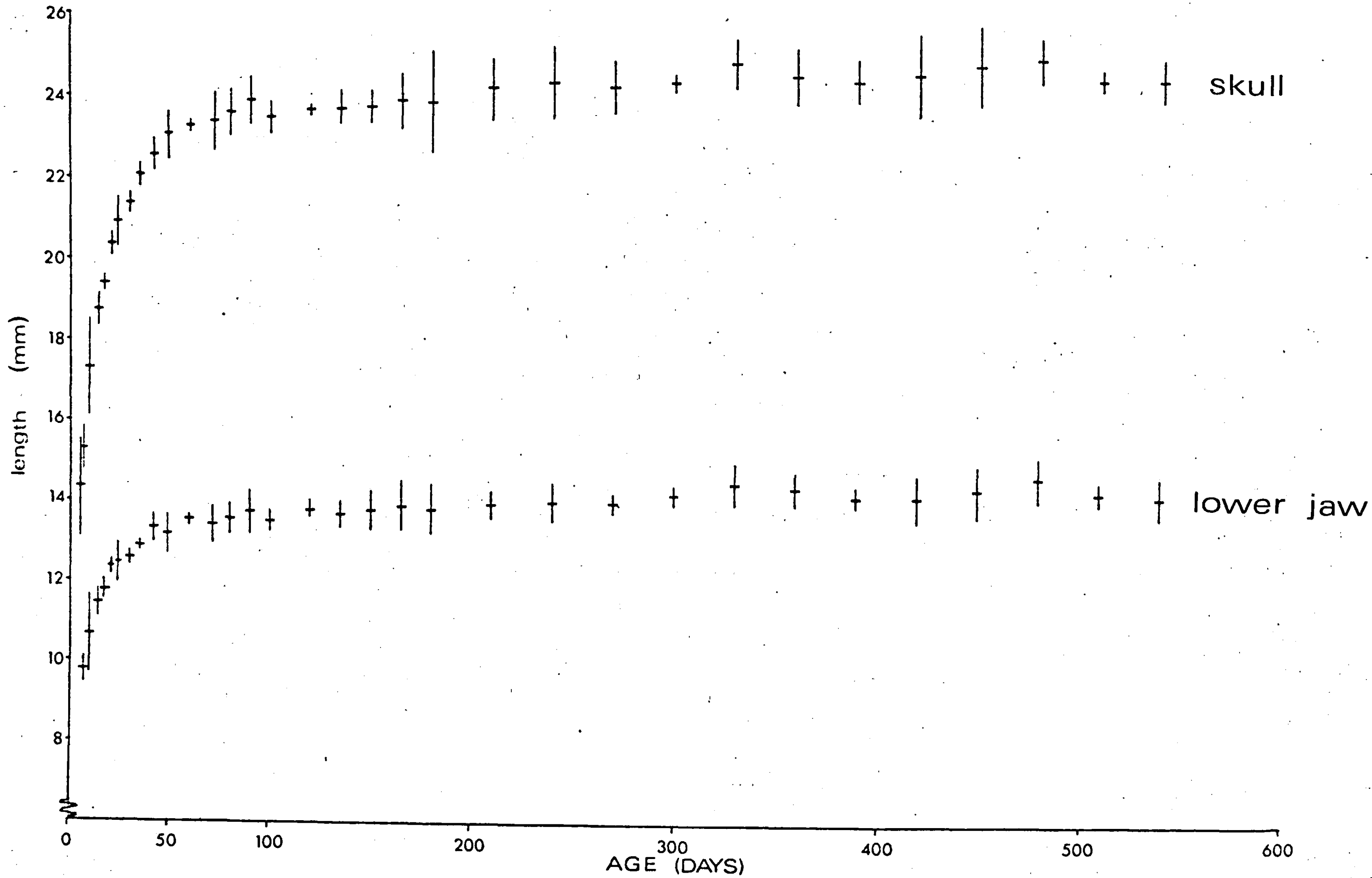


Fig. 15. Growth curves for the skull and the lower jaw lengths of the Skomer vole. (see Fig. 13 for explanation).

Only 6 voles out of the whole sample (3.6%) had skulls over 25 mm long. These voles were 11, 14, 15, & 16 months old.

The correlation coefficient for the whole sample was 0.61.

b.1.b. Estimating the age from the skull length:

The whole sample was divided into 16 groups according to the skull length (Table 15).

Accuracy for estimating the age of voles with a skull length of up to 22.5 mm was high (groups 1 to 10) representing a maximum mean age of 39.2 days. It decreased in voles with longer skulls, reaching its lowest at a skull length of 23.6 to 23.9 mm (group 13). The variability in the distribution of the material in the latter group was high (v=62.67). The accuracy for estimating the age of voles with this skull length, was ± 47.7 days for a mean age of 184.6 days.

Variability decreased in the last 3 groups, corresponding to a high accuracy for estimating the age of voles with a skull length of 24 to 25.34 mm (groups 14 to 16).

Table 15. Numerical data for estimating the age of the Skomer vole from the skull length:

G. No	SK 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	14.0-14.5	2	5 days	5.0± -	-	-	5.0 days
2	14.6-15.9	4	7 days	7.0± -	-	-	7.0 days
	16.0-16.5*						
3	16.6-17.9	3	10 days	10.0± -	-	-	10.0 days
4	18.0-18.9	3	14 days	14.0± -	-	-	14.0 days
5	19.0-19.9	5	14- 17	16.4± 0.60	1.34	8.18	14.7- 18.1
6	20.0-20.5	3	21 days	21.0± -	-	-	21.0 days
7	20.6-20.9	5	21- 30	24.6± 1.47	3.29	13.36	20.5- 28.7
8	21.0-21.5	8	24- 30	29.3± 0.75	2.12	7.25	27.5- 31.0
9	21.6-21.9	6	30- 35	33.3± 1.05	2.58	7.75	30.6- 36.0
10	22.0-22.5	5	35- 49	39.2± 2.80	6.26	15.97	31.4- 47.0
11	22.6-22.9	9	35-100	57.0± 6.73	20.19	35.42	41.5- 72.6
12	23.0-23.5	29	49-240	100.8± 9.74	52.45	52.02	80.9-120.8
13	23.6-23.9	25	60-450	184.6±23.13	115.67	62.67	136.9-232.2
14	24.0-24.5	35	80-540	310.7±25.20	149.07	47.98	259.3-362.1
15	24.6-24.9	18	180-540	343.3±27.78	117.87	34.33	285.3-401.4
16	25.0-25.34	6	330-480	410.0±26.46	64.81	15.81	342.0-478.0

* Data for this measurement were not available.

b.2. The zygomatic breadth:

b.2.a. Growth curve of the zygomatic breadth:

The growth of the zygomatic breadth was very fast during the first month. It slowed down afterwards, but continued in a regular way throughout the animal's life.

Four age groups could be identified on the basis of average values of the zygomatic breadth, these were:

1. Voles under 21 days old with a mean zygomatic breadth of less than 12 mm.

2. Voles between 21 and 42 days old with a mean zygomatic breadth of 12 to 12.85 mm.

3. Voles between 42 and 180 days old with a mean zygomatic breadth of 13 to 13.97 mm (the mean zygomatic breadth being 13.19 mm for 42 days old voles and 13.97 mm for 180 days old voles).

4. Voles 7 months and older with a mean zygomatic breadth of more than 14 mm.

The skulls of only 2 voles out of the whole sample (1.2%) had their zygomatic breadth 15 and 15.1 mm. They were 14 & 11 months old respectively.

The correlation coefficient for the whole sample was 0.67. It was 0.93 for voles under 42 days old.

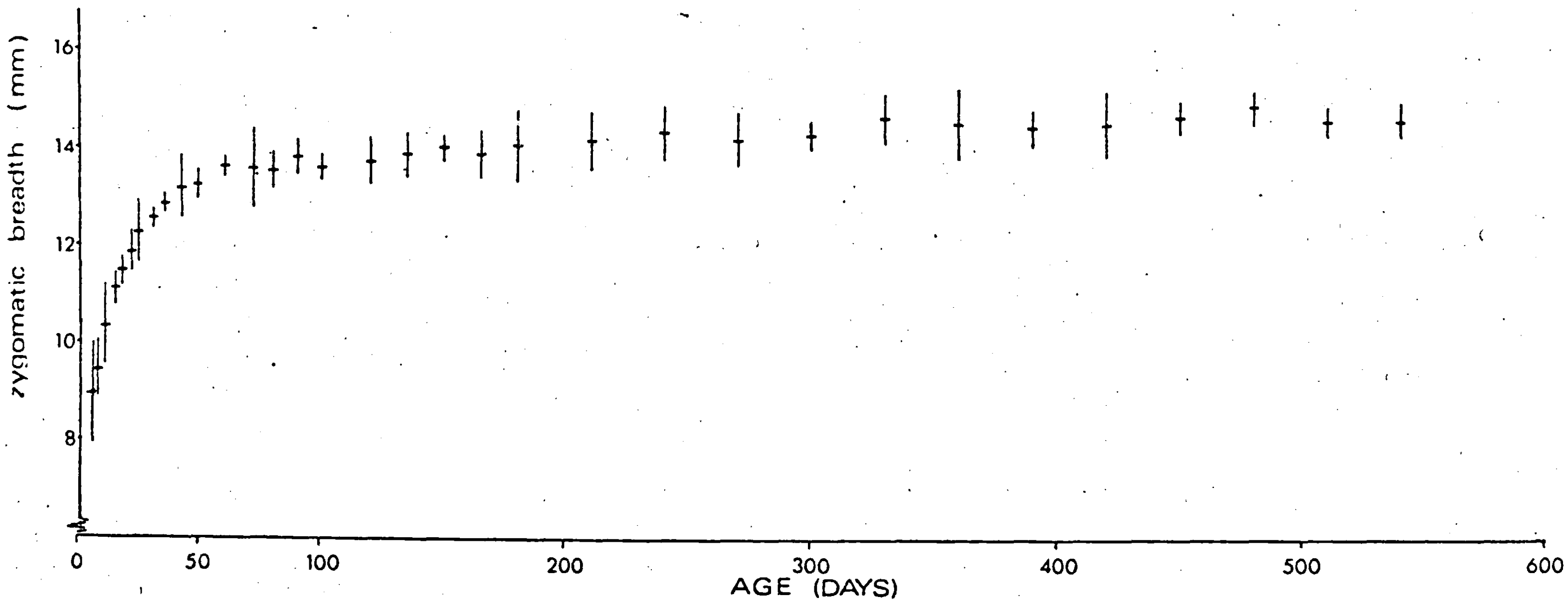


Fig. 16. Growth curve for the zygomatic breadth of the Skomer vole. (see Fig. 13 for explanation).

b.2.b. Estimating the age from the zygomatic breadth:

The whole sample was divided into 11 groups according to the zygomatic breadth. Data were treated as before (Table 16).

Accuracy for estimating the age of the Skomer vole from the zygomatic breadth was high in the first 7 groups corresponding to a maximum mean age of 31.7 days and a zygomatic breadth of up to 12.9 mm (group 7). The accuracy was also high in group 11, being ± 58.3 days for a mean age of 420 days and a zygomatic breadth of 14.6 to 15.1 mm.

Variability for the distribution of the material was high in groups 8, 9, & 10. These groups included voles with a zygomatic breadth of 13 to 14.5 mm but the accuracy for estimating their age is still high, due mainly to the artificial large sample size. The accuracy was, for example, ± 32.5 days for a mean age of 146.3 days (group 9).

The high accuracy for estimating the age, and the low variability make the zygomatic breadth a reliable index of age up to a breadth of 12.9 mm, but less reliable in voles with wider zygomatic breadth.

Table 16. Numerical data for estimating the age of the Skomer vole from the zygomatic breadth:

G. No	ZB L/ mm	F.	O. Range / days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	8.9- 9.05	2	5 days	5.0± -	-	-	5.0 days
2	9.1- 9.9	3	7 days	7.0± -	-	-	7.0 days
3	10.0-10.9	5	7- 14	10.2± 1.11	2.49	24.41	7.1- 13.3
4	11.0-11.5	5	14- 17	15.2± 0.73	1.64	10.81	13.2- 17.2
5	11.6-11.9	6	17- 24	20.2± 1.10	2.71	13.46	17.4- 23.0
6	12.0-12.5	10	21- 35	28.9± 1.46	4.61	15.94	25.6- 32.2
7	12.6-12.9	11	24- 35	31.7± 1.08	3.58	11.28	29.3- 34.1
8	13.0-13.4	29	35-210	79.2± 8.32	44.81	56.55	62.2- 96.3
9	13.5-13.9	29	60-360	146.3±15.86	85.42	58.39	113.8-178.8
10	14.0-14.5	51	60-540	279.8±19.53	139.44	49.83	240.6-319.1
11	14.6-15.1	16	180-540	420.0±27.39	109.54	26.08	361.7-478.3

b.3. The lower jaw length:

b.3.a. Growth curve of the lower jaw:

The lower jaw grew very quickly and regularly up to the age of 42 days (r=0.92). Growth then slowed down but continued throughout life. It was not as regular as the growth of the zygomatic breadth.

Four age groups could be identified on the basis of the lower jaw length, these were:

1. Voles 35 days and younger with a lower jaw mean length of less than 13 mm.

2. Voles between 42 and 150 days old with a mean lower jaw length of more than 13 mm and less than 13.79mm.

3. Voles between 165 days and 9 months old with a mean lower jaw length of more than 13.8 mm and less than 14 mm.

4. Voles 10 months and older with a mean lower jaw length of more than 14 mm.

Only 2 voles out of the whole sample (1.2%) had lower jaws 15 mm long. They were 11 & 16 months old.

The correlation coefficient for the whole sample was 0.64.

b.3.b. Estimating the age from the lower jaw length:

The whole sample was divided into 10 groups according to the lower jaw length (Table 17).

The most variable values of the lower jaw length were located within the range 13 to 13.9 mm. Skomer voles with this lower jaw length (group 8) would have a mean age of 202.9 days with a standard deviation of 136.3 days, a minimum age of 157.5 days, and a maximum of 248.4 days. This result is accurate with 0.05 probability . Variability in the distribution of voles with a lower jaw length of more than 14 mm and less than 13 mm was not high. For example, Skomer voles with 14 to 14.4 mm lower jaw length (group 9) would have a mean age of 322.5 days, a minimum age of 280.6 days, and a maximum of 364.4 days.

Lower jaw length is evidently useful as age index up to 13.5 mm, but less reliable above this length.

Table 17. Numerical data for estimating the age of the Skomer vole from the lower jaw length:

G. No	LJ 1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	9.0- 9.4	2	5 days	5.0± -	-	-	5.0 days
2	9.5- 9.9	3	7 days	7.0± -	-	-	7.0 days
3	10.0-10.9	3	7- 10	9.0± 1.00	1.73	19.25	4.7- 13.3
4	11.0-11.9	8	10- 17	14.6± 0.85	2.39	16.31	12.6- 16.6
5	12.0-12.5	12	17- 30	24.9± 1.39	4.81	19.32	21.9- 28.0
6	12.6-12.9	11	24- 35	31.6± 1.32	4.39	13.87	28.7- 34.6
7	13.0-13.5	42	30-240	90.0± 8.01	51.93	57.72	73.8-106.2
8	13.6-13.9	37	42-540	202.9±22.40	136.28	67.16	157.5-248.4
9	14.0-14.4	42	60-540	322.5±20.74	134.42	41.68	280.6-364.4
10	14.5-15.0	7	330-480	407.1±25.23	66.76	16.40	345.3-469.0

D. Discussion:

The skull in the mainland bank vole and the Skomer vole grow quickly only during the first 2 months of their life, after this, the growth decreases in a way which differs from one measurement to another.

The zygomatic breadth grows regularly throughout the vole's life. It is the best age indicator among the three skull measurements which have been investigated. Skull length is next in its value, and then the lower jaw length.

Skull measurements have been used by some authors in ageing different species of mammals. Alexander (1960) recommended the use of the zygomatic breadth as an age indicator in the muskrat (Ondatra zibethicus) where there is a 1.5% decrease in the zygomatic breadth after the skull dries. Since all the skull measurements in the bank voles were recorded one week after they had been cleaned and dried, the measuring error should be uniform, and the data are still valid.

Chipman (1965) identified four age groups on the basis of the zygomatic breadth in the cotton rat (Sigmodon hispidus). Green & Jameson (1975) confirmed Chipman's suggestion in using the zygomatic breadth in Sigmodon hispidus as an age indicator. They mentioned that this character is useful in separating juveniles from adults. They added also that estimation of age from the zygomatic arch in laboratory and field populations are the same.

Skull length was held by Prychodko (1951) to be a dimension which constantly increases in C. glareolus. Wasilewski (1952), disagreed. According to him, the condylobasal length increases more slowly in autumn than in spring. While Adamczewska-Andrzejewska (1973 b) found the condylobasal length to exhibit a regular course of growth in <u>Apodemus agrarius</u>, she supported Wasilewski in agreeing that the condylobasal growth was influenced by season.

In the present study, seasonal variations were assumed to have been excluded by the maintenance of uniform laboratory conditions, and from the observation that all skull measurements reflected growth throughout life (see Chapter IV). Under these conditions, growth of the skull was found to be less variable than body weight and body measurements, which might mean that any factor, whether it is internal or external, is less likely to affect skull measurements, and therefore, skull measurements are more reliable age criteria than the body measurements. Moreover, sexual maturity had no effect on the rate of growth of the skull, as the latter continued to grow after the voles attained sexual maturity. Therefore, age is the main factor which influence the skull growth.

II. 4. The molar teeth

A. Introduction:

I. Development and growth of the tooth roots:

The molar teeth in the bank vole (Fig. 17) are characterized by having a single root ('neck') which becomes divided into two at a definite age. The length of roots increases with age. Therefore, the onset of this phenomenon, and the speed with which it progresses ought to be related to age.

Zimmerman (1937) first drew attention to the use of this character as an age criterion in his work on *C. glareolus* in Germany. This method has since been used by many other authors working on different species of this genus in Europe and also in Asia. Wrangle (1939), and Prychodko (1951) used it on *C. glareolus* in Germany ; Koshkina (1955) applied it to *C. glareolus*, *C. rufocanus*, & *C. rutilus* in Russia; Shaw *et al* (1959) on *C. rutilus* in China; Zejda (1955 & 1961), & Mazak (1963), on *C. glareolus* in Czechoslovakia; Wasilewski (1952), Haitlinger (1965), Tupikova *et.al* (1968), and Pucek & Zejda (1968) on *C. glareolus* in Pland; Viitala (1971) on *C. rufocanus* in Finland; Delany & Bishop (1960) on *C. glareolus* in Britain.

Lowe (1971) in England, studied during the years 1955 & 1956, the root growth of laboratory and field populations of *C. g. britannicus*. He injected the voles with alizarin red to stain the calcium being deposited in the roots. He did not succeed in studying the root growth in the laboratory-raised population, and his results were derived from the

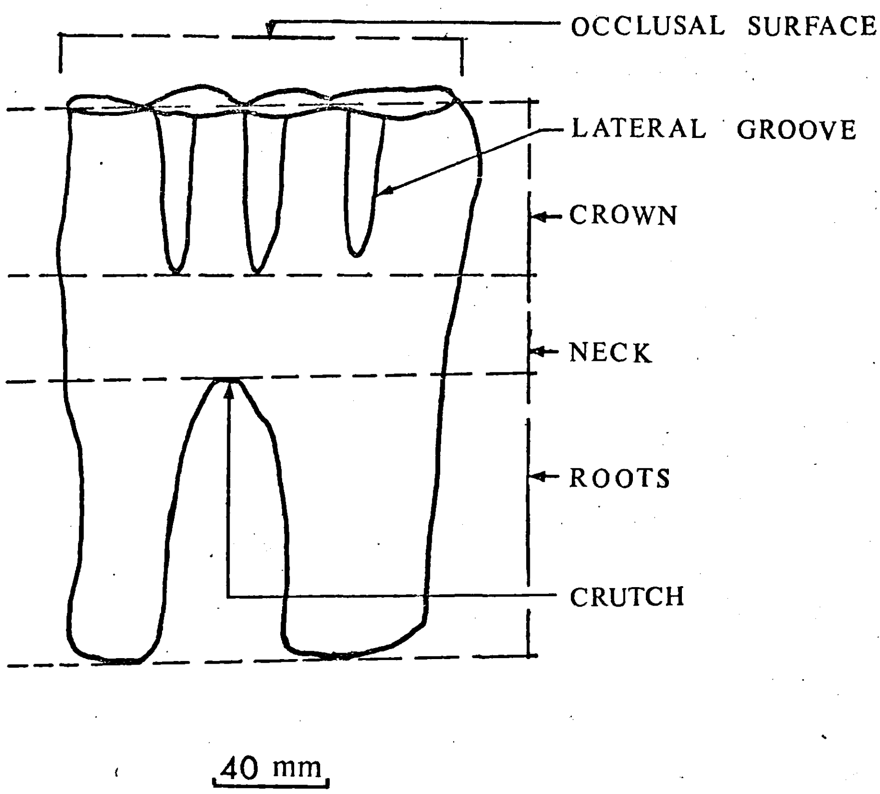


Fig. 17. A diagram for the first lower molar of a male <u>C</u>. <u>g</u>. <u>britannicus</u>.

study of a field population.

In studying the development and growth of the molar roots, M_1 has usually been used. But Koshkina (1955), Tupikova et al (1968), and Viitala (1971) used M^2, and Delany & Bishop (1960) used M^3 for the same purpose.

Most of the investigations which have been made, showed that the roots started to appear at the age of 2 to 4 months in C. glareolus, and at 7 to 8 months in C. rufocanus (Koshkina, 1955). Zimmerman (1937) mentioned that the roots develop at the age of 6 months in C. glareolus.

Lowe (1971) found that the tooth roots of laboratory-raised voles did not develop throughout the first six months of life. He mentioned also that in the field population, the onset of molar root development was variable (2 to 4.5 months) depending on the season of birth. And the root growth rates varied from 0.05 to 0.55 mm per month.

Regarding the Skomer vole, nothing has been published concerning the growth and development of the roots of the molar teeth.

II. Tooth wear:

It is known that the teeth of any animal are worn away progressively with age as a result of their use for feeding and other purposes throughout life.

In the case of the genus Clethrionomys, the growth of the molar crowns ceases at a certain age, but they continue to wear down throughout the animal's life. At the same time the roots continue to grow until, in old animals only the roots remain with a thin crown. As a result the root length/ crown height ratio increases with age.

Review of the literature indicated tooth wear to be a reliable criterion of age for several species of small mammals, such as the cotton rat (Sigmodon hispidus), Chipman, 1965; the brown rat (Rattus norvegicus), Tanaka, 1968; the brown and black rats (R. norvegicus and R. rattus), Karnoukhova, 1971; the lesser jerboa (Allactaga elater), Smirnov et al, 1971; and the striped field mouse (Apodemus agrarius), Adamczewska-Andrzejewska, 1973 b.

Nothing has been written, however regarding the use of tooth wear (as distinct from root growth) to determine the age of Clethrionomys.

In view of the above studies the present work was undertaken to:

1. Obtain a correlation between age and molar root growth.
2. To find out which of the molars gives the best correlation with age.
3. Study the tooth wear and its value for use as an age criterion.

B. Methods:

In order to study the root development and growth, and tooth wear, all the molars of the left maxilla and right mandible were used.

Extracting the teeth was done by boiling the skull in very dilute KOH solution, less than 1%, for 10 minutes.

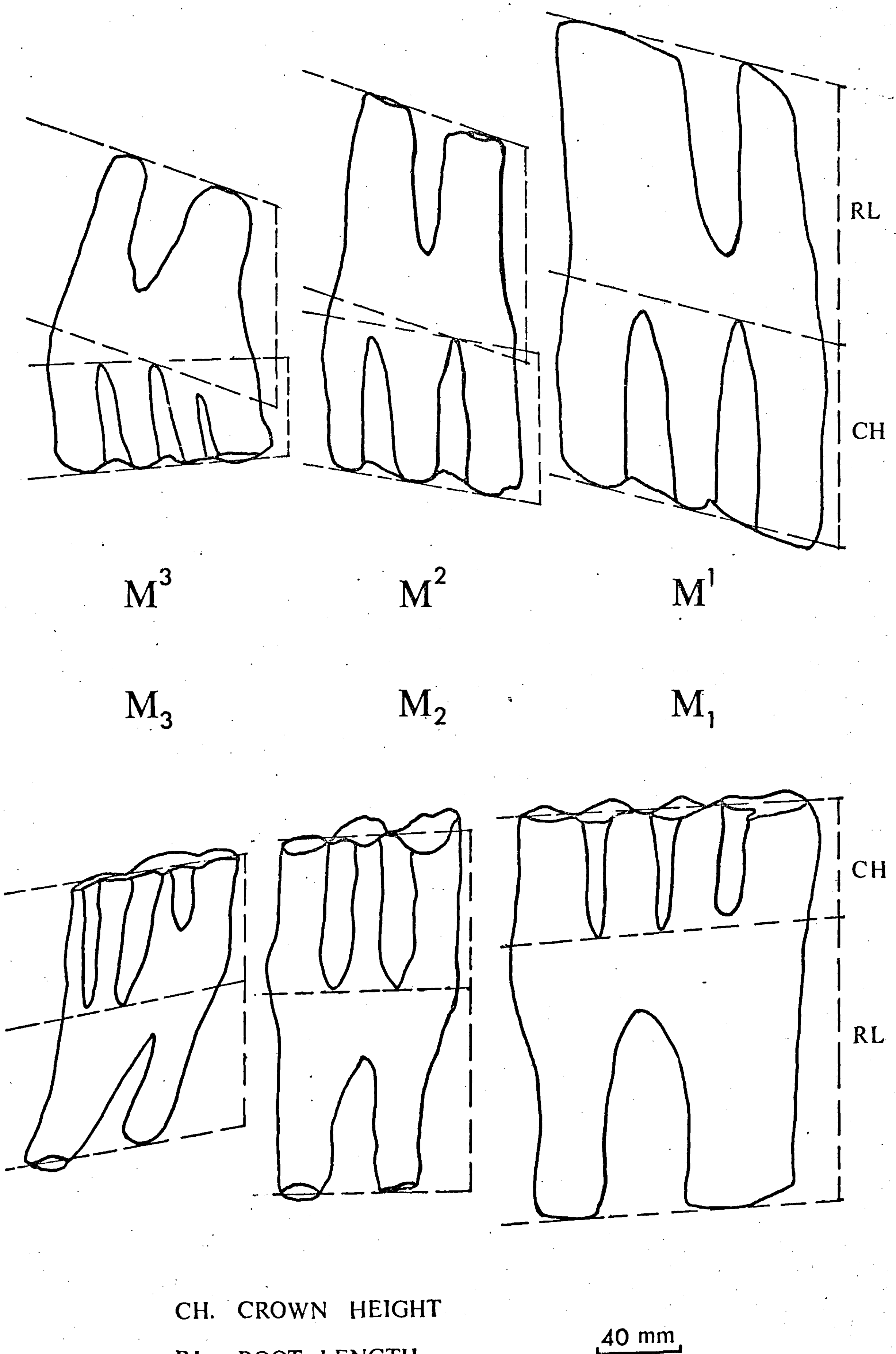
With fine forceps, each tooth was pulled out, put on a file card with its buccal (external) face, facing upwards, and then covered by Sellotape.

A low power vernier measuring microscope (Utilex), (Swift Microscopes-London) with an eyepiece of x6 magnification was used for recording the tooth measurements. The eyepiece was provided with a graticule consisting of a single line crossed by two parallel lines 0.2 mm apart. These lines were used to determine the starting and ending points of each measurement. A micrometer screw, fitted with a calibrated drum, which is mounted on one end of the casting, adjusts the movable stage. It moves for distances up to 25 mm and measurements were made entirely on the micrometer drum to a reading of 0.01 mm. The tooth to be measured was put on a glass stage and then the table was moved along the desired amount and the measurement read off the microdrum.

Two measurements were recorded for each of the six molars (Fig. 18). The first was the crown height. In young animals, it was the whole length of the tooth. In the adults its length extended from the occlusal surface to the end of the longest groove after the latter has been closed. The second measurement was the length of the roots. It is the distance between the end of the longest closed groove to the line connecting the free end of the two roots .

After a preliminary study of the neck height, variability was found to occur, in voles of the same age, which in turn would affect the time when the crutch started to develop (see Fig. 17). Moreover, Lowe (1971) stated that the crutch does not remain strictly constant because layers of cementum are continually being added to all tooth

Fig. 18. Molar teeth of a male mainland bank vole, 315 days old, showing the two measurements which were taken for each of them.



CH. CROWN HEIGHT
RL. ROOT LENGTH

surfaces below gum level throughout life. Therefore, the neck height was included in the root measurement in the present study.

C. Results:

I. Root development and growth:

a. The mainland bank vole:

Data for the sexes are combined, as no significant differences were found between them. The results of applying the t test on the whole sample (141 specimens between the ages 42 to 540 days) are:

Root	length	of	the	first lower	molar	(RM_1):	$t_{48}=0.26$,	$P>0.8$
"	"	"	"	second	"	(RM_2):	$t_{48}=0.26$,	$P>0.7$
"	"	"	"	third	"	(RM_3):	$t_{48}=0.30$,	$P>0.7$
"	"	"	"	first upper	"	(RM^1):	$t_{46}=0.18$,	$P>0.8$
"	"	"	"	second "	"	(RM^2):	$t_{48}=0.27$,	$P>0.7$
"	"	"	"	third "	"	(RM^3):	$t_{46}=0.41$,	$P>0.6$

a.1. Development and growth curves of the neck and roots of the three lower molars:

These data are presented in Figs. 19, 20, 21, and Appendices 18, 19, and 20.

The neck of the three lower molars started to develop after the closure of all the lateral grooves, which are found on the crowns. This closure occurred at the age of

35 to 42 days. The neck continued to grow with its lower end open. This end started to close, at its lower middle point, at the age of 72 to 90 days in M_1 and M_2, and at the age of 90 to 120 days in M_3, the time when the roots started to develop.

The roots of M_1 and M_2 grew regularly throughout life. Growth slowed down above the age of 14 months, but it never ceased. The growth of the roots of M_3 was also regular, but the root shape was not regular, and rather difficult to measure.

The average monthly increase in the root length, of voles 90 to 420 days old was 0.16 mm for RM_1, 0.13 mm for RM_2, and 0.08 mm for RM_3. It was 0.14 mm, 0.10 mm, and 0.07 mm, in voles 90 to 540 days old.

The correlation coefficient between age and the length of roots of the lower molars were: 0.96 for RM_1 & RM_2, and 0.95 for RM_3 .

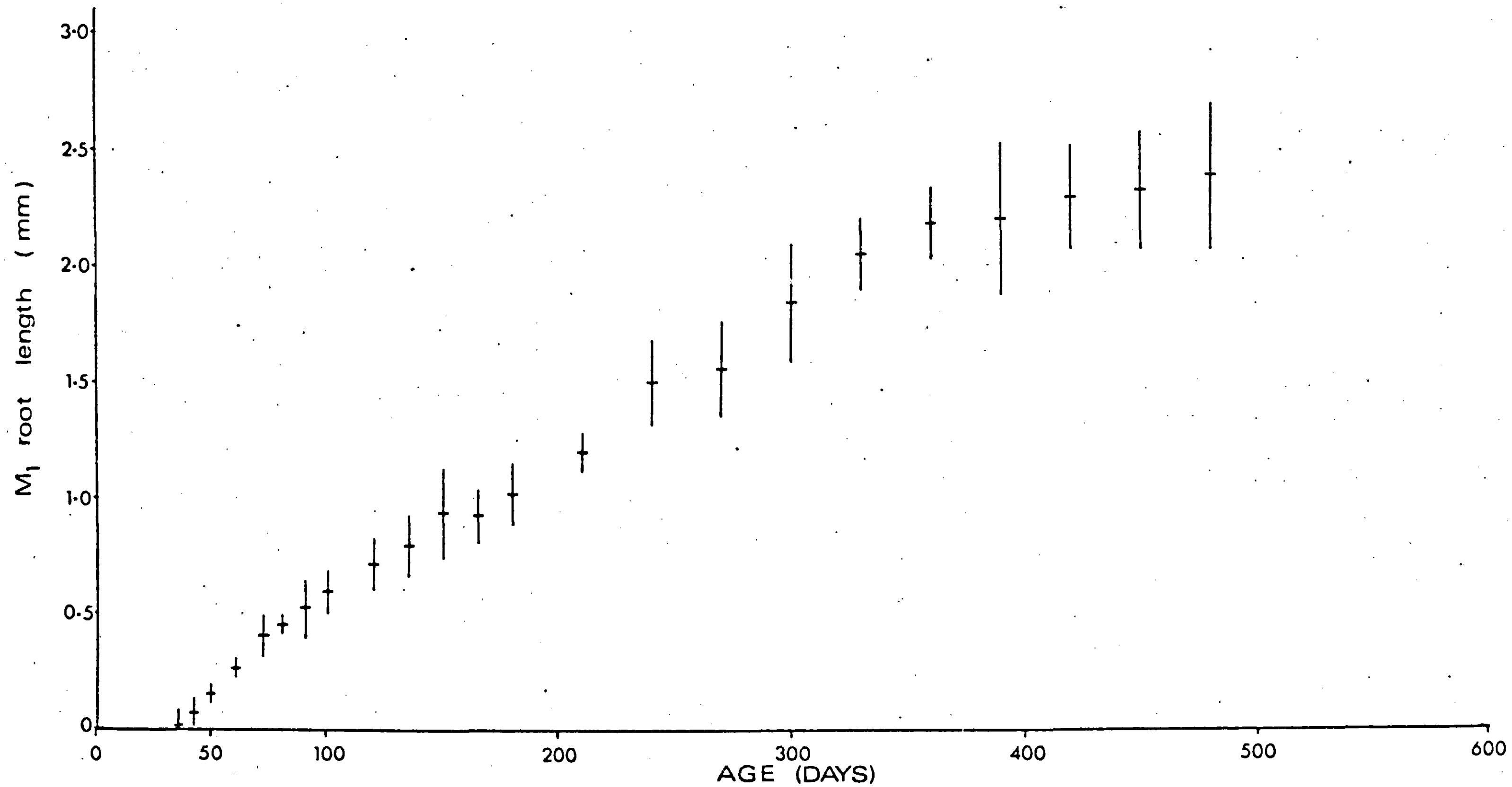


Fig. 19. Growth curve for the root length of M_1 of the mainland bank vole. The horizontal line represents the mean, and the vertical line represents one 95% confidence limits on each side of the mean.

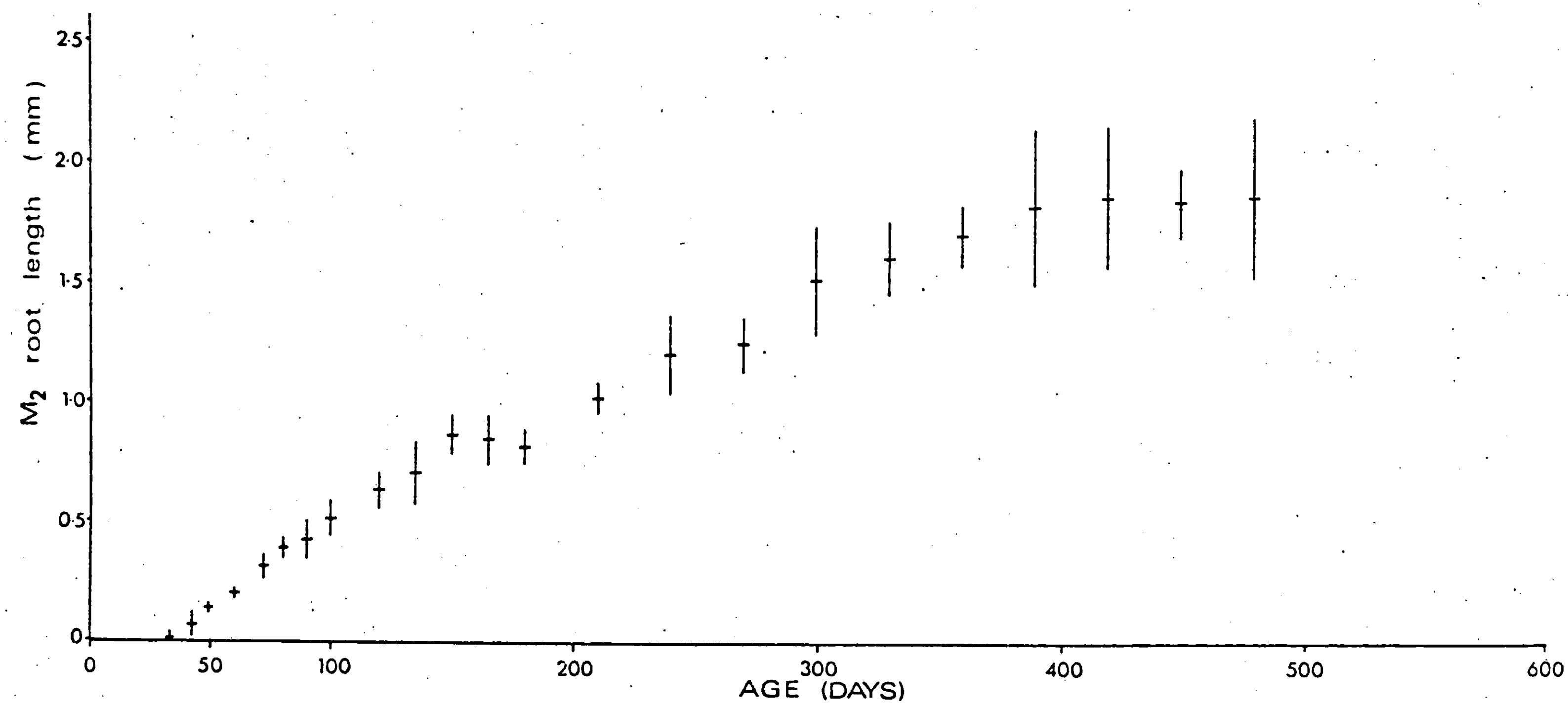


Fig. 20. Growth curve for the root length of M_2 of the mainland bank vole. (see Fig. 19 for explanation).

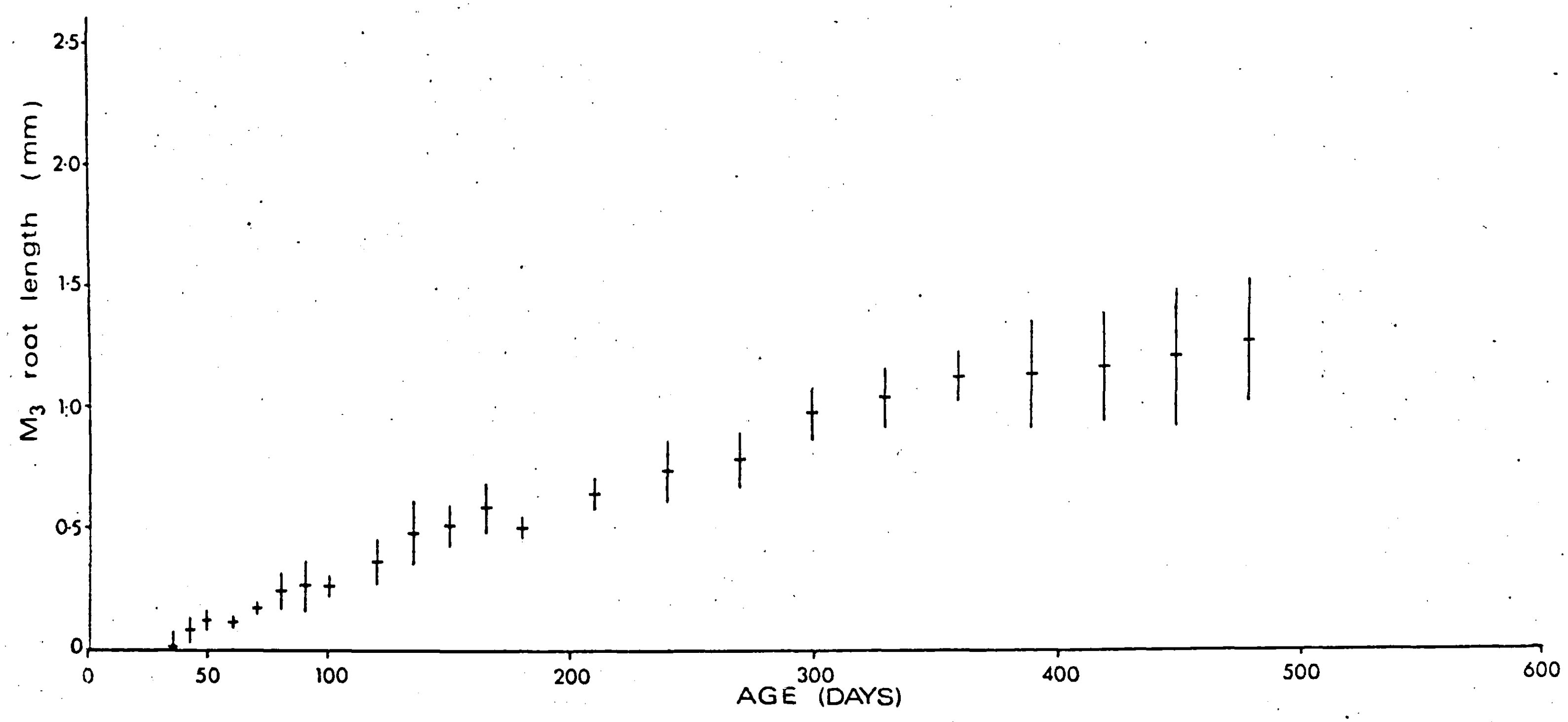


Fig. 21. Growth curve for the root length of M_3 of the mainland bank vole. (see Fig. 19 for explanation).

a.2. Estimating the age from the length of the neck and roots of the lower molars:

1. RM_1:

The whole sample was divided into 22 groups according to M_1 root length. The mean age, standard deviation, standard error, and coefficient of variation were taken for each size-group and 95% confidence limits were attached to the mean age, (Table 18).

Variability and standard deviation, for the distribution of the material within each group were low, and therefore accuracy for estimating the age of voles from the root length of M_1 is high, extending from ± 1.9 day for a mean age of 59.2 days (group 3), to ± 85.9 days for a mean age of 378 days (group 19).

The most variable root length value was 0.7 to 0.79 mm (group 8). The accuracy for estimating the age of voles with this root length is still high (being ± 18.4 days), because the age of most of the specimens belonging to this group concentrated around the mean age of the group, and therefore voles with this root length would most likely have a mean age of 133.5 days, a minimum age of 115 days, and a maximum age of 151.9 days.

The high correlation coefficient (r=0.96), the low variability ($\bar{v}$=14.29), and the high accuracy for estimating the age, made the use of M_1 root length of high value as an age indicator throughout life.

Table 18. Numerical data for estimating the age of the mainland bank vole from the root length of M_1 :

G. No	RM_1 l/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.03-0.09	4	35- 49	42.0± 2.86	5.72	13.61	32.9- 51.1
2	0.1-0.19	14	42- 60	50.4± 1.55	5.79	11.49	47.0- 53.7
3	0.2-0.29	13	49- 60	59.2± 0.85	3.05	5.16	57.3- 61.0
4	0.3-0.39	15	60-100	71.9± 3.21	12.43	17.30	65.0- 78.7
5	0.4-0.49	12	60-100	79.7± 3.00	10.40	13.06	73.1- 86.3
6	0.5-0.59	12	80-120	98.3± 4.41	15.28	15.53	88.6-108.0
7	0.6-0.69	8	90-150	119.4± 8.68	24.56	20.57	98.8-140.0
8	0.7-0.79	13	100-180	133.5± 8.46	30.51	22.86	115.0-151.9
9	0.8-0.89	6	120-180	147.5±10.55	25.84	17.52	120.4-174.6
10	0.9-0.99	8	120-210	163.1±13.12	37.12	22.76	132.0-194.2
11	1.0-1.09	15	150-270	186.0± 8.64	33.45	17.98	167.5-204.5
12	1.1-1.19	9	150-270	203.3±12.02	36.06	17.73	175.6-231.1
13	1.2-1.21	6	180-240	210.0± 7.74	18.97	9.04	190.1-229.9
14	1.3-1.49	8	180-240	213.8± 6.80	19.23	8.99	197.6-229.9
15	1.5-1.59	6	240-270	260.0± 6.32	15.49	5.95	243.8-276.2
16	1.6-1.79	7	240-330	278.6±12.62	33.38	11.98	247.7-309.5
17	1.8-1.99	5	240-360	300.0±21.21	47.43	15.81	241.0-359.0
18	2.0-2.09	7	270-450	355.7±23.08	61.06	17.17	299.2-412.3
19	2.1-2.19	5	330-480	378.0±30.89	69.07	18.27	292.1-463.9
20	2.2-2.39	16	330-540	433.1±17.10	68.38	15.79	396.7-469.6
21	2.4-2.59	5	390-510	444.0±19.90	44.50	10.02	388.7-499.3
22	2.6-2.80	3	480-540	510.0±17.32	30.00	5.88	435.5-584.5

2. $\underline{RM_2}$:

The whole sample was divided into 17 RM_2-length groups. Data were treated as before (Table 19).

Although, M_2 has not been thought of, by many, as a tooth useful for age determination, it proved, in the present study, to be of high value for this purpose. The accuracy for estimating the age from the root length of M_2 was found to be very high, extending from ± 3.4 days for a mean age of 52.7 days and 63 days and root length of 0.1 to 0.29 mm (groups 2 & 3), to ± 48 days for a mean age of 431.3 days and root length of 1.8 to 1.89 mm (group 16).

The most variable root length value was 0.7 to 0.79 mm (v=15.92), corresponding to a mean age of 160.5 days, a minimum age of 142 days and a maximum age of 178.8 days (group 8).

The accuracy for estimating the age of voles from the root length of M_2. were higher than those obtained for the root length of M_1.

The high accuracy, in addition to the low variability in the distribution of the material ($\bar{v}$=11.68) make the use of the root length of M_2 of higher value than M_1 throughout life.

Table 19. Numerical data for estimating the age of the mainland bank vole from the root length of M_2 :

G. No	RM_2l/ mm	F.	O. Range// days	Mean±S.E.	S.D	V.	Estimated age range/95%c.l.
1	0.03-0.09	4	35- 42	40.3± 1.75	3.50	8.70	34.7- 45.8
2	0.1-0.19	17	42- 60	52.7± 1.62	6.67	12.65	49.3- 56.1
3	0.2-0.29	12	60- 72	63.0± 1.57	5.43	8.61	59.6- 66.5
4	0.3-0.39	14	60- 90	77.7± 2.07	7.76	9.99	73.2- 82.2
5	0.4-0.49	10	80-100	93.0± 2.60	8.23	8.85	87.1- 98.9
6	0.5-0.59	10	80-120	105.0± 4.53	14.34	13.65	94.8-115.2
7	0.6-0.69	9	100-135	122.2± 4.80	14.39	11.77	111.1-133.3
8	0.7-0.79	10	120-180	160.5± 8.08	25.54	15.92	142.2-178.8
9	0.8-0.89	12	150-210	173.8± 6.25	21.65	12.46	160.0-187.5
10	0.9-0.99	13	135-210	184.6± 7.48	26.96	14.60	168.3-200.9
11	1.0-1.09	10	210-270	231.0± 7.81	24.70	10.69	213.4-248.7
12	1.1-1.29	13	210-270	237.7± 7.17	25.87	10.88	222.1-253.3
13	1.3-1.39	5	270-300	276.0± 6.00	13.42	4.86	259.3-292.7
14	1.4-1.59	10	240-360	306.0±14.00	44.27	14.47	274.4-337.6
15	1.6-1.79	16	300-480	386.3±14.46	57.84	14.97	355.5-417.1
16	1.8-1.89	8	360-510	431.3±20.39	57.68	13.37	382.9-479.6
17	1.9-2.29	10	390-540	483.0±17.00	53.76	11.13	444.6-521.4

3. $\underline{RM_3}$

The whole sample was divided into 14 RM_3-length groups (Table 20).

Variability in the distribution of the material within each size-group was higher than in RM_1 and RM_2 ($\bar{v}$=16.78), and therefore the accuracy for estimating the age of voles from the root length of M_3 was lower. It extended from ± 4.8 days for a mean age of 51.8 days and a root length of 0.04 to 0.09 mm (group 1), to ± 86 days for a mean age of 470 days and a root length of 1.4 to 1.49 mm (group 13).

The most variable root length value was 0.2 to 0.29 mm corresponding to a mean age of 85.7 days. This might be due to individual variations in the onset of root development. The accuracy for estimating the age of voles in this group was ± 10.9 days (group 3).

Although the correlation coefficient between age and the growth of the roots of this molar was very high (r=0.95), there was high variability ($\bar{v}$=23.23, Appendix 20), and standard deviations, in addition to irregularities in the root shape. All these factors reduce the value of using this tooth compared with the two other lower molars.

Table 20. Numerical data for estimating the age of the mainland bank vole from the root length of M_3:

G. No	RM_3l/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.04-0.09	15	35- 60	51.8± 2.26	8.75	16.90	47.0- 56.6
2	0.1-0.19	26	42-100	67.7± 3.30	16.83	24.84	60.9- 74.5
3	0.2-0.29	18	49-120	85.7± 5.14	21.79	25.44	74.8- 96.5
4	0.3-0.39	14	80-135	101.8± 4.37	16.36	16.07	92.4-111.2
5	0.4-0.49	12	135-210	168.8± 7.64	26.47	15.68	151.9-185.6
6	0.5-0.59	22	120-240	174.6± 7.62	35.72	20.46	158.7-190.4
7	0.6-0.69	17	165-270	221.5± 9.50	39.16	17.68	201.3-241.6
8	0.7-0.79	11	135-270	222.3±11.23	37.24	16.75	197.2-247.3
9	0.8-0.99	11	210-450	297.3±19.59	64.98	21.86	253.6-341.0
10	1.0-1.09	12	270-480	352.5±18.14	62.83	17.82	312.6-392.4
11	1.1-1.19	8	330-450	371.3±15.97	45.18	12.17	333.4-409.1
12	1.2-1.39	13	360-540	456.9±17.37	62.63	13.71	419.1-494.8
13	1.4-1.49	3	450-510	470.0±20.00	34.63	7.37	384.0-556.0
14	1.5-1.55	2	480-540	510.0±30.00	42.43	8.32	*

* The 95% confidence limits were not attached to the mean age because the sample size was small.

a.3. Development and growth curves of the neck and roots of the three upper molars:

The relevant data are presented in Figs. 22, 23, & 24 and Appendices 21, 22, & 23.

The lateral grooves on the crown of each of the three upper molars started to close, at their 'upper'* end, at the age of 42 days in M^1 and M^3, and at the age of 35 days in M^2, the time when the neck started to develop. The neck grew with its 'upper' end open until the age of 72 to 90 days in M^1 and M^2, and 80 to 90 days in M^3. The roots developed afterwards, and grew regularly with an average monthly increase of 0.14 mm in RM^1; 0.12 mm in RM^2; and 0.10 mm in RM^3, in voles 90 to 420 days old. The growth of the roots slowed down afterwards, and the average monthly increase in voles 90 to 540 days old was 0.13 mm, 0.08 mm, and 0.06 mm, respectively.

The correlation coefficient between age and the length of the roots were 0.96 for RM^1; 0.95 for RM^2 and RM^3.

* or alveolar end.

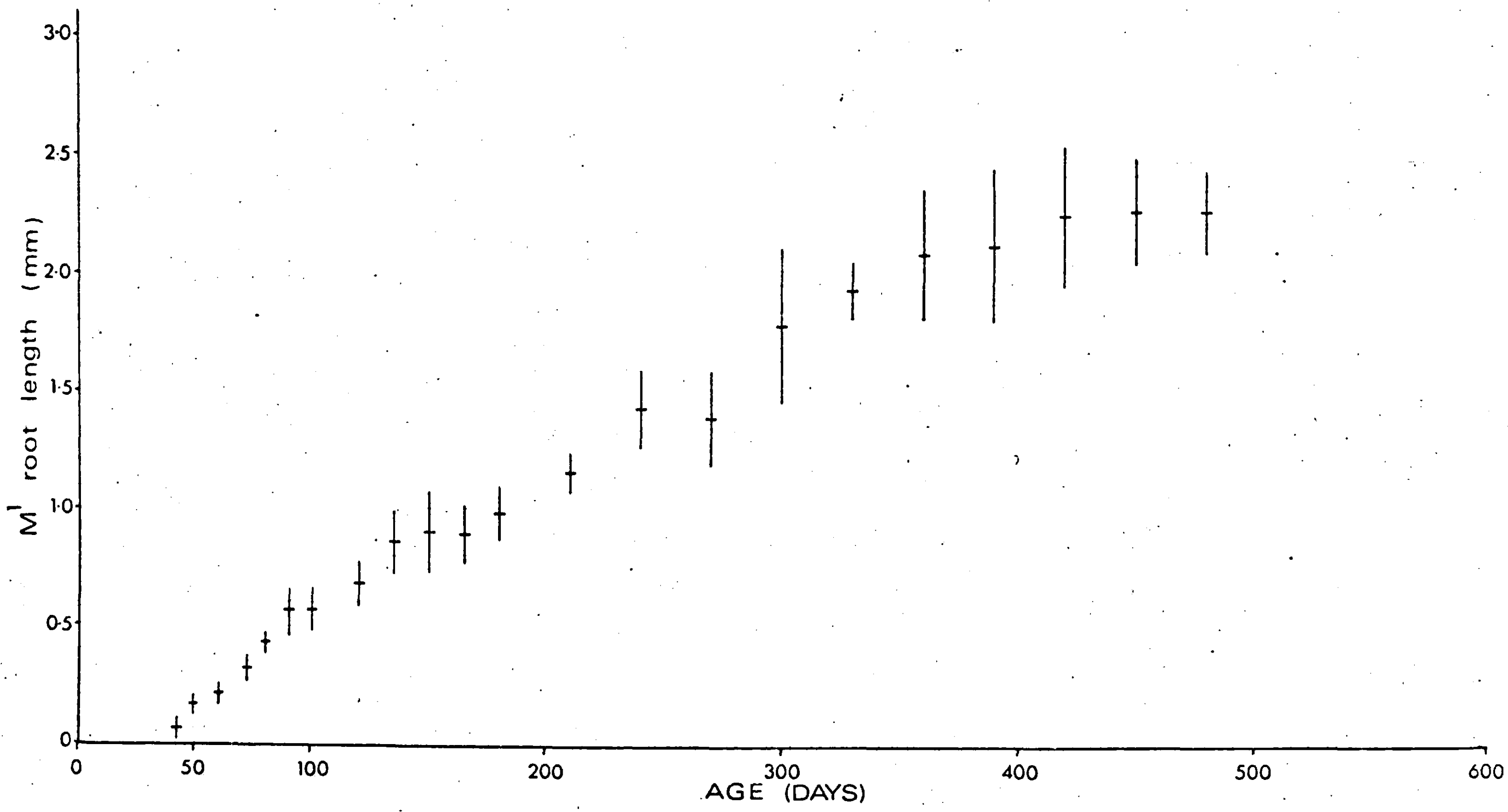


Fig. 22. Growth curve for the root length of M^1 of the mainland bank vole. (see Fig. 19 for explanation).

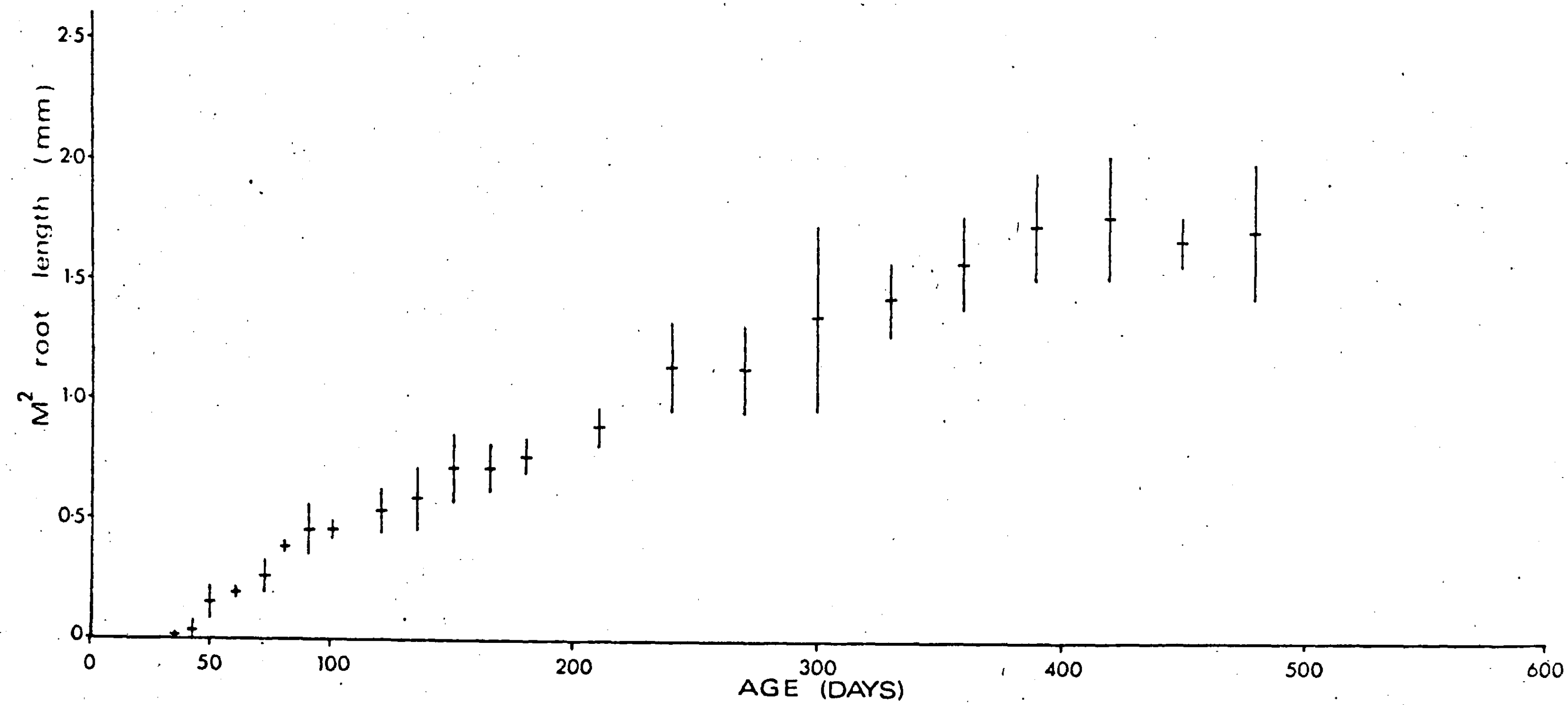


Fig. 23. Growth curve for the root length of M^2 of the mainland bank vole. (see Fig. 19 for explanation).

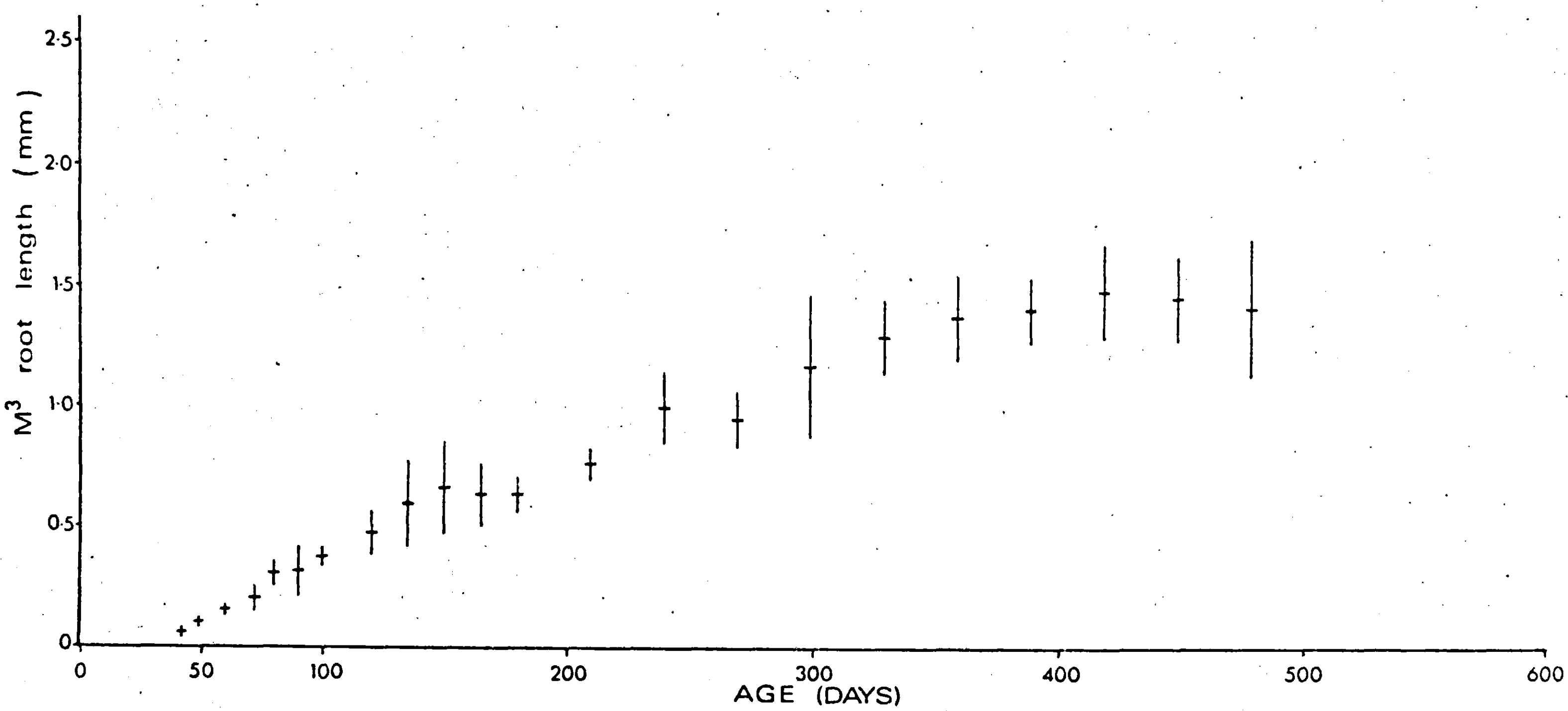


Fig. 24. Growth curve for the root length of M^3 of the mainland bank vole. (see Fig. 19 for explanation).

a.4. Estimating the age from the neck and root length of the upper molars:

1. RM^1:

The whole sample was divided into 20 RM^1-length groups (Table 21).

Variability in the distribution of the material within each size-group was not high ($\bar{v}$=14.86). The accuracy for estimating the age of voles from the root length of M^1 is high, extending from ± 4.5 days for a mean age of 52.4 and 60.2 days, and a root length of 0.1 to 0.29 mm (groups 2 & 3), to ± 62.4 days for a mean age of 288 days and a root length of 1.5 to 1.69 mm (group 15).

The most variable root length value was 0.8 to 0.89 mm, (v=22.87) corresponding to an average age of 152.9 days, a minimum age of 132.7 and a maximum of 173 days (group 9).

The variability for the distribution of the material was found to be lower above an average age of 210 days with the root length being more than 1.1 mm (groups 12 & 20).

The high accuracy for estimating the age of bank voles from the root length of M^1 as has been shown in table 21, along with the high correlation coefficient made the use of this character for determining the age of the bank vole of a high value.

Table 21. Numerical data for estimating the age of the main-land bank vole from the root length of $_{M}1$:

G. No	RM^1 l/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.04-0.09	9	42- 60	50.3± 2.62	7.86	15.61	44.3- 56.4
2	0.1-0.19	12	42- 60	52.4± 2.06	7.15	13.65	47.9- 56.9
3	0.2-0.29	14	49- 72	60.2± 2.09	7.82	12.98	55.7- 64.7
4	0.3-0.39	12	60- 80	69.0± 2.47	8.55	12.39	63.6- 74.4
5	0.4-0.49	12	80-120	90.8± 3.58	12.40	13.65	83.0- 98.7
6	0.5-0.59	8	80-120	97.5± 5.90	16.69	17.12	83.5-111.5
7	0.6-0.69	11	90-150	104.6± 5.62	18.64	17.82	92.0-117.1
8	0.7-0.79	10	120-180	150.0± 7.74	24.49	16.33	132.5-167.5
9	0.8-0.89	14	100-210	152.9± 9.34	34.96	22.87	132.7-173.0
10	0.9-0.99	7	135-210	171.4± 9.18	24.28	14.16	148.9-193.9
11	1.0-1.09	15	135-270	190.0±10.82	41.92	22.06	166.9-213.2
12	1.1-1.19	5	180-240	210.0± 9.49	21.21	10.10	183.6-236.4
13	1.2-1.29	9	180-270	220.0±11.18	35.54	15.25	194.2-245.8
14	1.3-1.49	13	210-270	242.3± 7.18	25.87	10.68	226.7-258.0
15	1.5-1.69	5	240-360	288.0±22.45	50.20	17.43	225.6-350.4
16	1.7-1.89	6	240-390	320.0±20.00	48.99	15.31	268.6-371.4
17	1.9-1.99	7	270-360	321.4±14.22	37.61	11.70	286.6-356.3
18	2.0-2.19	10	300-540	432.0±22.45	70.99	16.43	381.3-482.7
19	2.2-2.49	15	330-540	426.0±15.55	60.21	14.13	392.7-459.3
20	2.5-2.84	4	450-540	502.5±18.88	37.75	7.51	442.5-562.5

2. RM^2:

The whole sample was divided into 18 RM^2-length groups (Table 22).

The regularity in the distribution of the material according to RM^2 length, the reasonably low standard deviation, in addition to the low coefficient of variation ($\bar{v}$=15.72), gave this molar a high indication for use as a criterion of age.

It is not the first time that RM^2 has been used as an age criterion. It has been used for this purpose by Koshkina (1955); Tupikova et al (1968); and Viitala (1971). Their results will be discussed later.

3. RM^3:

The whole sample was divided into 15 RM^3-length groups (Table 23).

Variability for the distribution of the material within each size-group was not high ($\bar{v}$=15.22). The accuracy for estimating the age, extended from ± 2.2 days for a mean age of 45.8 days and a root length of 0.01 to 0.09 mm (group 1), to ± 74.5 days for a mean age of 480 days and a root length of 1.6 to 1.83 mm (group 15).

The most variable root length value was 0.4 to 0.49 mm (v=23.3),(individual variations in the onset of root development), corresponding to a mean age of 115.9 days and an accuracy of ± 18.2 days (group 5).

The small overlap of the data between the size-groups, in addition to the high correlation coefficient, suggest that the root length of M^3 is a reliable age indicator.

Table 22. Numerical data for estimating the age of the mainland bank vole from the root length of $_{M}2$:

G. No	RM^2l/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.02-0.09	6	35- 49	43.2± 2.15	5.27	12.21	37.6- 48.7
2	0.1-0.19	19	49- 72	57.2± 1.70	7.41	12.94	53.6- 60.8
3	0.2-0.29	11	49- 72	60.2± 2.20	7.28	12.09	55.3- 65.1
4	0.3-0.39	13	72-100	82.0± 2.58	9.31	11.35	76.4- 87.6
5	0.4-0.49	18	80-135	103.3± 4.18	17.74	17.17	94.5-112.2
6	0.5-0.59	10	90-165	115.5± 7.65	24.20	20.96	98.2-132.8
7	0.6-0.69	11	120-180	155.5± 7.64	25.34	16.30	138.4-172.5
8	0.7-0.79	16	135-210	182.8± 7.15	28.58	15.63	167.6-198.0
9	0.8-0.89	13	150-270	210.0±11.64	41.98	19.99	184.6-235.4
10	0.9-0.99	7	180-270	214.3±12.12	32.07	14.97	184.6-244.0
11	1.0-1.09	7	210-270	235.7±10.20	26.99	11.45	210.7-260.7
12	1.1-1.19	6	240-300	270.0±10.95	26.83	9.94	241.9-298.1
13	1.2-1.29	6	240-360	305.0±18.03	44.16	14.48	258.7-351.3
14	1.3-1.49	7	210-480	325.7±33.01	87.34	26.82	244.8-406.6
15	1.5-1.59	11	240-540	390.0±27.14	90.00	23.08	329.5-450.5
16	1.6-1.79	15	270-540	410.0±19.79	76.63	18.69	367.7-452.4
17	1.8-1.89	5	360-510	432.0±27.82	62.21	14.40	354.7-509.3
18	1.9-2.15	4	420-540	487.5±25.62	51.23	10.51	406.0-569.0

Table 23. Numerical data for estimating the age of the mainland bank vole from the root length of M^3 :

G. No	RM^3 l/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.01-0.09	13	42- 49	45.8± 1.01	3.63	7.94	43.6- 48.0
2	0.1-0.19	19	49- 72	60.7± 1.13	6.07	10.00	58.4- 63.1
3	0.2-0.29	17	60- 90	76.9± 2.50	10.30	13.39	71.6- 82.2
4	0.3-0.39	15	80-120	100.7± 3.71	14.38	14.28	92.7-108.6
5	0.4-0.49	11	80-165	115.9± 8.14	27.00	23.30	97.8-134.1
6	0.5-0.59	11	120-210	169.1± 9.51	31.53	18.65	147.9-190.3
7	0.6-0.69	15	120-210	173.0± 8.52	32.99	19.07	154.8-191.2
8	0.7-0.79	8	135-210	176.3± 9.30	26.29	14.92	154.2-198.3
9	0.8-0.89	19	135-270	222.6± 9.89	43.09	19.35	201.9-243.4
10	0.9-0.99	5	210-270	228.0±12.00	26.83	11.77	194.6-261.4
11	1.0-1.19	13	240-360	288.5±12.50	45.06	15.62	261.2-315.7
12	1.2-1.29	10	240-480	363.0±21.19	67.01	18.46	315.1-410.9
13	1.3-1.39	15	270-540	416.0±20.67	80.07	19.25	371.8-460.2
14	1.4-1.59	15	330-540	422.0±19.56	67.53	16.00	380.1-463.9
15	1.6-1.83	3	360-510	480.0±17.32	30.00	6.25	405.5-554.5

b. The Skomer vole:

Data for the development of the neck and roots of the lower and upper molars in the Skomer vole are presented for the two sexes combined, as no significant differences were found between them. The results of applying the t test on a sample of 136 specimens, 35 to 540 days old are:

Root length of the first lower molar, (RM_1): $t48=0.17$, $P > 0.8$
" " " " second " " , (RM_2): $t48=0.15$, $P > 0.8$
" " " " third " " , (RM_3): $t44=0.29$, $P > 0.7$

" " " " first upper " , (RM^1): $t46=0.14$, $P > 0.8$
" " " " second " " , (RM^2): $t46=0.06$, $P > 0.9$
" " " " third " " , (RM^3): $t46=0.16$, $P > 0.8$

b.1. Development and growth curves of the neck and roots of the three lower molars:

The relevant data are presented in Figs 25, 26, & 27, and Appendices 24, 25, & 26 .

The lateral grooves on the crowns of the lower molars started to close at their lower end at the age of 35 to 42 days in M_1 and M_2, and over the age of 42 days in M_3. The neck developed then, and grew until the central part of its lower end closed, and then the roots started to develop. This usually occurred at the age of 72 to 100 days in M_1 and M_2, though was sometimes delayed until 120 days. In M_3 it occurred when the voles were 90 to

120 days old.

The roots then grew regularly throughout life, with an average increase of 0.14 mm in RM_1, 0.12 mm in RM_2, and 0.07 mm in RM_3.

The length of the neck and roots was highly correlated with age, (r=o.98 for RM_1 and RM_2, and r=0.96 for RM_3).

Variability in the growth of RM_1 and RM_2 was not high, ($\bar{v}$=14.69 for RM_1, starting from the age of 49 days onward; $\bar{v}$=13.35 for RM_2, starting from the age of 42 days onward). They were higher in RM_3, ($\bar{v}$=19.96 for the whole sample).

In spite of the growth of RM_3 length being regular and highly correlated with age, the irregular shape of the roots made measuring their length very difficult, and the high variability decreased their value as age indicator.

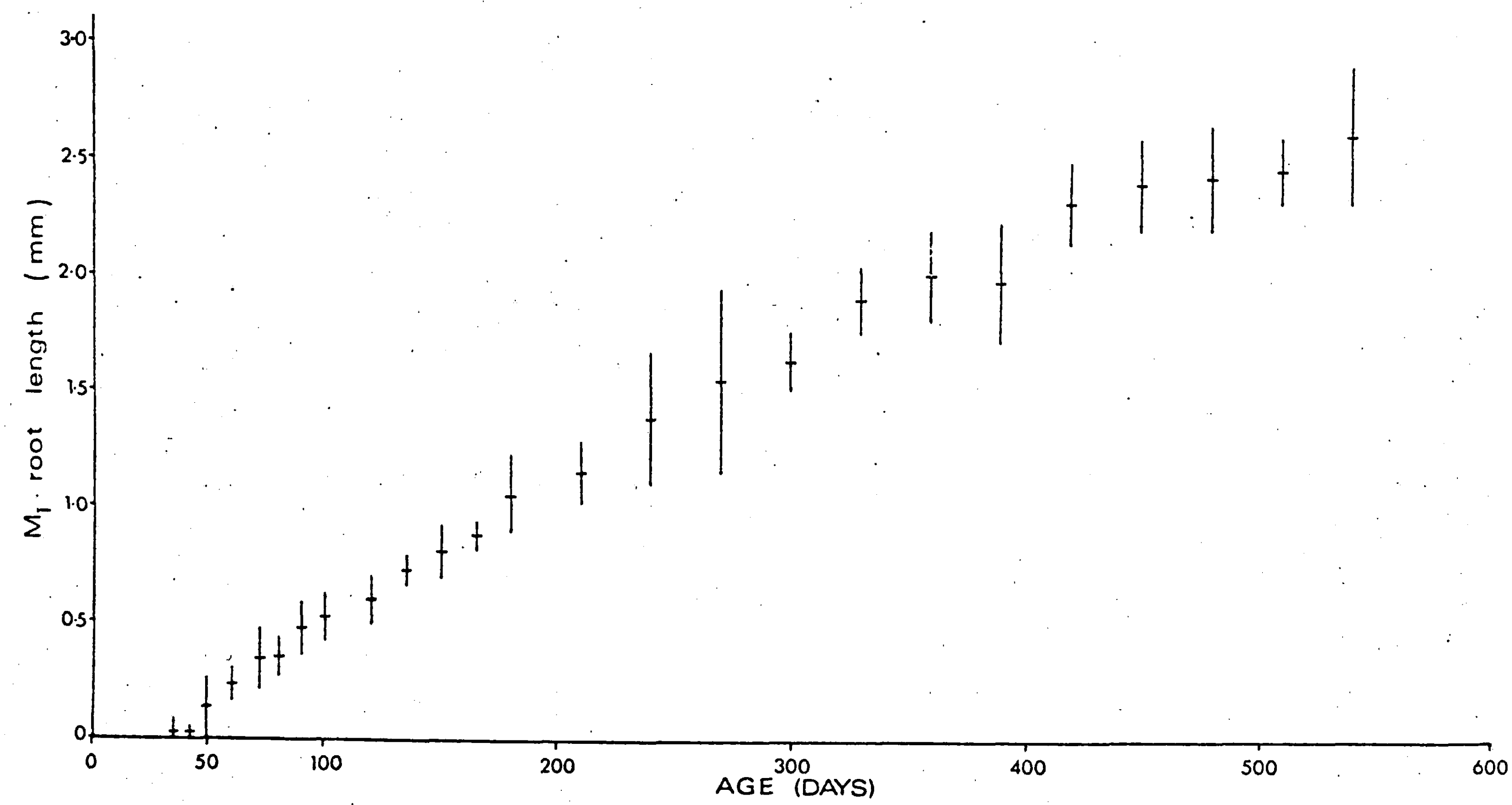


Fig. 25. Growth curve for the root length of M_1 of the Skomer vole. (see Fig. 19 for explanation).

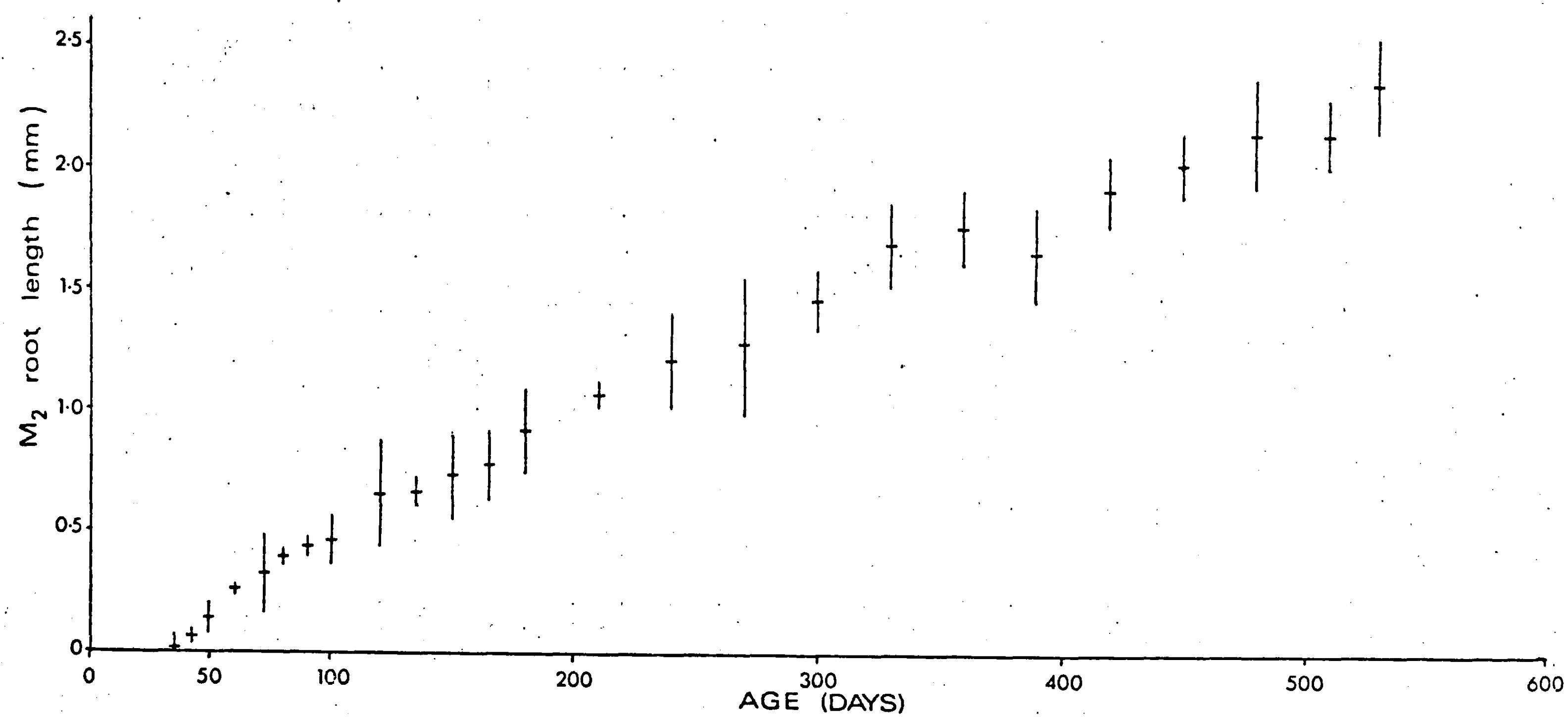


Fig. 26. Growth curve for the root length of M_2 of the Skomer vole. (see Fig. 19 for explanation).

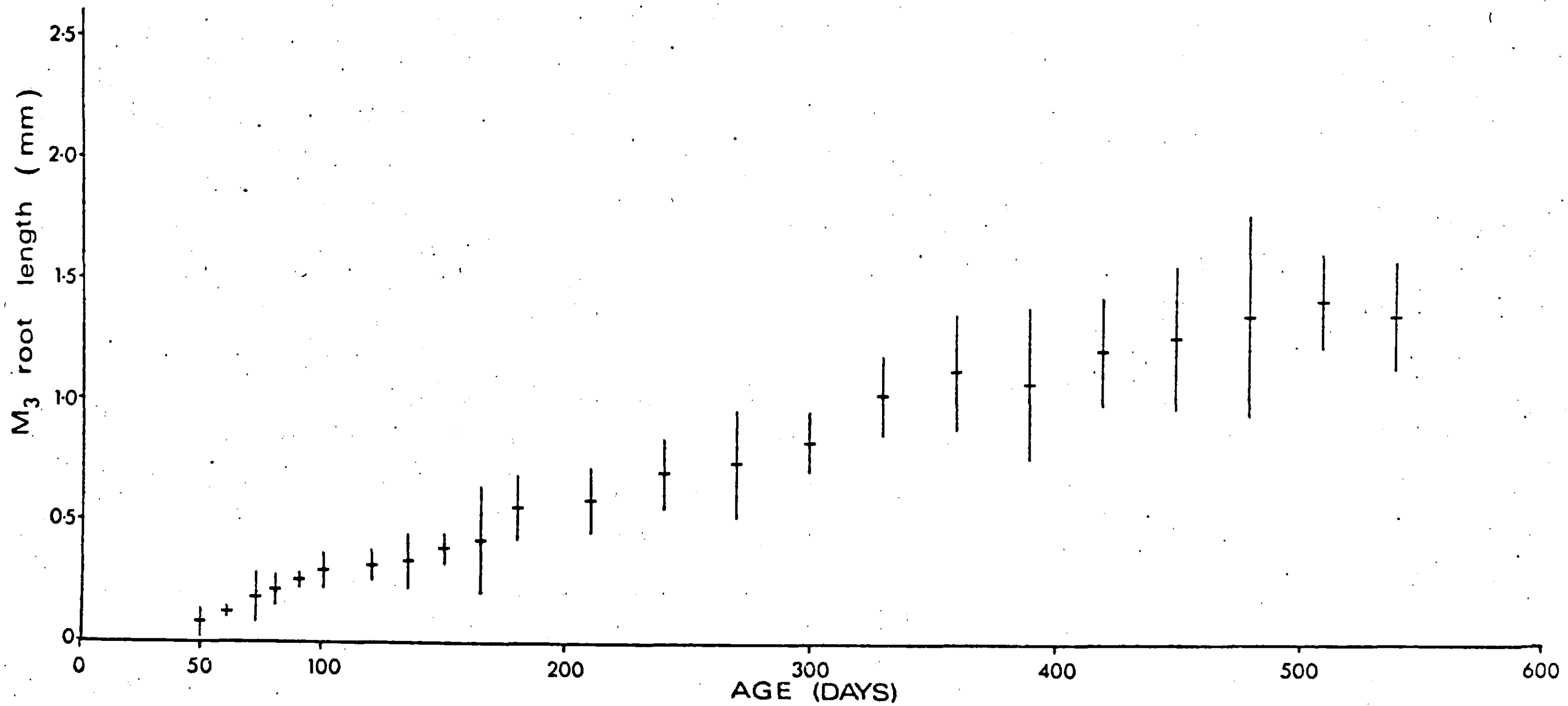


Fig. 27. Growth curve for the root length of M_3 of the Skomer vole. (see Fig. 19 for explanation).

b.2. Estimating the age of Skomer voles from the length of the neck and roots of the lower molars:

1. RM_1:

The whole sample was divided into 20 groups according to the length of the neck and roots of M_1 (Table 24).

Variability in the distribution of the material within each size-group was not high ($\bar{v}$=10.95). The accuracy for estimating the age was high extended from ± 4.7 days for a mean age of 58.2 days and a root length of 0.1 to 0.19 mm (group 2), to ± 61.3 days for a mean age of 375 and 486 days and a root length of 2.0 to 2.19 mm, and 2.4 to 2.49 mm, respectively (groups 16 & 19).

The most variable measurement for RM_1 length was 0.4 to 0.49 mm, (v=20.25). This group included voles with an average age of 85.3 days, a standard deviation of 17.3 days, a minimum age of 67.2 days, and a maximum age of 103.5 days (group 5).

The regular growth of the roots of M_1, the low variability and standard deviations, and the high correlation with age, made the use of M_1 root length value as an indicator of age.

Table 24. Numerical data for estimating the age of the Skomer vole from the root length of M_1 :

G. No	RM_1 l/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.04-0.09	5	35- 49	43.4± 2.62	5.86	13.49	36.1- 50.7
2	0.1-0.19	6	49- 60	58.2± 1.83	4.49	7.72	53.5- 62.9
3	0.2-0.29	7	49- 72	60.1± 2.51	6.64	11.05	54.0- 66.3
4	0.3-0.39	10	60- 90	76.4± 3.33	10.53	13.79	68.9- 83.9
5	0.4-0.49	6	60-100	85.3± 7.05	17.28	20.25	67.2-103.5
6	0.5-0.59	8	90-120	103.8± 4.98	14.08	13.57	92.0-115.6
7	0.6-0.69	5	100-135	118.0± 7.84	17.54	14.86	96.2-139.8
8	0.7-0.79	4	135-150	142.5± 4.33	8.66	6.08	128.7-156.3
9	0.8-0.89	6	135-165	155.0± 5.00	12.25	7.90	142.2-167.9
10	0.9-0.99	3	150-165	160.0± 3.85	8.66	5.41	143.4-176.6
11	1.0-1.19	10	180-240	204.0± 7.48	23.66	11.60	187.1-220.9
12	1.2-1.39	4	210-270	240.0±17.32	34.64	14.43	184.9-295.1
13	1.4-1.59	7	240-300	270.0±11.34	30.00	11.11	242.2-297.8
14	1.6-1.79	7	270-390	321.4±15.65	41.40	12.88	283.1-359.8
15	1.8-1.99	9	270-390	340.0±13.23	39.69	11.67	309.4-370.6
16	2.0-2.19	4	330-420	375.0±19.27	38.73	10.33	313.7-436.7
17	2.2-2.29	6	360-450	415.0±14.32	35.07	8.45	378.2-451.8
18	2.3-2.39	6	420-510	480.0±13.42	32.86	6.85	445.5-514.5
19	2.4-2.49	5	420-540	486.0±22.05	49.30	10.14	424.7-547.3
20	2.5-2.82	6	450-540	510.0±15.39	37.95	7.44	470.5-549.6

2. $\underline{RM_2}$:

The whole sample was divided into 20 RM_2-length groups (Table 25).

The distribution of the material within each group was regular, resulting in an average coefficient of variation, for the whole sample, of 10.07. The accuracy for estimating the age was very high and extended from ± 3 days, for a mean age of 40.8 days and a root length of o.o2 to 0.09 mm (group 1), to ± 60 days for a mean age of 412.5 days and a root length of 1.9 to 1.99 mm (group 16).

The most variable value for the root length was 0.5 to 0.59 mm (group 6), corresponding to a mean age of 114 days and an accuracy for estimating the age of ± 27.2 days.

The very low variability and standard deviations, in addition to the high correlation coefficient suggest that M_2 root length is a highly reliable indication of age.

3. $\underline{RM_3}$:

The whole sample was divided into 13 RM_3-length groups (Table 26).

Variability in the distribution of the material within each group were higher than in RM_1 and RM_2, ($\bar{v}$=16.08). Growth abnormalities in RM_3 were frequently encountered. The accuracy for estimating the age from the root length of M_3 was less than from M_1 and M_2. It extended from ± 4.8 days for a mean age of 55.9 days and a root length of 0.06 to 0.09 mm (group 1), to ± 74.5 days for a mean age of 510 days and a root length of 1.5 to 1.73 mm (group 13).

The most variable root length value was 0.2 to 0.29 mm (v=27.52), corresponding to a mean age of 102.8 days, and an accuracy for estimating the age of ± 13.6 days.

Although, the root length of M_3 was less accurate for estimating the age of the Skomer vole than M_1 and M_2, it is still a reliable criterion, but less so than the other two lower molars.

Table 25. Numerical data for estimating the age of the Skomer vole from the root length of M_2 :

G. No	RM_2l/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.02-0.09	6	35- 42	40.8± 1.17	2.85	7.00	37.8- 43.8
2	0.1-0.19	6	49- 60	52.7± 2.32	5.68	10.78	46.7- 58.6
3	0.2-0.29	10	60- 72	62.4± 1.60	5.06	8.11	58.8- 66.0
4	0.3-0.39	8	60-100	76.5± 5.93	16.76	21.91	62.5- 90.6
5	0.4-0.49	8	72-100	87.8± 3.49	9.88	11.26	79.5- 96.0
6	0.5-0.59	5	100-150	114.0± 9.80	21.91	19.22	86.8-141.2
7	0.6-0.69	6	120-165	135.0± 6.71	16.43	12.17	117.8-152.2
8	0.7-0.79	7	135-180	154.3± 6.31	16.69	10.82	138.8-169.8
9	0.8-0.99	4	150-165	157.5± 4.33	8.66	5.50	143.7-171.3
10	1.0-1.19	12	180-270	212.5± 7.80	27.01	12.71	195.3-229.7
11	1.2-1.39	8	240-300	266.3± 8.85	25.04	9.40	245.3-287.2
12	1.4-1.59	8	300-390	333.8±14.39	40.69	12.19	300.0-367.9
13	1.6-1.69	5	270-390	342.0±20.35	45.50	13.30	285.4-398.6
14	1.7-1.79	6	300-420	350.0±18.44	45.17	12.90	302.6-397.4
15	1.8-1.89	4	360-420	382.5±14.36	28.72	7.51	336.8-428.2
16	1.9-1.99	4	360-450	412.5±18.88	37.75	9.15	352.5-472.5
17	2.0-2.09	5	420-510	462.0±15.30	34.21	7.40	419.5-504.5
18	2.1-2.19	6	450-510	490.0±10.00	24.49	5.00	464.3-515.7
19	2.2-2.39	5	480-540	522.0±12.00	26.83	5.14	488.6-555.4
20	2.49 mm	1	540 days	540.0± -	-	-	540.0 days

Table 26. Numerical data for estimating the age of the Skomer vole from the root length of M_3 :

G. No	RM_3l/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.06-0.09	8	49- 60	55.9± 2.01	5.69	10.19	51.1- 60.6
2	0.1-0.19	12	49- 80	62.8± 2.33	8.08	12.88	57.6- 67.9
3	0.2-0.29	19	72-165	102.8± 6.49	28.30	27.52	89.2-116.5
4	0.3-0.39	12	100-165	128.8± 6.43	22.27	17.30	114.6-142.9
5	0.4-0.49	5	135-180	165.0±13.42	30.00	18.18	127.7-202.3
6	0.5-0.59	6	165-270	212.5±15.69	38.44	18.09	172.2-252.4
7	0.6-0.69	6	165-300	212.5±20.65	50.57	23.80	159.4-265.6
8	0.7-0.79	10	210-390	270.0±16.73	52.92	19.60	232.2-307.8
9	0.8-0.89	5	240-360	306.0±19.90	44.50	14.54	250.7-361.3
10	0.9-1.09	11	270-390	346.4±13.64	45.23	13.06	315.9-367.8
11	1.1-1.29	12	330-540	447.5±16.29	56.43	12.61	411.7-483.3
12	1.3-1.49	10	360-540	453.0±22.11	69.93	15.44	403.0-503.0
13	1.5-1.73	3	480-540	510.0±17.32	30.00	5.88	435.5-584.5

b.3. Development and growth curves of the neck and roots of the three upper molars:

The relevant data are presented in Figs. 28, 29, & 30, and Appendices 27, 28, & 29.

The lateral grooves on the crowns of the upper molars closed at their 'upper'* end when the voles were 35 to 42 days old. The neck then developed and grew until it had its middle 'upper' point closed at the age of 72 to 100 days, though was sometimes delayed until 120 days in M^2 only. The earliest closure for the neck of M^2 was recorded in only one vole 60 days old. The roots then developed and grew regularly throughout life with an average monthly increase of 0.1mm in RM^1, 0.11 mm in RM^2, and 0.09 mm in RM^3.

The growth of the neck and roots of the upper molars was highly correlated with age, ($r=0.95$ for RM^1; $r=0.96$ for RM^2 and RM^3).

Variability was not high in the root length of M^1 and M^2, as the mean value for the coefficient of variation for the whole sample ($\bar{v}$) was 15.5 & 16.35 respectively. The variability was higher in RM^3, ($\bar{v}=20.04$).

* alveolar end.

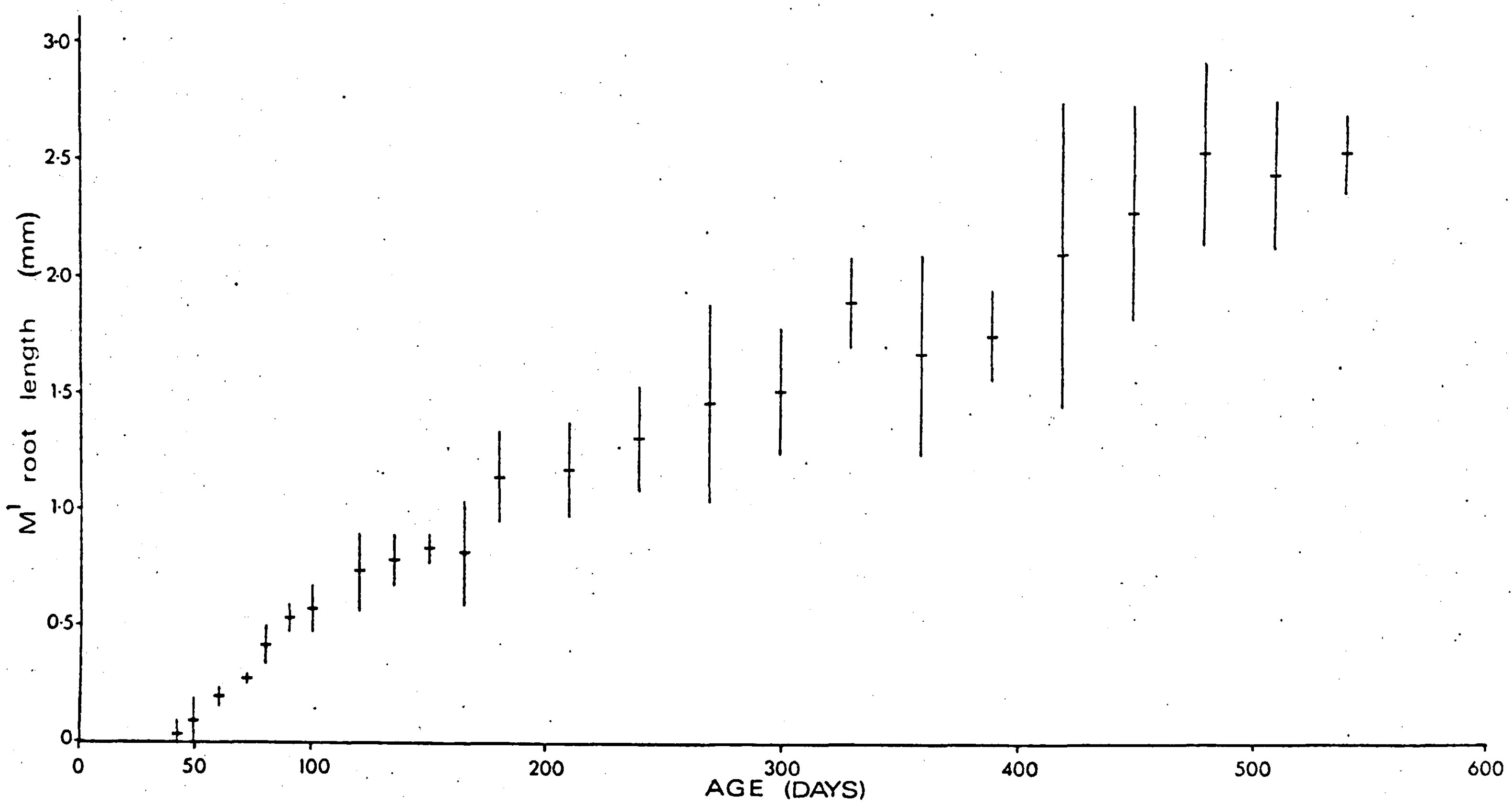


Fig. 28. Growth curve for the root length of M^1 of the Skomer vole. (see Fig. 19 for explanation).

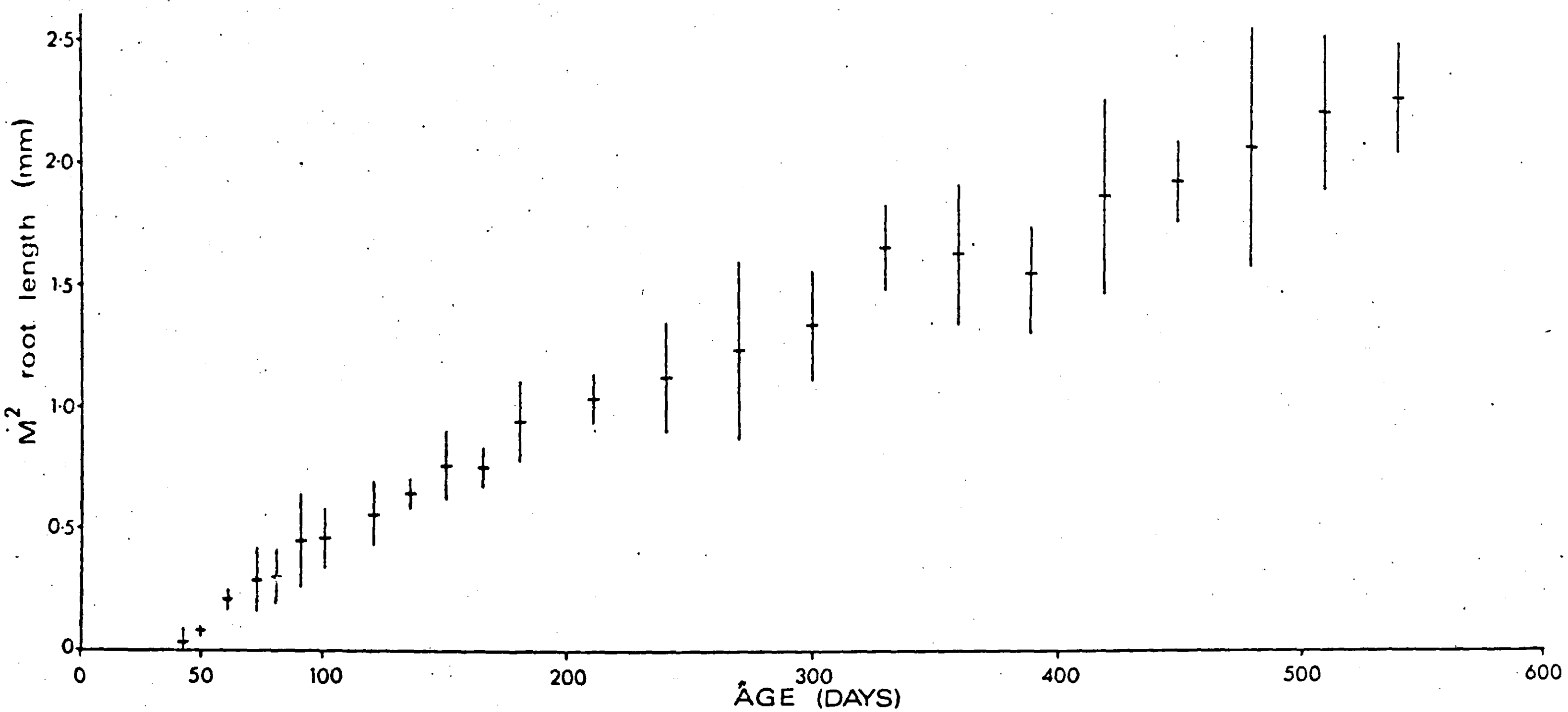


Fig. 29. Growth curve for the root length of M^2 of the Skomer vole. (see Fig. 19 for explanation).

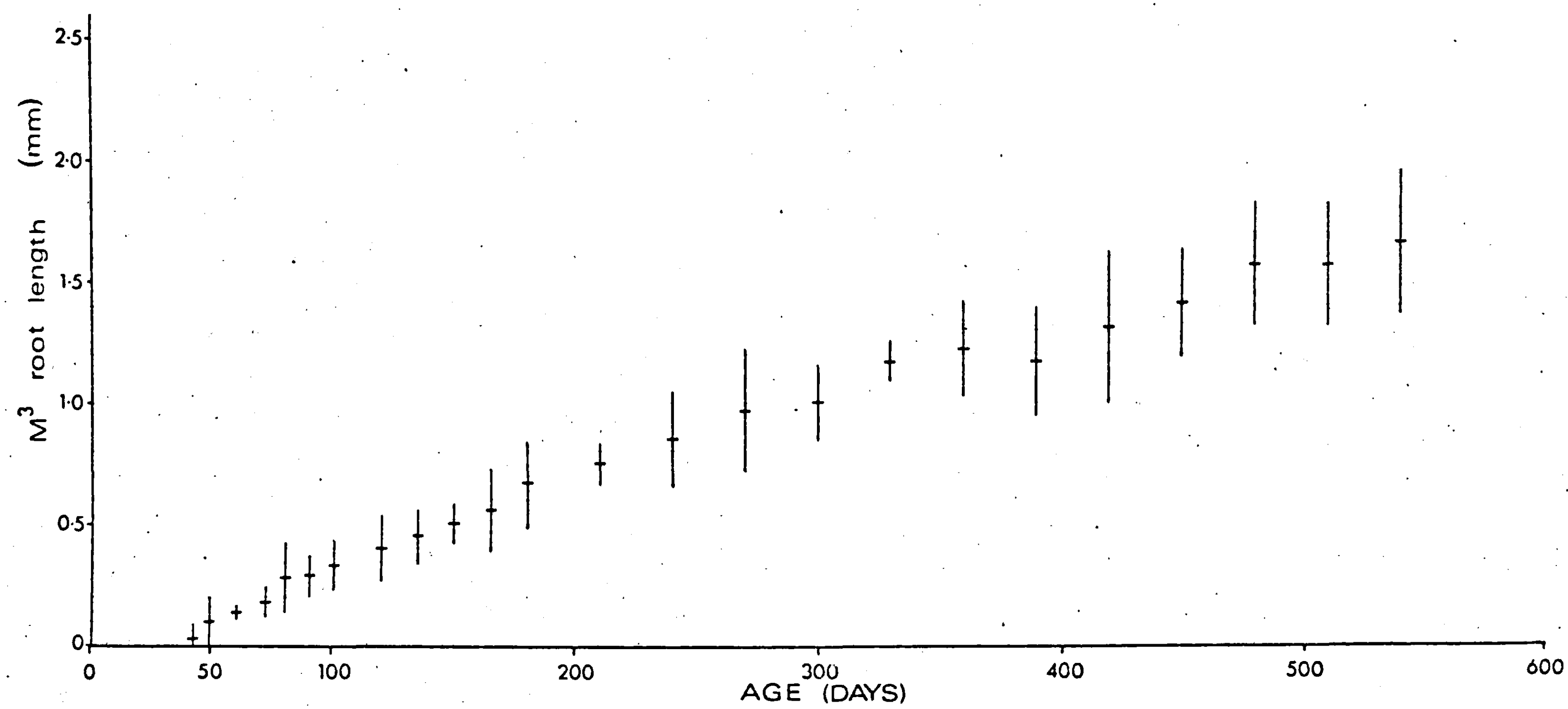


Fig. 30. Growth curve for the root length of M^3 of the Skomer vole. (see Fig. 19 for explanation).

b.4. Estimating the age of the Skomer vole from the length of the neck and roots of the upper molars:

1. RM^1:

The whole sample was divided into 17 groups according to the length of the neck and roots of M^1. The mean age, standard deviation, standard error, and coefficient of variation were taken for each group, and are presented in table 27. The 95% confidence limits were attached to the mean age of each size-group.

The root length of M^1 proved to be a reliable criterion as an age indicator. Variability within each group is low ($\bar{v}$=12.41). The accuracy for estimating the age was high, extended from ± 4.5 days for a mean age of 57.1 days and a root length of 0.1 to o.19 mm (group 2), to ± 74.5 days (groups 10 & 17). The low accuracy for the latter two groups was mainly due to the small sample size (only 3 specimens comprised each of them).

The most variable root length value was 1.1 to 1.29 mm (group 11) corresponding to a mean age of 242.7 days, and an accuracy for estimating the age of ± 39.8 days.

Table 27. Numerical data for estimating the age of the Skomer vole from the root length of $_{M}1$:

G. No	$RM^1$1/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.02-0.09	4	42- 49	47.3± 1.75	3.50	3.50	41.7- 52.8
2	0.1-0.19	10	42- 60	57.1± 2.00	6.33	11.09	52.6- 61.6
3	0.2-0.39	9	60- 80	67.6± 2.53	7.60	11.25	61.7- 73.4
4	0.4-0.49	7	80-100	87.1± 3.59	9.51	10.92	73.3- 95.9
5	0.5-0.59	5	90-100	92.0± 2.00	4.47	4.86	86.4- 97.6
6	0.6-0.69	7	100-165	117.1± 9.50	25.14	21.46	93.9-140.4
7	0.7-0.79	6	120-165	137.5± 7.16	17.54	12.75	119.1-155.9
8	0.8-0.89	8	120-165	144.4± 4.86	13.74	9.52	132.9-155.9
9	0.9-0.99	4	165-210	180.0±10.65	21.21	11.79	146.1-213.9
10	1.0-1.09	3	210-270	240.0±17.32	30.00	12.50	165.5-314.5
11	1.1-1.29	11	180-360	242.7±17.84	59.18	24.38	203.0-282.5
12	1.3-1.49	4	210-300	240.0±21.22	42.43	17.68	172.5-307.5
13	1.5-1.69	9	240-420	320.0±21.21	63.64	19.89	271.0-369.0
14	1.7-1.99	13	270-450	355.4±12.64	45.57	12.82	327.8-383.0
15	2.0-2.39	7	420-510	462.9±14.43	38.17	8.25	427.5-498.2
16	2.4-2.59	9	420-540	496.7±14.24	42.72	8.60	463.8-529.6
17	2.6-2.80	3	480-540	510.0±17.32	30.00	5.88	435.5-584.5

2. RM^2:

The whole sample was divided into 20 RM^2-length groups (Table 28).

The distribution of the material within each group was regular and the variability was not high ($\bar{v}$=14.6). The accuracy for estimating the age extended from ± 5.6 days (group 1), to ± 98.4 days (group 19). The low accuracy for the latter group and also for group 14 (accuracy being ± 90.3 days) was mainly due to the small sample size.

The most variable root length value was 0.8 to 0.89 mm (v=24.44) corresponding to an average age of 182.1 days (group 9).

Therefore, the root length of M^2 is considered to be a good index of age, but is less reliable than the root length of M^1.

3. RM^3:

The whole sample was divided into 14 RM^3-length groups (Table 29).

Variability in this molar was higher than in RM^1 and RM^2 ($\bar{v}$=16.33). The accuracy for estimating the age extended from ± 4.2 days (group 2), to ± 70.9 days (group 9). The most variable root length value was 0.4 to 0.49 mm (v= 24.94).

Again this measurement is a good index, but it is less reliable than RM^1 and RM^2.

Table 28. Numerical data for estimating the age of the Skomer vole from the root length of $_{M}2$:

G. No	$RM^2$1/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.06-0.09	4	42- 49	47.3± 1.73	3.50	7.41	41.7- 52.8
2	0.1-0.19	7	42- 60	55.9± 2.78	7.36	13.17	49.1- 62.7
3	0.2-0.29	10	60- 80	66.4± 2.74	8.68	13.08	60.2- 72.6
4	0.3-0.39	12	60-100	82.8± 4.20	14.56	17.58	73.6- 92.1
5	0.4-0.49	3	80-120	100.0±11.55	20.00	20.00	50.3-149.7
6	0.5-0.59	7	90-135	109.3± 6.02	15.92	14.57	94.5-124.0
7	0.6-0.69	7	90-150	130.7± 7.82	20.70	15.84	111.6-149.9
8	0.7-0.79	5	135-165	159.0± 6.00	13.42	8.44	142.3-175.7
9	0.8-0.89	7	150-270	182.1±19.91	44.52	24.44	133.4-230.9
10	0.9-0.99	4	180-240	217.5±14.36	28.72	13.21	171.8-263.2
11	1.0-1.09	8	180-300	232.5±17.70	50.07	21.54	190.6-274.5
12	1.1-1.29	5	210-360	270.0±26.83	60.00	22.22	195.4-344.6
13	1.3-1.39	5	240-390	294.0±25.81	57.71	19.63	222.3-365.8
14	1.4-1.49	4	300-420	337.5±28.40	56.79	16.83	247.2-427.8
15	1.5-1.59	5	270-390	348.0±22.45	50.20	14.43	285.6-410.4
16	1.6-1.69	4	360-390	367.5± 7.50	15.00	4.08	343.7-391.4
17	1.7-1.89	9	300-480	383.3±21.08	63.25	16.50	334.6-432.0
18	1.9-2.09	9	360-540	470.0±17.32	51.96	11.06	430.0-510.0
19	2.1-2.29	4	420-540	472.5±30.93	61.85	13.09	374.1-570.9
20	2.3-2.50	5	480-540	516.0±11.22	25.10	4.86	484.8-547.3

Table 29. Numerical data for estimating the age of the Skomer vole from the root length of M^3 :

G. No	RM^3l/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.04-0.09	7	42- 60	50.1± 2.81	7.43	14.81	43.3- 57.0
2	0.1-0.19	11	49- 72	61.2± 1.89	6.27	10.26	57.0- 65.4
3	0.2-0.29	14	60-100	79.6± 3.65	13.66	17.17	71.7- 87.5
4	0.3-0.39	8	90-135	110.0± 6.20	17.53	15.93	95.3-124.7
5	0.4-0.49	8	80-165	128.1±11.30	31.95	24.94	101.4-154.9
6	0.5-0.59	8	100-165	140.0± 7.38	20.87	14.91	122.5-157.5
7	0.6-0.69	6	135-240	187.5±14.36	35.18	18.76	150.6-224.4
8	0.7-0.79	7	165-270	210.0±14.27	37.75	17.98	175.0-245.0
9	0.8-0.89	6	180-360	250.0±27.57	67.53	27.01	179.2-320.9
10	0.9-1.09	14	240-420	306.4±14.13	52.86	17.25	275.9-337.0
11	1.1-1.29	9	270-420	350.0±15.00	45.00	12.86	315.4-384.7
12	1.3-1.39	7	300-510	415.7±24.87	65.79	15.83	354.8-476.6
13	1.4-1.59	12	360-510	447.5±18.26	63.26	14.14	407.3-487.7
14	1.6-1.90	7	450-540	510.0±13.07	34.64	6.79	478.0-542.0

II. Tooth wear:

The whole sample of each subspecies was divided into two groups, according to the presence or absence of a neck & roots in their molar teeth. The first group included all young voles up to 35 days old. The growth of their molar crowns was studied. The second group included all voles 42 days and older. The wear of their molar crowns was studied.

a. The mainland bank vole:

Data for tooth wear in the mainland bank vole are presented combined for the two sexes, as no significant differences were found between them. The results of applying the t test on 199 specimens, 5 to 540 days old, are:

Crown of the	first lower	molar,	(CM_1):	$t_{64}=0.18$,	$P>0.8$
" " "	second "	"	(CM_2):	$t_{64}=0.26$,	$P>0.7$
" " "	third "	"	(CM_3):	$t_{64}=0.16$,	$P>0.8$
" " "	first upper	"	(CM^1):	$t_{64}=0.42$,	$P>0.6$
" " "	second "	"	(CM^2):	$t_{64}=0.32$,	$P>0.7$
" " "	third "	"	(CM^3):	$t_{60}=0.31$,	$P>0.7$

a.1. Growth and wear of molar crowns:

Data for the growth and wear of each of the six molars in the mainland bank vole are presented in Figs. 31 to 36 and Appendices 30 to 35.

The crown, of each molar, grew very quickly during the first month of the vole's life. It reached its maximum height at an age extending from 30 to 35 days in CM_1, (average height was 3.34 to 3.35 mm); 30 days in CM_2, (average, 3.04 mm); 35 days in CM_3, (2.7 mm); 35 to 42 days in CM^1, (3.92 mm); 35 days in CM^2, (3.23 mm); and 35 to 42 days in CM^3 (2.38 mm).

The crown height, over the age of 14 days, was affected by wear, as the voles had started to eat solid food by that time. Since the growth was very fast during the first month, tooth wear was not obvious.

The crown, after reaching its maximum height, ceased to grow. Its height started to decrease, as a result of wear, and continued throughout life, with a monthly average rate of 0.14 mm in CM_1; 0.12 mm in CM_2; 0.09 mm in CM_3; 0.16 mm in CM^1; 0.13 mm in CM^2; and 0.08 mm in CM^3.

The growth and wear of the crowns of all the lower and upper molars were highly correlated with age. Variability was not high throughout life (Table 30).

Table 30. The correletion coefficient between age and crown height, and the mean coefficient of variation for the growth and wear of the six molar crowns in the mainland bank vole:

Character	CM_1	CM_2	CM_3	CM^1	CM^2	CM^3
r up to the age of 35 days	0.80	0.79	0.87	0.86	0.86	0.85
r between the ages 42 days & 18 months	-0.90	-0.90	-0.93	-0.93	-0.93	-0.91
Average coefficient of variation up to the age of 35 days	5.09	6.55	6.37	5.96	5.47	8.15
Average coefficient of variation over the age of 42 days onward	13.26	12.33	10.89	14.95	13.75	13.50

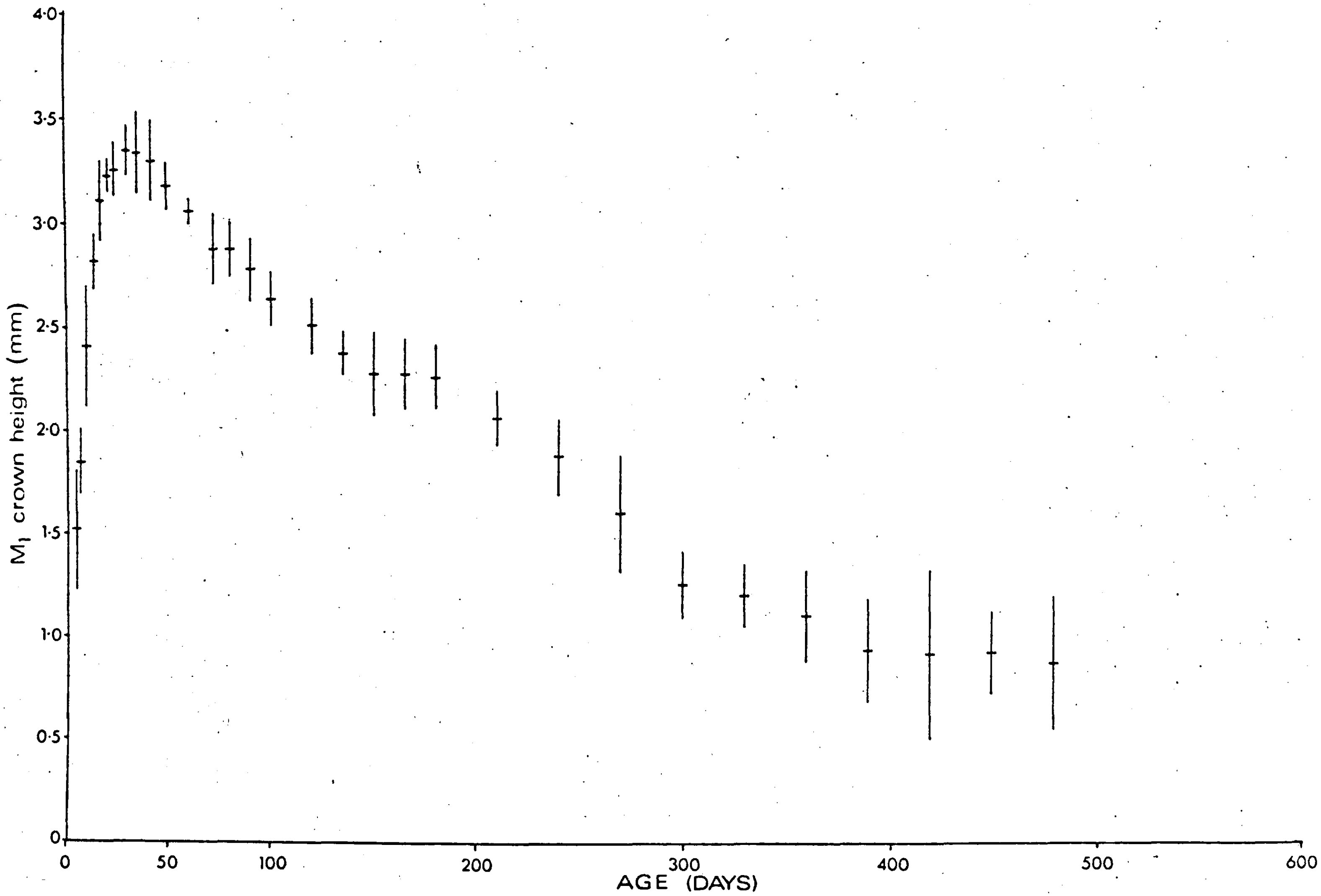


Fig. 31. Growth and wear curve for the crown height of M_1 of the mainland bank vole. (see Fig. 19 for explanation).

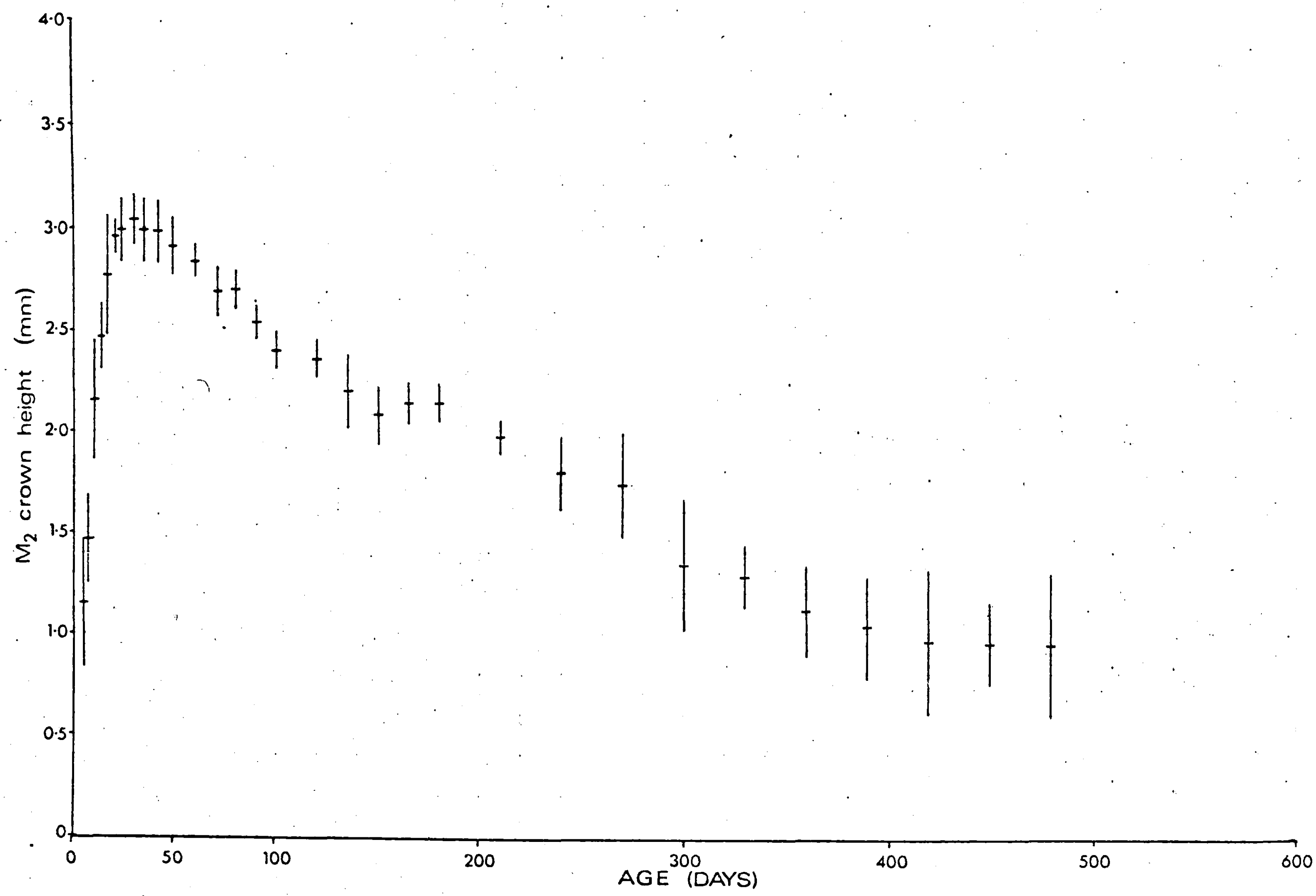


Fig. 32. Growth and wear curve for the crown height of M_2 of the mainland bank vole. (see Fig. 19 for explanation).

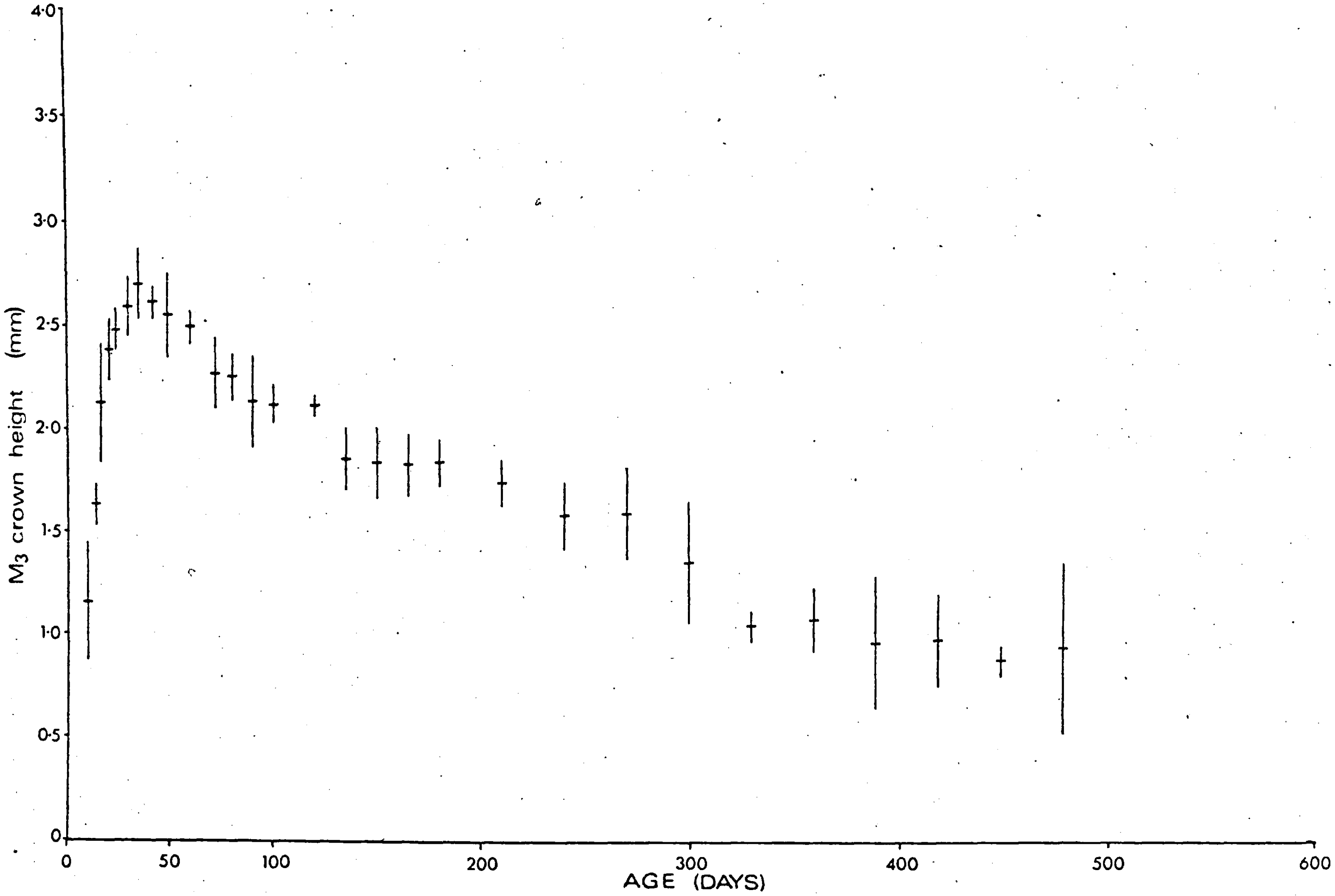


Fig. 33. Growth and wear curve for the crown height of M_3 of the mainland bank vole. (see Fig. 19 for explanation).

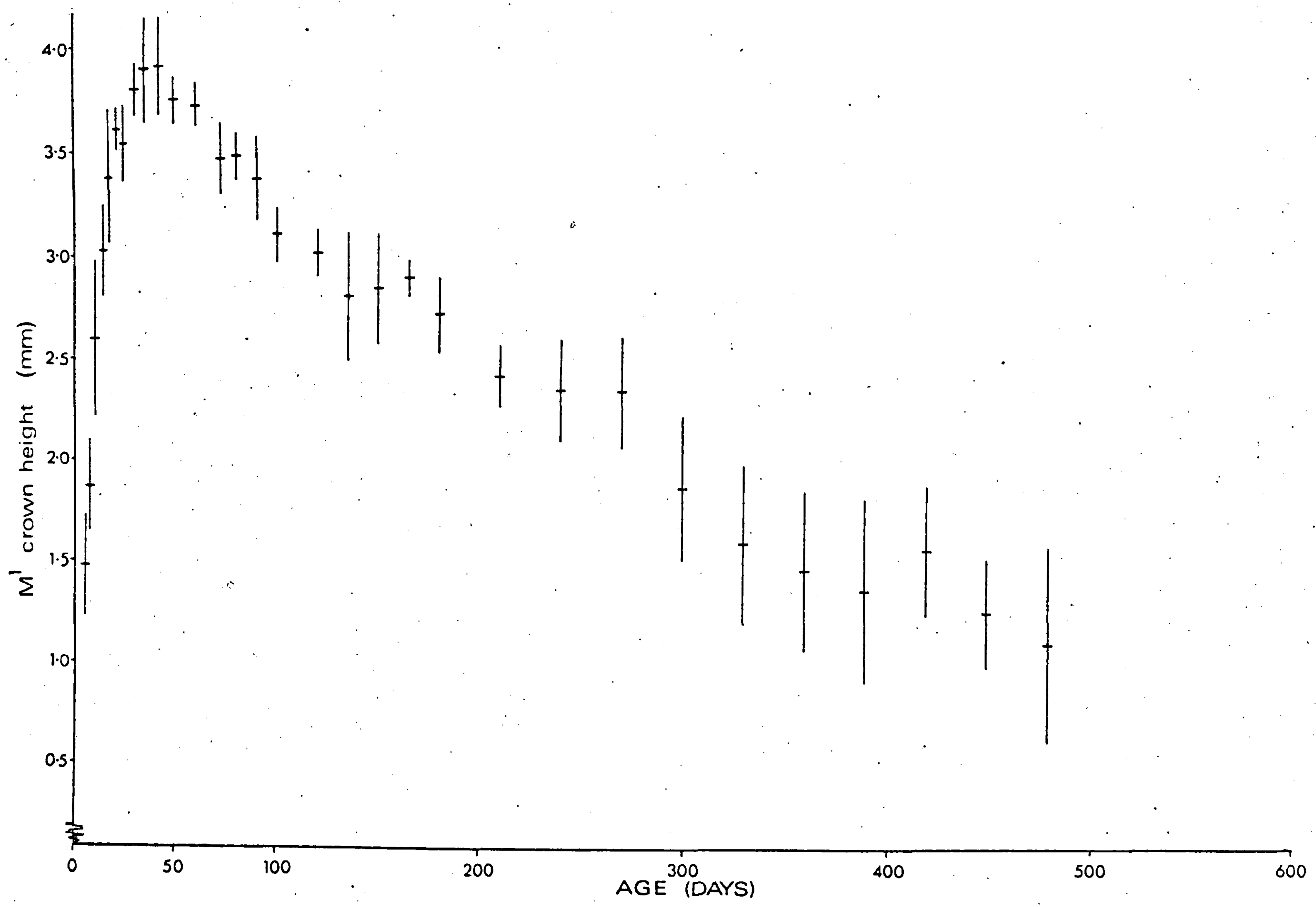


Fig. 34. Growth and wear curve for the crown height of M^1 of the mainland bank vole. (see Fig. 19 for explanation).

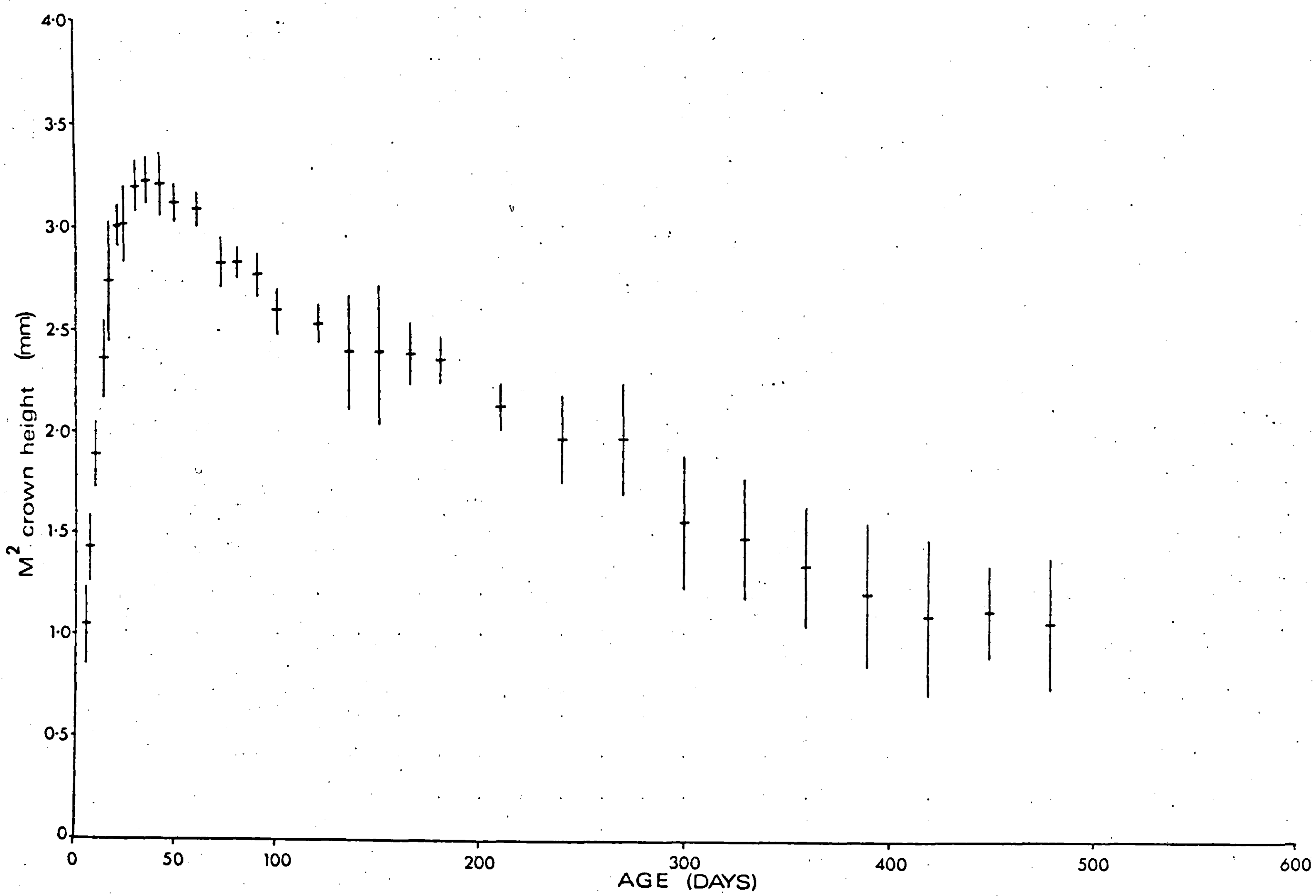


Fig. 35. Growth and wear curve for the crown height of M^2 of the mainland bank vole. (see Fig. 19 for explanation).

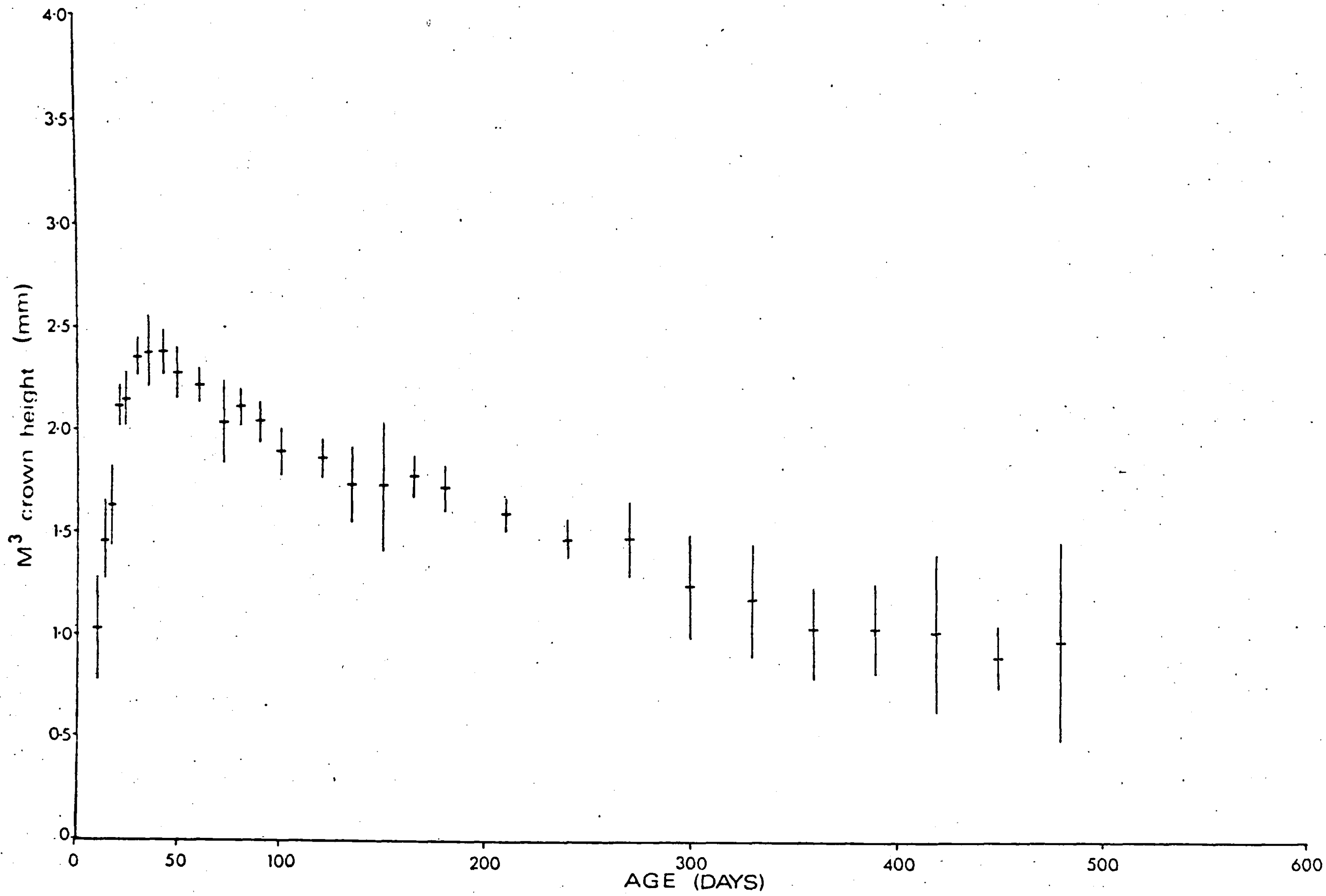


Fig. 36. Growth and wear curve for the crown height of M^3 of the mainland bank vole. (see Fig. 19 for explanation).

a.2. Estimating the age of the mainland bank vole from the height of the molar crowns:

1. CM_1:

The whole sample was divided into two main categories on the basis of the presence or absence of a neck and roots in the first lower molar. The first group included all voles 30 days and younger, whose first lower molars had not yet developed necks. This group was divided into 7 groups according to the height of the whole molar. The second group included all voles 35 days and older, whose first lower molars had developed necks and roots. This group was divided into 16 categories according to the height of the crown.

The mean age, standard deviation, standard error, and coefficient of variation were computed for each category and 95% confidence limits were attached to the mean age (Table 31).

The accuracy for estimating the age of voles of the first main group (groups 1 to 7), was very high, as the variability was low ($\bar{v}$=9.41). The lowest accuracy was ± 3.7 days for a mean age of 22.1 days and a molar crown height of 3.2 to 3.29 mm (group 6). The accuracy was still high in the second main group ($\bar{v}$=17.05), extended from ± 5.1 days for a mean age of 66 days and a crown height of 3.09 to 2.9 mm (group 12), to ± 61.1 days for a mean age of 365 days and a crown height of 1.29 to 1.2 mm (group 20).

Because of the low variability, the high accuracy for estimating the age, the crown height of M_1 is considered a reliable index for ageing the mainland bank vole.

Table 31. Numerical data for estimating the age of the mainland bank vole from the crown height of M_1 :

G. No	CM_1h/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1.3-1.79	6	5- 7	5.7± 0.42	1.03	18.22	4.6- 6.8
2	1.8-1.99	2	7 days	7.0± -	-	-	7.0 days
3	2.0-2.69	6	10 days	10.0± -	-	-	10.0 days
4	2.7-2.89	4	14 days	14.0± -	-	-	14.0 days
	2.9-2.99*	-					
5	3.0-3.19	8	17- 24	21.0± 1.22	3.46	16.50	18.2- 23.8
6	3.2-3.29	7	17- 30	22.1± 1.52	4.02	18.15	18.4- 25.9
7	3.3-3.59	9	21- 30	27.7± 1.20	3.61	13.03	24.9- 30.4
8	3.59-3.4	4	35- 42	38.5± 2.02	4.04	10.50	32.1- 44.9
9	3.39-3.3	4	42- 49	47.3± 1.75	3.50	7.41	41.7- 52.8
10	3.29-3.2	10	35- 60	51.4± 3.74	11.82	22.99	43.0- 59.9
11	3.19-3.1	9	42- 80	55.6± 4.94	14.81	26.65	44.2- 67.0
12	3.09-2.9	24	49- 90	66.0± 2.46	12.06	18.28	60.9- 71.1
13	2.89-2.8	7	60-100	80.3± 6.48	17.14	21.35	64.4- 96.2
14	2.79-2.6	20	72-120	95.3± 3.91	17.49	18.35	87.1-103.5
15	2.59-2.4	19	100-210	147.6± 7.34	31.99	21.67	132.2-163.0
16	2.39-2.2	20	100-210	164.0± 8.42	37.65	22.96	146.4-181.6
17	2.19-2.0	18	150-240	192.5± 7.79	33.04	17.17	176.1-208.9
18	1.99-1.7	15	180-270	234.0± 7.86	30.43	13.00	217.2-250.8
19	1.69-1.3	10	240-360	297.0±13.00	41.11	13.84	267.6-326.4
20	1.29-1.2	6	300-450	365.0±23.77	58.22	15.95	303.9-426.1
21	1.19-1.0	9	300-510	393.3±23.69	71.06	18.07	338.6-448.1
22	0.99-0.8	12	330-540	420.0±16.92	58.62	13.96	382.8-457.2
23	0.79-0.6	10	390-540	477.0±15.80	49.90	10.46	441.3-512.7

* These measurements were not available in the sample.

2. $\underline{CM_2}$:

The whole sample was divided into 2 main groups on the same basis which has been used on CM_1. The first group was divided into 7 and the second into 15 crown-height sub-groups (Table 32).

Variability in the distribution of the material within each size-group was not high ($\bar{v}$=7.21 for the first main group -groups 1 to 7- , and $\bar{v}$=15.94 for the second -groups 8 to 22-). The accuracy for estimating the age was high. The lowest was ± 56.9 days (group 20).

The low variability, along with the high correlation coefficient made the use of the crown height of M_2, as an age indicator, of a high value throughout life.

3. $\underline{CM_3}$:

The whole sample was divided into two main groups. The first group was, in turn, divided into 6 sub-groups, and the second into 13 (Table 33).

The distribution of the material within each sub-group was less regular than in CM_1 and CM_2, and the variability was higher, ($\bar{v}$=8.29 for the first main group, and 19.69 for the second). But the accuracy for estimating the age was high enough to make the crown height of M_3 a reliable index of age.

Table 32. Numerical data for estimating the age of the mainland bank vole from the crown height of M_2 :

G. No	CM_2h/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1.0-1.49	6	5- 7	5.7± 0.42	1.03	18.22	4.6- 6.8
2	1.5-1.59	2	7 days	7.0± -	-	-	7.0 days
	1.6-1.99*	-					
3	2.0-2.29	4	10 days	10.0± -	-	-	10.0 days
4	2.3-2.59	4	14 days	14.0± -	-	-	14.0 days
5	2.6-2.79	3	17 days	17.0± -	-	-	17.0 days
6	2.8-2.99	10	17- 30	23.3± 1.30	4.11	17.64	20.4- 26.2
7	3.0-3.29	11	21- 30	26.7± 1.18	3.90	14.59	24.1- 29.4
8	3.29-3.2	2	35- 49	42.0± 7.00	9.90	23.57	▲
9	3.19-2.9	15	35- 60	48.5± 2.43	9.40	19.40	43.3- 53.7
10	2.89-2.7	26	35- 80	62.2± 2.75	14.02	22.56	56.5- 67.8
11	2.69-2.6	9	60-100	78.0± 5.44	16.31	20.91	65.4- 90.6
12	2.59-2.5	10	72-120	91.4± 5.51	17.41	19.05	79.0-103.9
13	2.49-2.4	5	90-120	100.0± 5.48	12.25	12.25	84.8-115.2
14	2.39-2.2	24	100-210	140.0± 6.94	33.98	24.27	125.6-154.4
15	2.19-2.0	25	120-270	190.2± 7.28	36.41	19.15	175.2-205.2
16	1.99-1.8	16	135-270	216.6± 9.39	37.54	17.33	196.6-236.6
17	1.79-1.6	6	210-270	245.0±12.04	29.50	12.04	214.1-275.9
18	1.59-1.3	12	240-360	302.5±11.94	41.37	13.68	276.2-328.8
19	1.29-1.2	8	330-480	386.3±20.78	58.78	15.22	337.0-435.0
20	1.19-1.0	11	270-540	395.5±25.53	84.66	21.41	338.5-452.4
21	0.99-0.8	10	360-480	426.0±14.00	44.27	10.39	394.0-457.6
22	0.79-0.6	7	420-540	492.9±17.12	45.36	9.20	450.9-534.8

* These measurements were not available in the sample.

▲ The 95% confidence limits were not attached to the mean age because the sample size was small.

Table 33. Numerical data for estimating the age of the mainland bank vole from the crown height of M_3 :

G. No	CM_3h/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1.0-1.39	4	10 days	10.0± -	-	-	10.0 days
	1.4-1.49*	-					
2	1.5-1.69	4	14 days	14.0± -	-	-	14.0 days
	1.7-1.89*	-					
3	1.9-2.19	4	17- 21	18.0± 1.00	2.00	11.11	14.8- 21.2
	2.2-2.29*						
4	2.3-2.39	2	17- 24	20.5± 3.50	4.95	24.15	▲
5	2.4-2.59	13	21- 30	24.9± 1.04	3.75	15.06	22.7- 27.2
6	2.6-2.89	4	30 days	30.0± -	-	-	30.0 days
7	2.99-2.9	2	35- 49	42.0± 7.00	9.90	23.57	▲
8	2.89-2.6	17	35- 60	46.2± 2.26	9.30	20.11	41.7- 50.8
9	2.59-2.5	6	42- 80	58.5± 5.27	12.90	22.04	45.0- 72.0
10	2.49-2.3	19	49- 90	65.7± 2.45	10.67	16.24	60.5- 70.8
11	2.29-2.1	26	49-120	92.7± 4.30	21.91	23.63	83.8-101.6
12	2.09-1.9	23	72-210	145.1± 9.37	44.95	30.98	125.7-164.5
13	1.89-1.6	42	100-270	197.3± 7.38	47.80	24.23	182.4-212.2
14	1.59-1.4	9	210-300	250.0±12.25	36.74	14.70	221.7-278.3
15	1.39-1.2	7	210-480	300.0±35.25	93.27	31.09	213.6-386.4
16	1.19-1.1	8	300-420	356.3±13.22	37.39	10.50	324.9-387.6
17	1.09-0.9	16	330-540	403.1±18.16	72.64	18.02	364.5-441.8
18	0.89-0.8	6	360-510	440.0±20.00	48.99	11.13	388.6-491.4
19	0.79-0.7	8	390-540	476.3±16.47	46.58	9.78	437.2-515.3

* These measurements were not available in the sample.

▲ The 95% confidence limits were not attached to the mean age because the sample size was small.

4. CM^1:

The whole sample was divided into two main groups on the basis of the presence or absence of a neck and roots in the first upper molar. The first group was divided into 7 sub-groups, and the second into 17, according to the crown height of the first upper molar. Data for each sub-group were treated as before and presented in table 34.

The distribution of the material within each group was regular. Variability was very low in the first 7 sub-groups, ($\bar{v}$=4.91). They were higher in sub-groups 8 to 24, ($\bar{v}$=19.0). Accuracy for estimating the age was high. The lowest, being ± 80.9 days (group 20), corresponding to a crown height of 2.09 to 2.2 mm. All other results showed in table 34 are accurate enough for CM^1 height to be used as an age indicator throughout life.

5. CM^2:

The whole sample was divided into two main groups. The first was, in turn, divided into 7 sub-groups and the second into 18 (Table 35).

The distribution of the material within each size-group was regular. Variability was not high, ($\bar{v}$=5.94 for the first main group, and $\bar{v}$=18.51 for the second). The accuracy for estimating the age was high, extended from ± 0.0 (groups 1 to 4), to ± 65.5 days (group 20). The latter represented a mean age of 360 days, and a crown height of 1.59 to 1.4 mm.

The height of CM^2 is again another reliable age index throughout life.

Table 34. Numerical data for estimating the age of the mainland bank vole from the crown height of $_{M}1$:

G. No	CM^1h/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1.3-1.69	4	5 days	5.0± -	-	-	5.0 days
2	1.7-1.99	4	7 days	7.0± -	-	-	7.0 days
	2.0-2.19*	-					
3	2.2-2.79	6	10 days	10.0± -	-	-	10.0 days
	2.8-2.89*	-					
4	2.9-3.19	4	14 days	14.0± -	-	-	14.0 days
5	3.2-3.49	8	17- 24	21.0± 1.22	3.46	16.50	18.1- 23.9
6	3.5-3.79	15	17- 30	24.5± 1.13	4.39	17.89	22.1- 27.0
7	3.8-3.99	4	30 days	30.0± -	-	-	30.0 days
8	4.29-4.08[illegible]	6[illegible]	35- 60	48.0± 4.20	10.30	21.45	37.2- 58.8
9	3.99-3.9	8	35- 60	49.6± 3.42	9.66	19.47	41.5- 57.7
10	3.89-3.7	17	35- 80	53.1± 2.89	11.93	22.46	47.0- 59.3
11	3.69-3.5	20	42- 90	65.3± 3.17	14.18	21.72	58.7- 71.9
12	3.49-3.4	6	60- 90	73.7± 4.91	12.03	16.33	61.1- 86.3
13	3.39-3.2	16	72-150	92.8± 4.97	19.88	21.43	82.2-103.3
14	3.19-3.1	7	90-135	109.3± 6.02	15.92	14.57	94.5-124.0
15	3.09-3.0	11	120-165	143.2± 5.49	18.20	12.71	130.9-155.4
16	2.99-2.8	21	100-240	156.2± 9.05	41.47	26.55	137.3-175.1
17	2.79-2.6	14	120-270	205.7±14.10	52.76	25.65	175.3-236.2
18	2.59-2.4	14	135-270	205.7±13.20	49.38	24.00	177.2-234.2
19	2.39-2.1	13	180-330	233.1±12.32	44.42	19.06	206.2-259.9
20	2.09-2.0	5	210-360	246.0±29.09	65.04	26.44	165.1-326.9
21	1.99-1.7	10	240-450	327.0±21.19	67.01	20.49	303.6-350.5
22	1.69-1.4	10	270-540	390.0±31.62	100.00	25.64	318.5-461.5
23	1.39-1.0	18	330-540	403.3±13.77	58.41	14.48	374.3-432.4
24	0.99-0.8	7	420-540	484.3±15.25	40.36	8.33	446.9-521.7

* These measurements were not available in the sample.

Table 35. Numerical data for estimating the age of the mainland bank vole from the crown height of $_{M}2$:

G. No	CM^{2}h/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.9-1.19	4	5 days	5.0± -	-	-	5.0 days
	1.2-1.29*	-					
2	1.3-1.59	4	7 days	7.0± -	-	-	7.0 days
	1.6-1.79*	-					
3	1.8-1.99	4	10 days	10.0± -	-	-	10.0 days
	2.0-2.19*	-					
4	2.2-2.59	4	14 days	14.0± -	-	-	14.0 days
5	2.6-2.99	9	17- 24	20.2± 1.09	3.27	16.17	17.7- 22.7
6	3.0-3.19	9	21- 30	24.7± 1.39	4.18	16.96	21.5- 27.9
7	3.2-3.39	6	24- 30	29.0± 1.00	2.45	8.45	26.4- 31.6
8	3.43-3.3	7	35- 60	46.1± 4.01	10.61	22.99	36.3- 56.0
9	3.29-3.1	15	35- 60	48.5± 2.52	9.77	20.15	43.1- 53.9
10	3.09-3.0	11	49- 80	59.9± 2.87	9.52	15.90	53.5- 66.3
11	2.99-2.9	9	49- 90	68.9± 4.97	14.90	21.62	57.4- 80.4
12	2.89-2.7	18	60-150	87.6± 5.10	21.64	24.72	76.8- 98.3
13	2.69-2.6	11	72-135	98.1± 6.14	20.38	20.78	84.4-111.8
14	2.59-2.5	11	100-180	125.0± 8.20	27.20	21.76	106.7-143.3
15	2.49-2.4	13	120-210	162.7± 7.75	27.96	17.19	145.8-179.6
16	2.39-2.2	21	100-270	200.5±10.44	47.83	23.86	178.7-222.3
17	2.19-2.1	9	135-270	200.0±14.36	43.08	21.54	166.8-233.2
18	2.09-1.9	12	135-330	228.8±14.20	49.18	21.50	197.5-260.0
19	1.89-1.6	11	210-360	283.6±16.86	55.91	19.71	246.0-321.2
20	1.59-1.4	10	240-540	360.0±28.98	91.65	25.46	294.5-425.5
21	1.39-1.2	9	300-510	403.3±24.04	72.11	17.88	347.8-458.9
22	1.19-1.0	8	330-540	412.5±26.44	74.79	18.13	349.8-475.2
23	0.99-0.9	5	360-480	420.0±21.21	47.43	11.29	361.0-479.0
24	0.89-0.8	4	420-480	450.0±12.25	24.49	5.44	411.0-489.0
25	0.79-0.7	3	510-540	520.0±10.00	17.32	3.33	477.0-563.0

* These measurements were not available in the sample.

6. CM^3:

The whole sample was divided into two main groups. The first of them was divided into 6 sub-groups, and the second into 15 (Table 36).

Variability in the distribution of the material, within each size-group, was somewhat, higher for this molar, than for CM^1 and CM^2, ($\bar{v}$=8.74 for the first main group, and $\bar{v}$=23.82 for the second). The highest variability (v being 32.99) occurred in voles with CM^3 height of 1.89 mm, a mean age of 146 days, a standard deviation of 53.6 days, a maximum age of 174.6 days, and a minimum age of 117.5 days with a probability of 0.05.

In spite of the slightly high variability, CM^3 height is still a reliable character for ageing the mainland bank vole (Table 36), as the accuracy is still high.

Table 36. Numerical data for estimating the age of the mainland bank vole from the crown height of $_{M}3$:

G. No	CM^{3}h/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.9-1.29	4	10 days	10.0± -	-	-	10.0 days
2	1.3-1.59	8	14- 17	15.5± 0.57	1.60	10.35	14.2- 16.9
3	1.6-1.99	4	17. 21	18.0± 1.00	2.00	11.11	14.8- 21.2
4	2.0-2.19	8	21. 24	22.5± 0.57	1.60	7.13	21.2- 23.9
5	2.2-2.29	6	21- 30	27.5± 1.63	3.99	14.50	23.3- 31.7
6	2.3-2.59	5	24- 30	28.8± 1.20	2.68	9.32	25.5- 32.1
7	2.59-2.5	3	35- 42	37.3± 2.33	4.04	10.83	27.3- 47.4
8	2.49-2.3	18	35- 60	49.4± 2.31	9.79	19.82	44.5- 54.3
9	2.29-2.2	9	49- 80	64.7± 3.97	11.91	18.41	55.5- 73.8
10	2.19-2.1	13	49-100	70.9± 4.55	16.39	23.13	60.9- 80.8
11	2.09-2.0	12	60-150	92.5± 7.08	24.54	26.53	76.9-108.1
12	1.99-1.9	14	60-180	109.1±10.07	37.68	34.55	87.3-130.8
13	1.89-1.8	16	72-270	146.1±13.41	53.64	36.75	117.5-174.6
14	1.79-1.7	17	72-270	169.5±13.57	55.93	32.99	140.8-198.3
15	1.69-1.6	11	100-240	175.5±12.91	42.81	24.40	146.7-204.2
16	1.59-1.5	15	135-270	210.0±10.04	38.87	18.51	188.5-231.5
17	1.49-1.4	13	150-360	258.5±16.12	58.14	22.50	223.3-293.6
18	1.39-1.2	10	150-480	294.0±29.93	94.66	32.20	226.4-361.6
19	1.19-1.1	8	270-540	367.5±28.77	81.37	22.14	299.3-435.7
20	1.09-0.9	14	270-540	409.3±21.00	78.59	19.20	363.9-454.7
21	0.89-0.6	15	330-540	434.0±17.29	66.95	15.43	397.0-471.0

b. The Skomer vole:

Data for tooth wear in the Skomer vole are presented combined for the two sexes, as no significant differences were found between them. Results of applying the t test on 169 specimens, aged 5 to 540 days, (64 degrees of freedom), are:

Crown of the first lower molar,	(CM_1):	t64=0.35,	$P > 0.7$
" " " second " " ,	(CM_2):	t64=0.58,	$P > 0.5$
" " " third " " ,	(CM_3):	t60=0.56,	$P > 0.5$
" " " first upper " ,	(CM^1):	t64=0.30,	$P > 0.7$
" " " second " " ,	(CM^2):	t64=0.42,	$P > 0.6$
" " " third " " ,	(CM^3):	t60=0.46,	$P > 0.6$

b.1. Growth and wear of molar crowns:

The relevant data are presented in Figs 37 to 42 and Appendices 36 to 41.

The lower and upper molars in the Skomer vole, grew very quickly during the first month of life. The crown, after reaching its maximum height, started to decrease, as a result of wearing, which started since the voles were 14 days old. Wear of the crown continued throughout life with an average monthly decrease which differs from one molar to another (Table 37).

The growth and wear of all the molar crowns were highly correlated with age and variability was not high (Table 38).

Table 37. Data showing the average maximum height of molar crowns in Skomer voles, the age of voles when their molar crowns reached this height, and the monthly average decrease of the crowns:

Character	CM_1	CM_2	CM_3	CM^1	CM^2	CM^3
Average maximum height/mm of the crown	3.74	3.38	2.92	4.21 & 4.23	3.59& 3.60	2.79& 2.80
Age of Skomer voles when they have the maximum crown height/days	42	35	35 & 42	42 & 49	42 & 49	42 & 49
Average monthly decrease of crown height/mm	0.15	0.15	0.11	0.16	0.14	0.10

Table 38. Data showing the correlation coefficients, and the average coefficients of variation of the molar crowns in the Skomer vole:

Character	CM_1	CM_2	CM_3	CM^1	CM^2	CM^3
r up to the age of 35 days	0.89	0.88	0.86	0.93	0.92	0.91
r between the ages 42 days & 18 months	-0.96	-0.96	-0.94	-0.95	-0.94	-0.94
Average coefficient of variation up to 35 days	2.07	2.51	4.74	2.30	2.94	4.36
Average coefficient of variation over 42 days onward	9.59	9.75	10.03	9.58	9.14	8.70

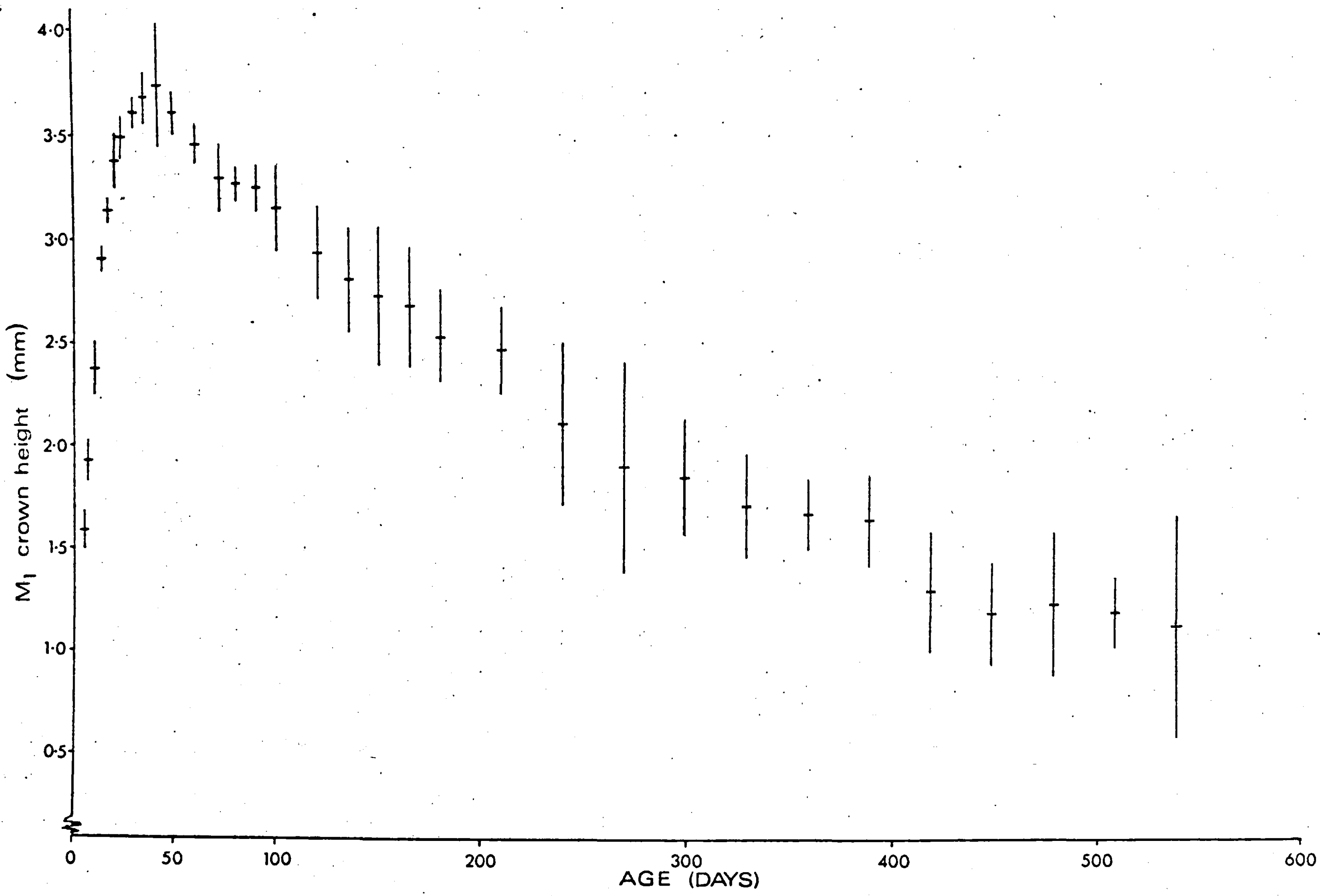


Fig. 37. Growth and wear curve for the crown height of M_1 of the Skomer vole. (see Fig. 19 for explanation).

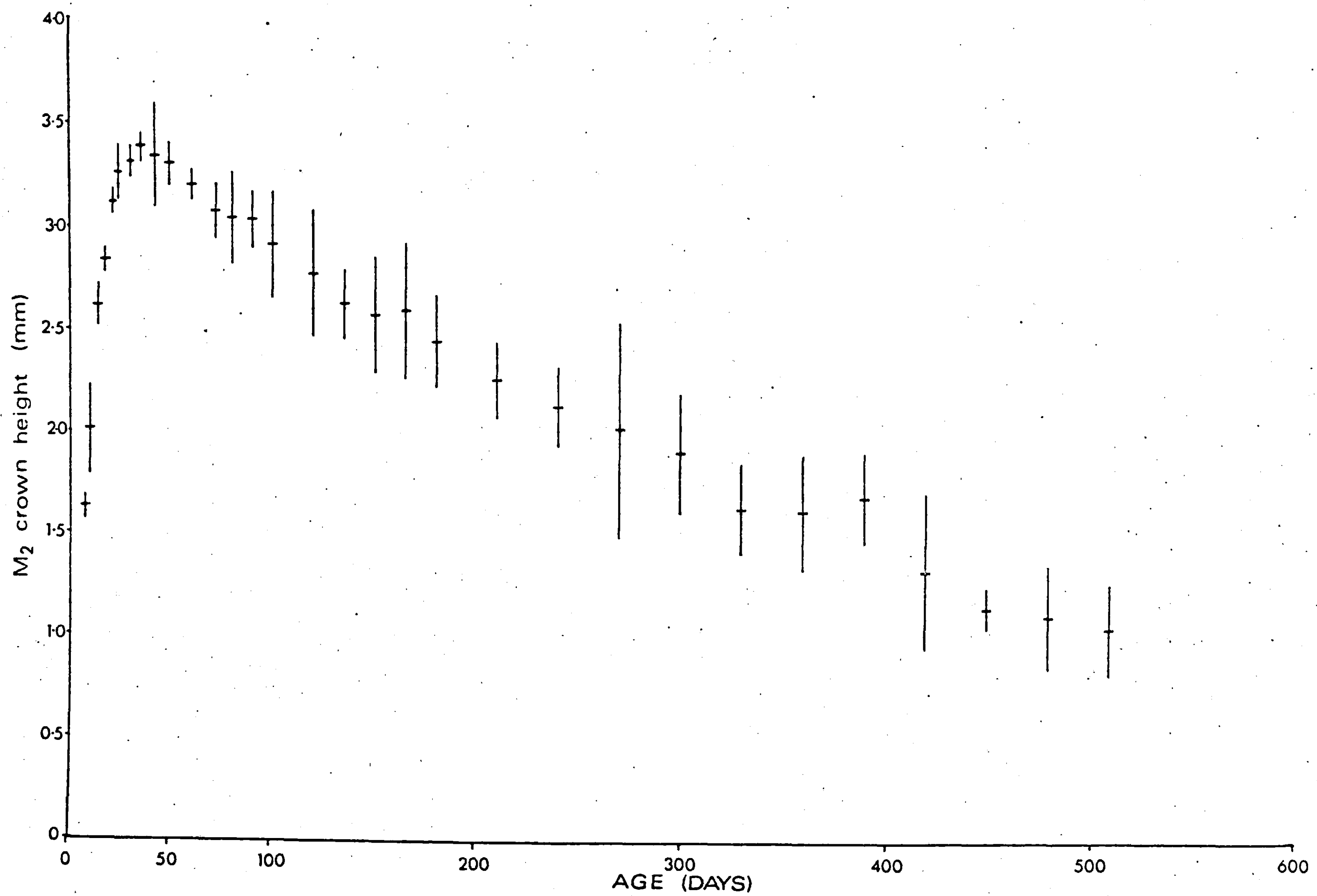


Fig. 38. Growth and wear curve for the crown height of M_2 of the Skomer vole. (see Fig. 19 for explanation).

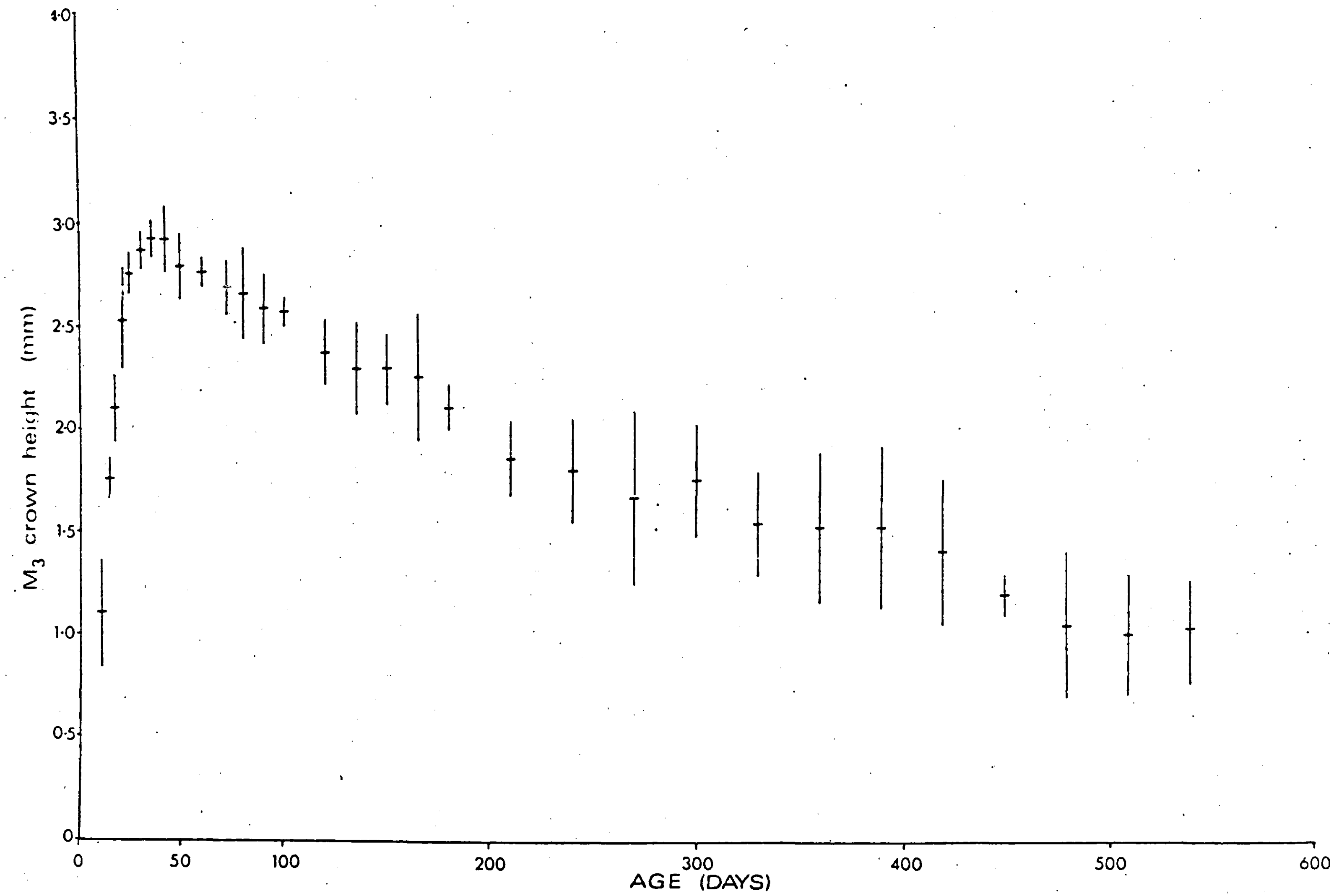


Fig. 39. Growth and wear curve for the crown height of M_3 of the Skomer vole. (see Fig. 19 for explanation).

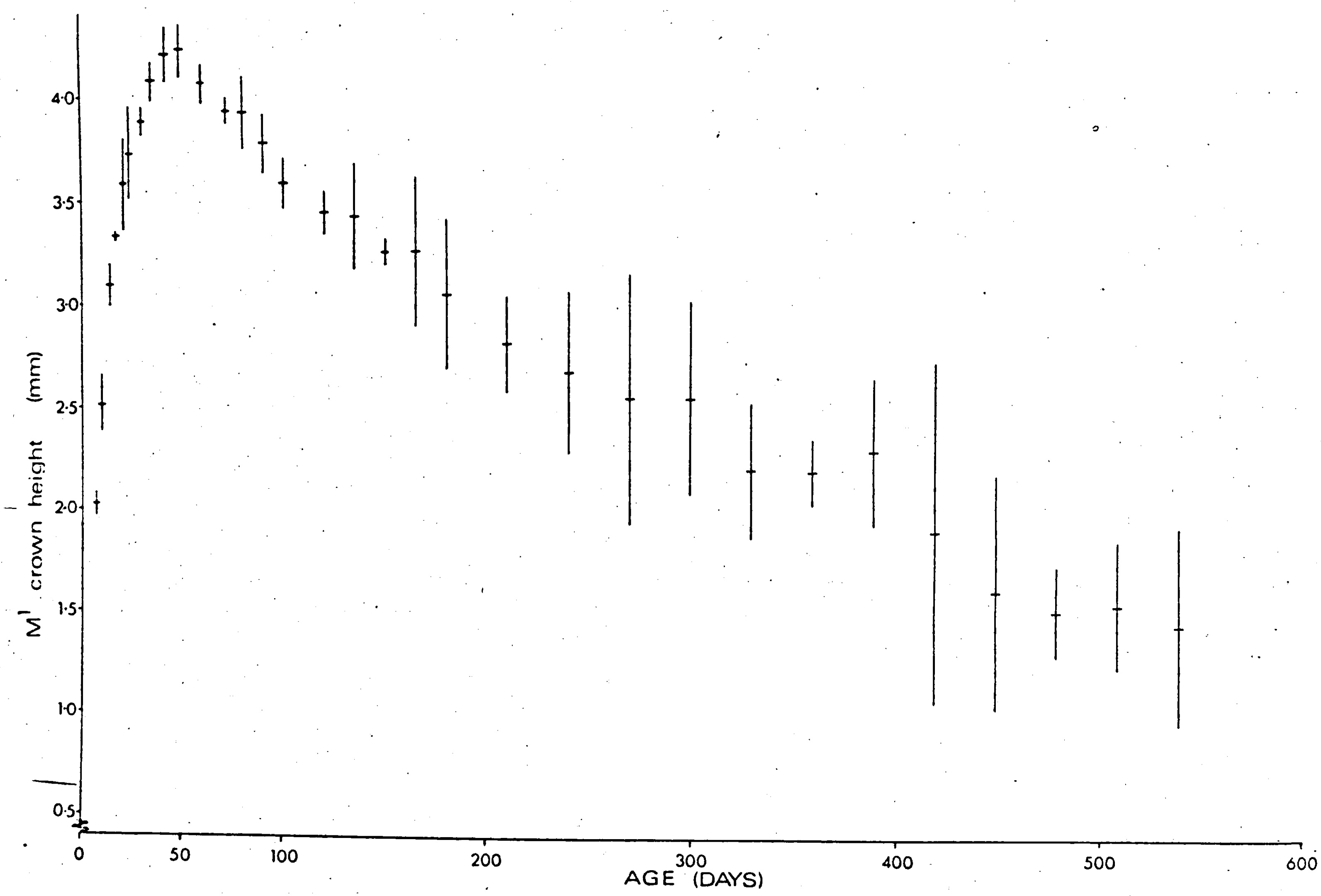


Fig. 40. Growth and wear curve for the crown height of M^1 of the Skomer vole. (see Fig. 19 for explanation).

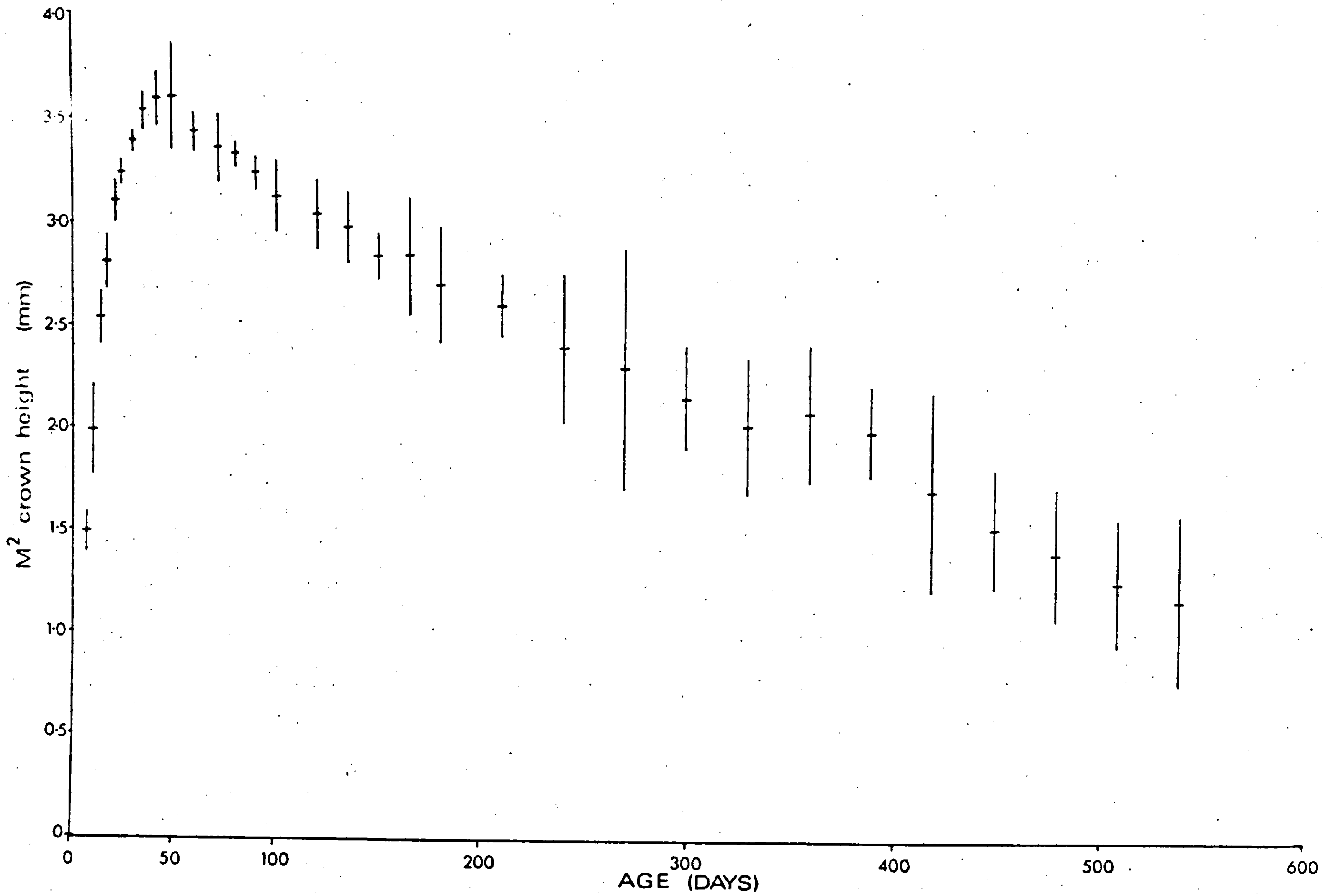


Fig. 41. Growth and wear curve for the crown height of M^2 of the Skomer vole. (see Fig. 19 for explanation).

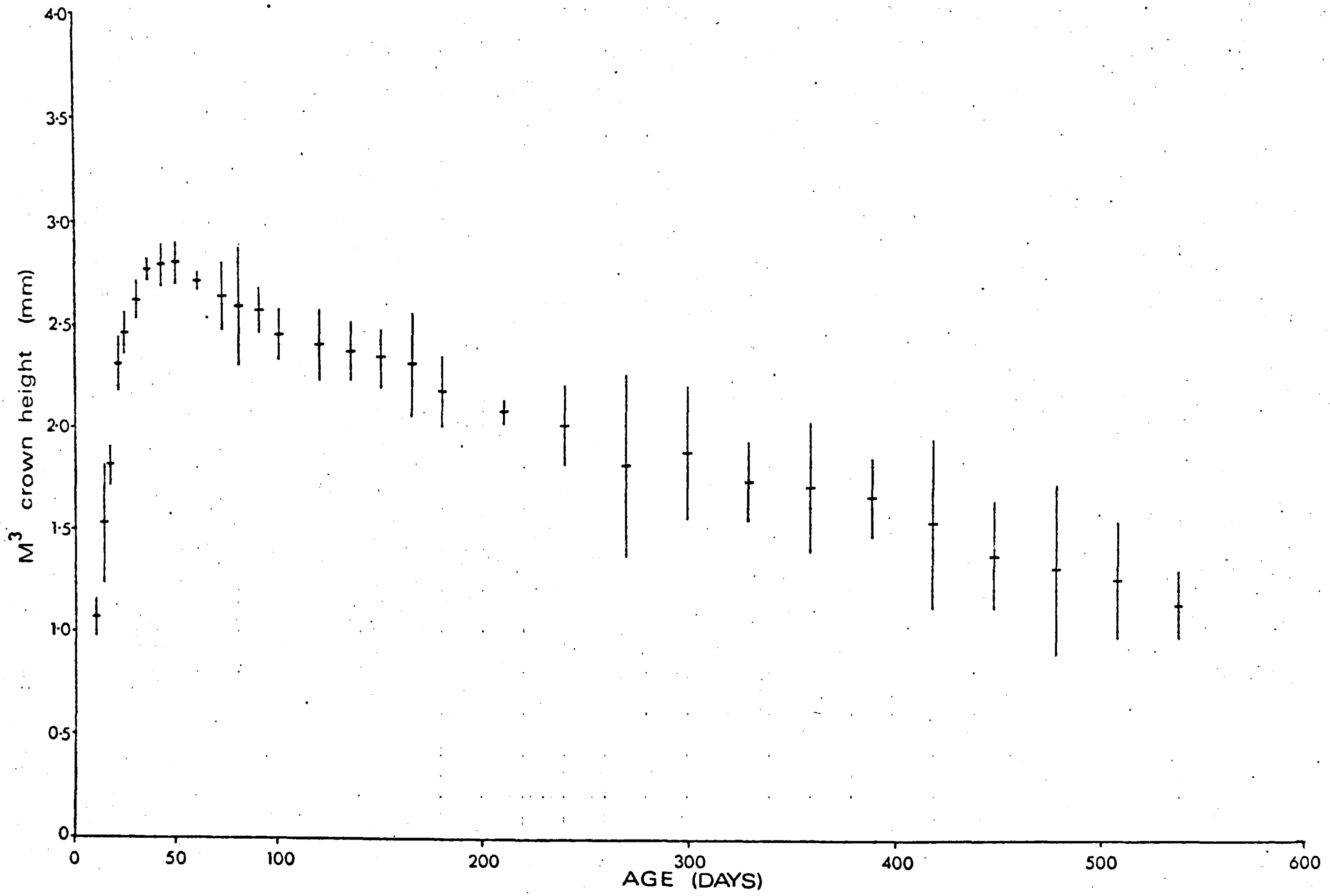


Fig. 42. Growth and wear curve for the crown height of M^3 of the Skomer vole. (see Fig. 19 for explanation).

b.2. Estimating the age of Skomer voles from the height of the molar crowns:

The whole sample was divided into two main groups, on the basis of the presence or absence of a neck and roots in each of the six molars which were analysed separatly. The first group included all voles 30 days and younger. The second, included all voles beyond the age of 35 days. Each of these two main groups, were divided into many other groups according to the crown height of each of the six molars which are presented as follow:

1. CM_1:

The first main group was divided into 8 and the second into 17 CM_1-height groups (Table 39).

Variability in the distribution of the material within each group was not high ($\bar{v}$=2.18 for groups 1 to 8, and $\bar{v}$= 13.3 for groups 9 to 25). The accuracy for estimating the age was high. It extended from ± 0.0 in groups 1 to 5 with a crown height of up to 3.19 mm; group 8 with a crown height of 3.6 to 3.79 mm; and in group 25 with a crown height of 0.94 to 0.82 mm, to ± 54.5 days (group 22), for a mean age of 390 days and a crown height of 1.59 to 1.4 mm.

The most variable crown height value was 2.99 to 2.9 mm (group 15) representing a mean age of 130 days and an accuracy for estimating the age of ± 36.5 days.

The regular distribution of the material, the low dispersion and the high accuracy, together with the high correlation coefficient enhance the value of CM_1 height as age indicator.

Table 39. Numerical data for estimating the age of the Skomer vole from the crown height of M_1 :

G. No	CM_1h/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1.5-1.59	2	5 days	5.0± -	-	-	5.0 days
	1.6-1.79*	-					
2	1.8-1.99	4	7 days	7.0± -	-	-	7.0 days
	2.0-2.29*	-					
3	2.3-2.49	3	10 days	10.0± -	-	-	10.0 days
	2.5-2.79*	-					
4	2.8-2.99	4	14 days	14.0± -	-	-	14.0 days
	3.0-3.09*	-					
5	3.1-3.19	4	17 days	17.0± -	-	-	17.0 days
	3.2-3.29*	-					
6	3.3-3.49	5	21- 24	21.6± 0.60	1.34	6.21	19.9- 23.3
7	3.5-3.59	8	24- 30	27.8± 1.10	3.11	11.19	25.1- 30.4
8	3.6-3.79	5	30 days	30.0± -	-	-	30.0 days
9	3.99-3.8	4	35- 42	36.8± 1.75	3.50	9.52	31.2- 42.3
10	3.79-3.6	8	35- 60	45.1± 2.96	8.37	18.56	38.1- 52.2
11	3.59-3.5	12	35- 60	51.3± 3.28	11.36	22.12	44.1- 58.6
12	3.49-3.4	2	60- 72	66.0± 6.00	8.49	12.86	▲
13	3.39-3.1	21	60-100	81.2± 3.03	13.89	17.10	74.9- 87.6
14	3.09-3.0	3	120-135	125.0± 5.00	8.66	6.93	103.5-146.5
15	2.99-2.9	5	100-165	130.0±13.13	29.37	22.59	93.5-166.5
16	2.89-2.8	4	120-150	138.8± 7.18	14.36	10.35	115.9-161.6
17	2.79-2.5	13	120-210	169.6± 8.20	29.61	17.46	151.7-187.5
18	2.49-2.3	7	150-240	201.4±12.62	33.38	16.57	170.5-232.4
19	2.29-2.0	7	210-330	278.6±15.62	41.40	14.86	240.3-316.8
20	1.99-1.7	10	240-390	309.0±16.76	53.00	17.16	271.1-346.9
21	1.69-1.6	4	330-390	360.0±12.25	24.49	6.80	321.0-399.0
22	1.59-1.4	12	270-540	390.0±24.77	85.81	22.00	335.5-444.5
23	1.39-1.3	3	420-450	430.0±10.00	17.32	4.03	387.0-473.0
24	1.29-1.0	12	420-540	482.5±10.08	34.93	7.24	460.3-504.7
25	0.94-0.82	2	540 days	540.0± -	-	-	540 days

* These measurements were not available in the sample.

▲ The 95% confidence limits were not attached to the mean age because the sample size was small.

2. $\underline{CM_2}$:

The first group was divided into 9 and the second into 16 CM_2-height groups (Table 40).

The distribution of the material within each group was regular. The accuracy for estimating the age was high, which extended up to ± 88.3 days (group 23) for a mean age of 440 days and a crown height of 1.39 to 1.2 mm. The most variable crown height value was 2.99 to 2.8 mm (v=28.13) representing a mean age of 116.4 days, an accuracy for estimating the age of ± 30.3 days (group 14). The variability in the distribution of the material for the whole sample was not high ($\bar{v}$=2.33 for the first 9 groups and $\bar{v}$=16.81 for groups 10 to 25). All these factors along with the high correlation coefficient, make CM_2 height a useful age indicator.

3. $\underline{CM_3}$:

The first main group was divided into 7 and the second into 16 CM_3-height groups (Table 41).

In spite of the third lower molar being not straight in shape, and therefore difficult to measure, results with high accuracy were obtained. Variability for the distribution of the material, within each size-group, was not high, ($\bar{v}$=3.24 for the first group, and $\bar{v}$=20.19 for the second).

Table 40. Numerical data for estimating the age of the Skomer vole from the crown height of M_2 :

G. No	CM$_2$h/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1.2-1.29	2	5 days	5.0± -	-	-	5.0 days
	1.3-1.59*	-					
2	1.6-1.69	4	7 days	7.0± -	-	-	7.0 days
	1.7-1.89*	-					
3	1.9-2.09	3	10 days	10.0± -	-	-	10.0 days
	2.1-2.49*	-					
4	2.5-2.69	4	14 days	14.0± -	-	-	14.0 days
	2.7-2.79*	-					
5	2.8-2.89	4	17 days	17.0± -	-	-	17.0 days
	2.9-2.99*	-					
6	3.0-3.19	4	21 days	21.0± -	-	-	21.0 days
7	3.2-3.29	7	24- 30	27.4± 1.21	3.21	11.60	24.5- 30.4
8	3.3-3.39	5	24- 30	28.8± 1.20	2.68	9.32	25.5- 32.1
9	3.4-3.49	2	30 days	30.0± -	-	-	30.0 days
10	3.59-3.4	4	35- 42	36.8± 1.75	3.50	9.52	31.2- 42.3
11	3.39-3.2	16	35- 60	47.6± 2.51	10.02	21.04	42.3- 55.0
12	3.19-3.1	13	60-100	70.3± 3.76	13.56	19.29	62.1- 78.5
13	3.09-3.0	6	60-100	80.7± 6.12	15.00	18.60	64.9- 96.4
14	2.99-2.8	7	80-165	116.4±12.38	32.75	28.13	86.1-146.8
15	2.79-2.7	8	100-165	133.8± 8.22	23.26	17.39	114.3-153.2
16	2.69-2.5	6	120-270	175.0±21.45	52.54	30.02	119.9-230.1
17	2.49-2.3	12	135-300	188.8±13.24	45.88	24.31	159.6-217.9
18	2.29-2.0	9	210-300	236.7±10.54	31.62	13.36	212.3-261.0
19	1.99-1.9	5	240-360	294.0±19.90	44.50	15.14	238.7-349.3
20	1.89-1.8	6	270-390	340.0±20.00	48.99	14.41	288.6-391.4
21	1.79-1.6	5	300-390	348.0±18.00	40.25	11.57	298.0-398.0
22	1.59-1.4	9	270-420	360.0±17.32	51.96	14.43	320.0-400.0
23	1.39-1.2	6	330-540	440.0±34.35	84.14	19.12	351.7-528.3
24	1.19-1.0	10	420-540	474.0±11.66	36.88	7.78	447.7-500.4
25	0.99-0.65	5	480-540	516.0±11.21	25.10	4.86	484.9-547.2

* These measurements were not available in the sample.

Table 41. Numerical data for estimating the age of the Skomer vole from the crown height of M_3 :

G. No	CM_3h/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1.0-1.19	3	10 days	10.0± -	-	-	10.0 days
	1.2-1.69*	-					
2	1.7-1.89	4	14 days	14.0± -	-	-	14.0 days
	1.9-1.99*	-					
3	2.0-2.19	4	17 days	17.0± -	-	-	17.0 days
	2.2-2.29*	-					
4	2.3-2.69	4	21 days	21.0± -	-	-	21.0 days
5	2.7-2.79	6	24- 30	27.0± 1.34	3.29	12.17	23.6- 30.4
6	2.8-2.89	4	24- 30	28.5± 1.50	3.00	10.53	23.7- 33.3
7	2.9-3.05	4	30 days	30.0± -	-	-	30.0 days
8	3.04-3.0	4	35- 42	36.8± 1.75	3.50	9.52	31.2- 42.3
9	2.99-2.9	5	35- 60	44.2± 4.73	10.57	23.91	31.1- 57.4
10	2.89-2.8	11	35- 80	53.6± 5.10	16.93	31.61	42.2- 64.9
11	2.79-2.7	11	49- 90	64.6± 4.49	14.88	23.02	54.6- 74.7
12	2.69-2.6	10	60-100	78.4± 6.06	19.16	24.43	64.7- 92.1
13	2.59-2.5	9	80-165	104.4± 9.91	29.73	28.47	81.6-127.3
14	2.49-2.4	6	90-165	123.3±12.63	30.93	25.08	90.9-155.8
15	2.39-2.3	6	120-165	137.5± 8.14	19.94	14.50	116.6-152.4
16	2.29-2.1	11	135-300	181.4±15.59	51.72	28.52	146.6-216.1
17	2.09-2.0	6	165-270	195.0±16.43	40.25	20.64	152.8-237.2
18	1.99-1.8	7	210-390	295.7±23.99	63.47	21.46	236.9-354.5
19	1.79-1.6	14	210-420	285.0±17.72	66.30	23.26	246.7-323.3
20	1.59-1.4	5	270-390	342.0±20.35	45.50	13.30	285.4-398.6
21	1.39-1.2	10	270-480	390.0±23.24	73.48	18.84	337.5-442.5
22	1.19-1.1	7	390-540	458.6±19.33	51.13	11.15	411.2-505.9
23	1.09-0.78	7	480-540	514.3±10.20	26.99	5.25	489.3-539.3

* These measurements were not available in the sample.

4. <u>CM[1]</u>:

The first main group was divided into 8 and the second into 15 CM^1-height groups (Table 42).

The distribution of the material according to CM^1 height was regular with low variability, ($\bar{v}$=2.26 for the first main group, and $\bar{v}$=20.87 for the second), which, with the high correlation coefficient, make CM^1 height a useful index.

5. <u>CM[2]</u>:

The first main group was divided into 8, and the second into 17 CM^2-height groups. Data for each size-group were treated as before and presented in table 43.

The regular distribution of the material according to CM^2 height, the low variability, ($\bar{v}$=0.0 for the first main group, $\bar{v}$=16.53 in the second), and the high accuracy for estimating the age , again make CM^2 height a reliable index.

6.<u>CM[3]</u>:

The first main group was divided into 7, and the second into 13 CM^3-height groups (Table 44).

The distribution of the material, according to CM^3 height, within each size-group was regular. Variability was low, ($\bar{v}$=3.18 for the first main group -groups 1 to 7 -, and $\bar{v}$=18.57 for the second, -groups 8 to 20-).

The accuracy for estimating the age was high, extended from ± 0.0 in groups 1 to 4, & 7, to ± 96.4 days (group 19). All these factors, along with the high correlation coefficient, enhance the value of CM^3 height to be used as an age indicator in the Skomer vole.

Table 48. Numerical data for estimating the age of the Skomer vole from the crown height of M^1 :

G. No	CM^1h/ mm	F.	O. Range/ days	Mean±S.E.		S.D.	V.	Estimated age range/95%c.l.
1	1.7-1.89	2	5 days	5.0±	-	-	-	5.0 days
	1.9-1.99*	-						
2	2.0-2.09	4	7 days	7.0±	-	-	-	7.0 days
	2.1-2.39*	-						
3	2.4-2.59	3	10 days	10.0±	-	-	-	10.0 days
	2.6-2.99*	-						
4	3.0-3.19	4	14 days	14.0±	-	-	-	14.0 days
	3.2-3.29*	-						
5	3.3-3.39	4	17 days	17.0±	-	-	-	17.0 days
6	3.4-3.69	6	21- 24	22.0±	0.63	1.55	7.04	20.4- 23.6
7	3.7-3.89	6	24- 30	28.0±	1.27	3.10	11.07	24.7- 31.3
8	3.9-3.99	6	30 days	30.0±	-	-	-	30.0 days
9	4.39-4.1	16	35- 60	48.1±	2.39	9.57	19.92	43.0- 53.1
10	4.09-4.0	11	35- 80	53.4±	5.71	18.93	35.48	40.6- 66.1
11	3.99-3.9	10	60- 90	68.6±	3.32	10.50	15.31	61.1- 76.1
12	3.89-3.8	5	80-100	88.0±	3.75	8.38	9.51	77.6- 98.4
13	3.79-3.6	6	90-165	119.2±	12.48	30.56	25.65	87.1-151.2
14	3.59-3.4	11	100-180	117.7±	7.24	24.02	20.40	101.6-133.9
15	3.39-3.2	10	135-300	175.5±	18.58	58.76	33.48	133.5-217.5
16	3.19-3.0	9	165-360	218.3±	23.20	69.60	31.88	164.7-271.9
17	2.99-2.6	11	180-420	250.9±	24.34	80.80	32.20	196.6-305.2
18	2.59-2.3	10	210-390	300.0±	16.73	52.92	17.64	262.2-337.8
19	2.29-2.0	10	240-390	330.0±	16.73	52.92	16.04	292.2-367.8
20	1.99-1.8	6	270-510	390.0±	37.15	90.99	23.33	294.5-485.5
21	1.79-1.6	6	330-540	455.0±	30.41	74.50	16.37	376.9-533.2
22	1.59-1.4	6	420-540	480.0±	17.32	42.43	8.84	435.5-524.5
23	1.39-1.0	6	480-540	505.0±	14.32	35.07	6.94	468.2-541.8

* These measurements were not available in the sample.

Table 43. Numerical data for estimating the age of the Skomer vole from the crown height of M^2 :

G. No	CM^2h/ mm	F.	O. Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1.2-1.29	2	5 days	5.0± -	-	-	5.0 days
	1.3-1.39*	-					
2	1.4-1.59	4	7 days	7.0± -	-	-	7.0 days
	1.6-1.89*	-					
3	1.9-2.09	3	10 days	10.0± -	-	-	10.0 days
	2.1-2.39*	-					
4	2.4-2.69	4	14 days	14.0± -	-	-	14.0 days
5	2.7-2.89	4	17 days	17.0± -	-	-	17.0 days
	2.9-2.99*	-					
6	3.0-3.19	4	21 days	21.0± -	-	-	21.0 days
7	3.2-3.29	4	24 days	24.0± -	-	-	24.0 days
8	3.3-3.49	10	30 days	30.0± -	-	-	30.0 days
9	3.75-3.7	3	35- 49	42.0± 4.04	7.00	16.67	▲
10	3.69-3.5	13	35- 60	46.5± 2.92	10.53	22.67	40.1- 52.8
11	3.49-3.4	9	35- 72	53.1± 5.06	15.24	28.69	41.4- 64.8
12	3.39-3.3	14	60-100	74.4± 4.01	15.01	20.17	65.8- 83.1
13	3.29-3.2	6	72-100	87.0± 3.96	9.70	11.14	76.8- 97.2
14	3.19-3.1	3	90-120	103.3± 8.82	15.28	14.78	65.4-141.3
15	3.09-2.9	15	100-180	136.0± 7.04	27.27	20.05	120.9-151.1
16	2.89-2.7	9	135-270	171.7±14.17	42.50	24.76	138.9-204.4
17	2.69-2.5	11	165-270	208.6± 9.59	31.79	15.24	187.3-230.0
18	2.49-2.3	6	210-360	280.0±24.08	58.99	21.07	218.1-341.9
19	2.29-2.1	8	270-390	307.5±13.59	38.45	12.50	275.3-339.7
20	2.09-1.9	9	240-420	320.0±33.91	101.73	31.79	241.7-398.3
21	1.89-1.7	5	270-360	330.0±16.74	36.74	11.13	284.3-375.7
22	1.69-1.6	7	300-480	415.7±22.13	58.55	14.09	361.5-469.9
23	1.59-1.3	8	420-540	480.0±13.89	39.28	8.18	447.1-512.9
24	1.29-1.10	4	480-540	510.0±12.25	24.49	4.80	471.0-549.0
25	1.09-0.8	3	510-540	530.0±10.00	17.32	3.27	487.0-573.0

* These measurements were not available in the sample

▲ The 95% confidence limits were not attached to the mean age because the sample size was small.

Table 44. Numerical data for estimating the age of the Skomer vole from the crown height of $_{M}3$:

G. No	CM^3h/ mm	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	1.0-1.10	3	10 days	10.0± -	-	-	10.0 days
	1.2-1.29*	-					
2	1.3-1.69	4	14 days	14.0± -	-	-	14.0 days
3	1.7-1.89	4	17 days	17.0± -	-	-	17.0 days
	1.9-2.19*	-					
4	2.2-2.39	4	21 days	21.0± -	-	-	21.0 days
5	2.4-2.49	4	24- 30	25.5± 1.50	3.00	11.76	20.7- 30.3
6	2.5-2.59	4	24- 30	28.5± 1.50	3.00	10.53	23.7- 33.3
7	2.6-2.79	6	30 days	30.0± -	-	-	30.0 days
8	2.89-2.8	7	35- 60	49.7± 3.95	10.44	20.99	40.0- 59.4
9	2.79-2.7	21	35- 80	51.8± 3.56	16.31	31.48	44.4- 59.3
10	2.69-2.6	10	60-100	72.4± 4.89	15.46	21.35	61.4- 83.5
11	2.59-2.5	4	72-100	85.5± 6.08	12.15	14.21	66.2-104.8
12	2.49-2.3	20	100-180	132.3± 5.68	25.42	19.22	120.4-144.1
13	2.29-2.1	14	80-300	200.7±17.22	64.42	32.09	163.5-237.9
14	2.09-2.0	8	165-240	200.6± 8.47	23.97	11.95	180.6-220.7
15	1.99-1.8	12	240-420	320.0±17.84	61.79	19.31	280.8-359.3
16	1.79-1.7	5	270-390	324.0±19.90	44.50	13.73	268.7-379.3
17	1.69-1.5	10	330-510	396.0±18.87	59.67	15.07	353.4-438.7
18	1.49-1.3	7	270-480	407.1±26.88	71.11	17.47	341.3-473.0
19	1.29-1.2	6	300-540	475.0±37.49	91.82	19.33	378.7-571.4
20	1.19-1.0	6	480-540	510.0±10.95	26.83	5.26	481.9-538.1

* These measurements were not available in the sample.

D. Conclusion and discussion:

I. Root growth and development:

The main purpose of studying the root growth and development of all the molars, in addition to discussing their relation with age, was to see which of them would give the best correlation with age. The study showed that the neck in the three lower molars started to develop at the age of 35 to 42 days, and at the age of 42 days in the three upper molars, in both, the mainland bank vole and the Skomer vole. The neck closed at its central lower end in the lower molars and at its central 'upper' end in the upper molars, at an age fluctuating between 72 and 100 days and sometimes as late as 120 days according to the different molars.

The roots then developed soon after the closure of the central end of the neck and grew with an average monthly increase which differed according to the different molars (Table 45).

Since the onset of root development, and the average monthly increase in root length were known, ageing voles would be easy by applying the following equation:

$$y = k + \left(\frac{M}{a}\right) 30 \text{ days}$$

y: Age in days.

k: Age of the vole at the onset of root development, (a minimum of 35 days for the lower molars and 42 days for the upper molars).

M: Root length + neck height.

a: Average monthly increase in the root length

Table 45. The average monthly increase in the molar roots of the mainland bank vole and the Skomer vole:

Average monthly increase/mm	RM_1	RM_2	RM_3	RM^1	RM^2	RM^3
mainland bank vole up to the age of 14 months	0.16	0.13	0.08	0.15	0.12	0.10
mainland bank vole up to the age of 18 months	0.13	0.10	0.07	0.13	0.08	0.06
Skomer vole up to the age of 18 months	0.14	0.12	0.07	0.10	0.11	0.09

For example, the age of a mainland bank vole with RM_1 length being 2.2 mm would be:

$$y = 35 + \left(\frac{2.2}{0.16}\right) 30$$

$$y = 35 + 412.5$$

$$y = 447.5 \text{ days}$$

This result does not differ much from that presented in table 18 (page 114), for voles having the same root length. The estimated age in table 18 was 433 days (group 20).

To compare the validity of each of the molars as age criterion, the correlation between their length and age was examined. Because all the six molars had almost the same correlation coefficient with age, the variability for the scatter of the measurements and the voles within each age-group sample and size-group was examined for every molar. The results showed that root length of M_2 had the lowest variability, and therefore the highest accuracy for estimating the age, then RM_1, RM^1, RM^2, RM^3, and RM_3 in order of reliability. This result applies to both the mainland bank vole and the Skomer vole.

M_1 and M^2 have been used by many authors to study root development, as an age criterion. The root length of M^3 has rarely been used as an ageing guide in British bank voles (Delany & Bishop, 1960) and (Bishop & Delany, 1963), but the method has not been discussed in detail.

The work which has been done on the roots of M^2 was by Koshkina (1955), on C. glareolus, C. rufocanus, and C. rutilus; Tupikova et al (1968), on C. glareolus, and C. rutilus; and Viitala (1971), on C. rufocanus. Their results showed that the formation of the neck of RM^2 occurred at 2 to 2.5 months in C. glareolus and C. rutilus (Tupikova et al, 1968 and Koshkina, 1955). While Koshkina (loc.cit.) recorded the appearance of roots at the age of 7 to 8 months in C. rufocanus, Viitala (1971), on the other hand, mentioned that the roots appear after the age of 65 days in this species.

The results of this study, on RM^2 of the two British races, C.g. britannicus, and C. g. skomerensis, showed that the neck (included with the roots in the material of the above authors), started to appear at the age of 42 days which is earlier than in the above species. The difference in the onset of root development between the British subspecies and the above species is probably specific. Feeding habits might speed up the development of the molar roots. Koshkina (loc.cit.) attributed the delay in the development of the molar roots to feeding habits also.

The average monthly increase in the roots of M^2 was found by Tupikova et al (loc.cit.) to be 0.1 to 0.2 mm in C. glareolus and C. rutilus. Viitala (loc.cit.) recorded it in C. rufocanus to be 0.16 mm in winter and 0.27 mm in males, 0.39 mm in females in summer months. In the present study, the average monthly increase of the root length of M^2 in C. g. britannicus, from 60 days and up to the age of 14 months, was 0.12 mm. In C. g. skomerensis, it was 0.11 mm, from 60 days up to 18 months of age.

The root length of M_1 has frequently been employed as an age indicator in C. glareolus by many authors including, Wrangle (1939), Prychodko (1951), Wasilewski (1952), Zejda (1961), Mazak (1963), Haitlinger (1965), Pucek & Zejda (1968), and Lowe (1971).

The results of their studies showed that the roots of M_1 (excluding the neck) started to develop during the third month of life or slightly later. Mazak (loc. cit.) for instance, recorded the root development to begin at the age of 3.5 months. Zejda (loc. cit.) stated that the neck formed during the third month of life and the roots could be measured at an age exceeding 3 months.

The results of the present study showed earlier development for the roots of M_1. The neck started to develop at 35 to 42 days in the two races. The roots could be measured starting at the age of 72 to 80 days and sometimes until the age of 4 months, the same result which was obtained for RM^2.

The monthly increase in the roots of M_1 of C. glareolus has been estimated by several authors, e.g. Prychodko (loc. cit.), and Haitliger (loc. cit.) recorded a monthly increase of 0.18 mm; Mazak (loc. cit.), 0.155 mm; Zejda (loc. cit.), 0.15 to 0.16 mm; Wasilewski (loc. cit), and Pucek & Zejda (loc. cit.), 0.15 mm. Lowe (loc. cit.) mentioned that the root growth rates varied with age and season ranging from 0.05 to 0.55 mm.

The results of the present study showed that the average monthly increase in the roots of M_1 for the mainland bank vole from the age of 60 days up to the age of 14 months, was 0.16 mm. It was 0.13 mm up to 18 months because of the slow growth of the roots above the age of 14 months, hence supporting Prychodko (1951) in his statement that growth of roots of M_1 is slower during the second year of life.

The average monthly increase in the roots of M_1 in the Skomer vole, from the age of 60 days up to the age of 18 months, was 0.14 mm.

Data on the development of molar roots in this study showed that they grew almost regularly throughout life (with a slowing of growth in old age) regardless of the different seasons. Overwintered voles did not have a slow-down in their molar root growth as it has been indicated by Zejda (1959), Haitlinger (1965), and Lowe (1971). My results are based upon a laboratory population and this regularity is probably due to the uniform conditions which prevented the environmental conditions from influencing the growth of molar roots. Mazak(1963) similarly reported a lack of seasonal effects in his laboratory population of C. glareolus.

Lowe (1971), in his study on the root development of the mainland bank vole, mentioned that the teeth of laboratory-bred animals proved aberrant in their development. He added that the first mandibular molars were rootless for at least the first 6 months of life. This abnormal growth has not occurred in the voles in the present study, and the roots in all cases were normal in their growth and development with regard to other authors' results. The abnormal growth of Lowe's laboratory animals is difficult to explain. However, his sample was possibly drawn from a small localised population with a 'defect' in tooth development. The founder members of his colony may have been few and all the descendents were the result of inbreeding among the original stock. However, he has not mentioned how many laboratory animals he used in his study.

Another possible explanation for the abnormal tooth growth is that alizarin injections might have affected the time of earliest root division in Lowe's laboratory voles, but his field animals showed no great effects of alizarin . If alizarin does have an effect, then it seems to be the only external factor that does.

II. Tooth wear:

The tooth wear has been used for ageing several big and small mammals. It has never been applied on *Clethrionomys*, mainly because of the most characteristic feature of the bank vole's molar teeth which develop roots at a definite age of life. Thus, investigators overlooked studying the tooth wear, as the **root length** was satisfactory for ageing the bank vole .

The occlusal surfaces of molar teeth in *Clethrionomys* are of the lophodont type, similar to those of the herbivores. In mammals with such teeth, the increasing area of exposed dentine on the occlusal surface of teeth has been measured to study tooth wear . Tanaka (1968), for instance, analysed the molar wear in the brown rat (*Rattus norvegicus*) by measuring the total size of occlusal area of the upper molars and calculating the molar wear index as a ratio of total worn surface to tooth row length times molar breadth.

In carnivores and insectivores, with their cheek teeth having pointed cusps, a linear measurement is taken to study tooth wear. This measurement is usually the distance between the gum line and the highest cusp.

Although, molar teeth in Clethrionomys are of the same type as the herbivorous mammals, their wear was studied by taking linear measurements for the crown height. The molar crown grew during the early stage of life, then stopped to grow at a definite age, and later, its height decreased with age.

Voles first take solid food when they are 14 days old and this is when wear starts. However, the degree of this wear cannot be measured quantitatively, until the age of 35 to 42 days, due to the continuous growth of the crown up to this age.

Tooth wear continued throughout the vole's life with a monthly average decrease in the crown height which differs in the different molars (Table 46).

Ageing voles from the crown height is easy if the age of voles having the maximum crown height, and the average monthly decrease of the crown height are known. This is accomplished by applying the following equation:

$$y = k + \left(\frac{M}{a}\right) 30 \text{ days}$$

Table 46. The average monthly decrease of molar crown height in the mainland bank vole and the Skomer vole:

/mm	CM_1	CM_2	CM_3	CM^1	CM^2	CM^3
mainland bank vole, 60 days up to 18 months	0.14	0.12	0.09	0.16	0.13	0.08
Skomer vole, 60 days up to 18 months	0.14	0.14	0.11	0.16	0.14	0.10

y: Age in days.

k: age of vole at the time of having the maximum crown height.

M: Crown height measurement.

a: Average monthly decrease in the crown height.

The molar growth (increase in crown height), and wear (decrease in crown height) were highly correlated with age. The correlation coefficient was almost the same in all the six molars, but variability within each age-group sample and size-group was found to differ among the different molars, and therefore according to this variability, the reliability of each molar, as an age criterion, was considered. The results of the present study showed the crown height of M_2 was the less variable character, then CM_1, CM^1, CM^2, CM^3, and CM_3. This result is applicable to the mainland bank vole and the Skomer vole.

Mazak (1963) mentioned the crown wear in C. glareolus. He recorded a decrease in the total height of the molar teeth which started above the age of 200 days, under the influence of crown wear. The results of the present study were dissimilar in that molars kept their height constant throughout life. This can be explained depending upon results which showed that the decrease in crown height was comparable to the increase in molar root length. Since crown heights always decreased above the age of 42 days, the crowns needed support from inside. This was accomplished by the continuous growth of the roots. The average monthly decrease in the crown height being almost comparable to the average monthly increase in the root length, gives support to the above speculation.

Although tooth wear proved to be a reliable age criterion in the bank vole and other small mammals, it has been shown to be highly unreliable for ageing certain species of bats, (Myotis lucifugus and M. keenii: Hall et al, 1957; and M. myotis: Sluiter, 1961).

Adamczewska-Andrzejwska (1973 b) also found some individual variations in tooth wear occurred within each age group in Apodemus agrarius. Individual variations were very low in bank voles raised in the laboratory. This was presumably due to the uniform hardness of the food pellets. Szabik (1973) in his work on the roe-deer, mentioned that the rate of tooth wear is connected with the hardness of food.

Tooth wear might be influenced by the hardness of teeth also. This hardness in turn is affected by different factors, such as the date of birth (seasonal factors), the quality of food the voles and their parents eat, the type of soil. and possibly hereditary factors.

Caution should be exercised when using tooth wear for ageing, as teeth are directly affected by external factors, (see chapter IV.).

II. 5. Fusion of epiphyses

A. Introduction:

The presence or absence of an epiphyseal cartilage in the subterminal regions of the long bones, between the epiphysis and metaphysis, has long been used as an age criterion for different mammalian species, (e.g. the cotton-tail rabbit (*Sylvilagus floridanus*), Thomsen & Mortensen, 1946; The grey and fox squirrels (*Sciurus carolinensis* & *S. niger*), Petrides, 1951, and Carson, 1961 ; the red & grey foxes (*Vulpes fulva* & *Urocyon cinereoargenteus*), Sullivan & Haugen, 1956; the European hare (*Lepus europaeus*), Bujalska *et al*, 1965; the cotton rat (*Sigmodon hispidus*), Chipman, 1965; the field voles (*Microtus gregalis* & *Lagurus lagurus*), Tarasov, 1966; the European hedgehog (*Erinaceus europaeus*), Morris, 1971; the red squirrel (*Sciurus vulgaris*), Davis & Sealander, 1971; the Danish red squirrel (*S. vulgaris*), Degn, 1973.

The use of this method is based on the fact that the epiphyseal cartilage is a growth centre which is after a certain interval, gradually replaced by a spongy bone while the animal grows older. Thus, the different stages of replacement of the epiphyseal cartilage could be closely connected with the age of any animal, and studying serial stages of replacement can give a key to the age of mammals. This method has never been used on *Clethrionomys* and the present work was carried out in order to find how far this method can be successfully applied to this genus.

B. Methods:

X-ray examination has been used by many authors to study the fusion of epiphyses, but Chipman (1965), in his work on *Sigmodon hispidus*, found that alizarin staining gave better results. Thomsen & Mortensen (1946), in their work on *Sylvilagus floridanus* came to the same conclusion. Palpating through the skin to feel the degree of formation of epiphyseal thickening,was used by Bujalska *et al* (1965) on *Lepus europaeus*. Hale (1949) examined cleaned bones to detect the epiphyseal cartilage of the humerus in *Sylvilagus floridanus*. He found bones easier to study than the x-ray and better in detecting remnants of cartilage that x-ray failed to show. Degn (1973), also examined cleaned bones to study the epiphysis of the distal end of the radius in *Sciurus vulgaris*.

In the present study, alizarin red-stained specimens were used, as they gave clear view of the bones and cartilages. X-ray has not been used in order to avoid pitfalls mentioned by the above authors. Results of alizarin red-stained specimens were found to be clear and easy to study than examining the bones. The technique of Mahoney (1966) has been followed. This, result in the flesh becoming transparent, leaving the red stained bones clearly visible in situ.

A low power binocular microscope was used to study the skeletons looking for stain-free cartilage (epiphyseal cartilage) between the epiphysis and the diaphysis. In studying areas of epiphyseal fusion, the degree of fusion was recorded and assigned to one of 4 categories. These are:

1. Open epiphysis: with a non-staining band of cartilage (did not take alizarin), between the epiphysis and the diaphysis.
2. Fusing epiphysis: with the band being narrower than in the first category, and the epiphysis has not fused to the diaphysis yet.
3. Fused epiphysis, suture visible: The epiphysis fused to the diaphysis and the suture line between them was visible.
4. Solidly fused epiphysis: The suture line disappeared.

A total of 55 mainland bank voles (26 females & 29 males), and 50 Skomer voles (24 females & 26 males) were examined in the present study for epiphyseal fusion.

C. Results:

Studying the alizarin stained skeletons of Clethrionomys revealed the presence of different sets of epiphyses. The most obvious ones, which formed the material for this study were:

1. Forelimb: Phalangeal, metacarpal, distal radio-ulnar, proximal humeral, and suprascapular.
2. Hind limb: Phalangeal, metatarsal, distal tibio-fibular, proximal tibiale, and distal femoral.

The tail was examined also to study the degree of fusion of the vertebral epiphysis, but after a preliminary study, its use was discontinued because variability was high between voles of the same age and the fusion was less correlated with age.

a. The mainland bank vole:

The forelimb was studied for areas of epiphyseal fusion. Results are summarized in Fig. 43.

The epiphyseal cartilage of the proximal phalanges remained unossified up to the age of 3 weeks. It reduced in size to a deeper staining suture line at the age of 30 days. The line disappeared soon afterwards. It was absent in specimens 42 days and older.

The metacarpal epiphyses were distinct and separate from the diaphyses in specimens 3 weeks old and younger. The epiphyseal cartilage was replaced by bone and the suture line remained obvious up to the age of 2 months, then disappeared.

The distal epiphyses of the radius and ulna remained separate from their diaphyses, up to the age of 2 months. The epiphyseal cartilage was replaced gradually during a time which extended to the seventh month of the vole's life. After the fusion of the epiphyses, the suture line remained visible up to the age of 14 months.

The proximal epiphysis of the humerus was distinct in specimens up to one month old. The ossification of the epiphyseal cartilage took place soon afterwards. At 9 months the epiphysis had fused to the diaphysis. The suture line was visible up to the age of 13 months, the time when it disappeared, but sometimes, traces of this line remained visible.

The suprascapular cartilage, at the corner between the vertebral and anterior borders of the scapula, started to take stain at the age of 21 days. Its ossification took place along the vertebral border. By 3 months a stain-free cartilage remained separating the ossified external parts of the suprascapular cartilage from the scapula. The ossification was completed at the age of 6 months. The suture line remained visible in specimens less than 12 months old. It was absent in voles above 12 months old.

The hind limb was studied for areas of epiphyseal fusion. Results are summarized in Fig. 43.

The phalangeal epiphyseal cartilage ossified very quickly. It was visible up to the age of 3 weeks. Ossification was complete at the age of one month and the suture line was absent in specimens aged, 2 months or older.

The metatarsal epiphyses remained separate from the diaphyses until the ossification of the epiphyseal cartilage, which took place over the age of one month, and was complete before the voles reached the age of 2 months. Suture lines were absent in specimens 72 days and older.

The distal epiphyses of the tibia and fibula were distinct in specimens up to 3 weeks old. Ossification of the epiphyseal cartilage continued until the age of 42 days. Suture lines were visible in specimens 42 and 60 days old but were absent in specimens aged 72 days and older.

The proximal epiphyses of the tibia and fibula were distinct in specimens younger than 2 months. Ossification of the epiphyseal cartilage took place in specimens 2 to 7 months old. The suture line was visible in specimens of 8

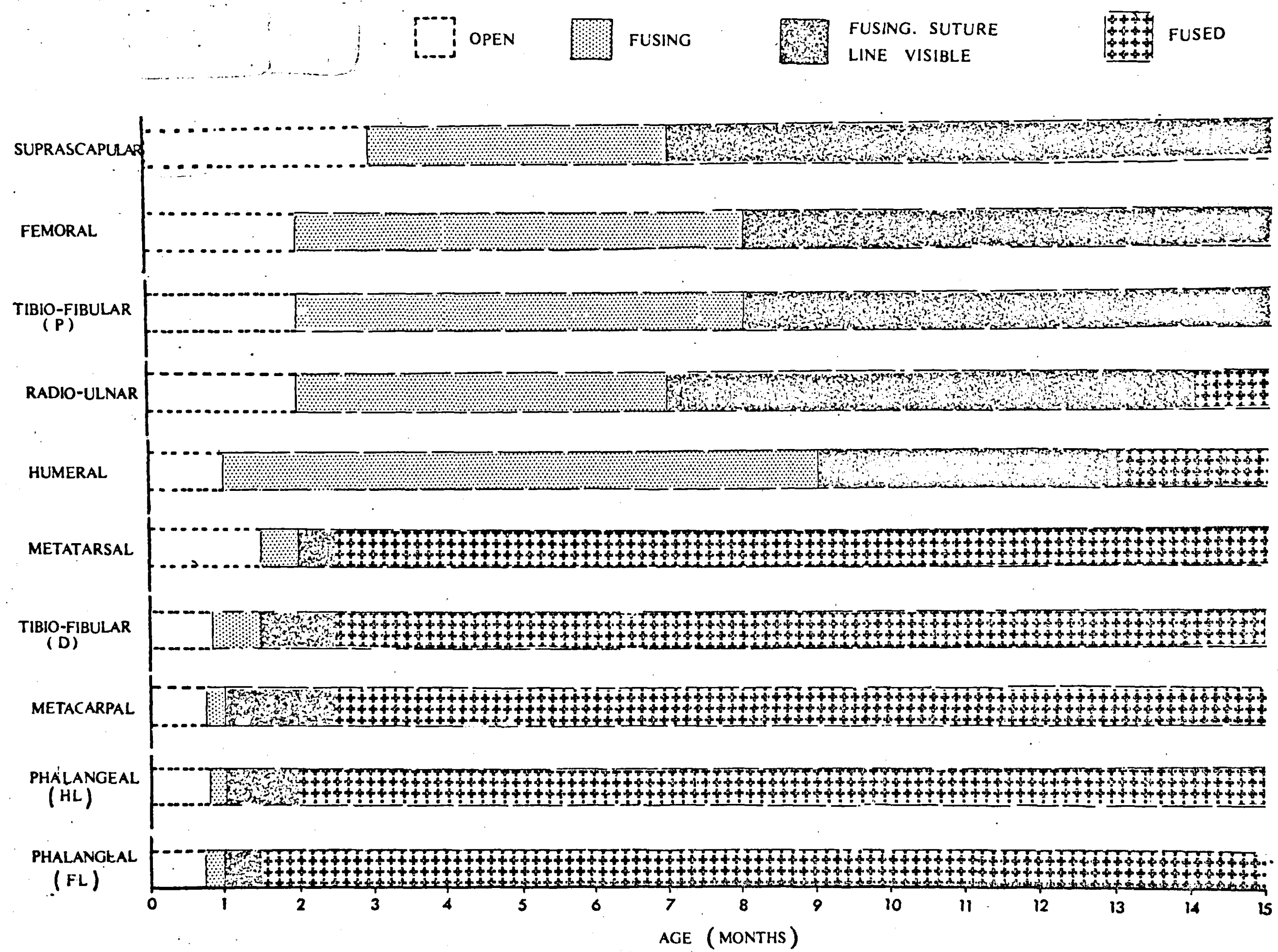


Fig. 43. Fusion of ten sets of epiphyses in the mainland bank vole.

months and older.

Changes in the distal epiphysis of the femur were very similar to the proximal epiphyses of the tibia and fibula. It was clearly distinct in specimens less than 2 months old, and fused to the diaphysis in specimens between 2 and 7 months old. The suture line was visible in specimens from 8 to 14 months old.

b. The Skomer vole:

The forelimb of the Skomer vole was studied and the results are summarized in Fig. 44.

The ossification of the phalangeal epiphyseal cartilage of the hand in the Skomer vole was similar to that in the mainland bank vole. The epiphyses were distinct in specimens up to 21 days old. Ossification took place in specimens 21 to 30 days old. Staining suture lines were absent in voles of 42 days and older.

The metacarpal epiphyses were distinct in specimens younger than one month. Ossification then occurred and the suture line was visible in specimens 42 days to 120 days old. It was absent in voles of 5 months and older.

The distal epiphyses of the radius and ulna showed no ossification in specimens aged 2 months and younger. Ossification started taking place at the age of 72 days, and continued in specimens 10 months old. The suture line was visible in voles 11 to 14 months old.

The proximal epiphysis of the humerus was separate from the diaphysis in specimens less than 2 months old. Ossification of the epiphyseal cartilage took place in specimens 2 to 3 months old. The staining suture line was visible in 4 to 12 months old voles. It was absent in voles of 13 months and older.

The suprascapular cartilage did not take stain in specimens less than 3 weeks old and a stain-free band continued to separate the ossifying external parts of the suprascapular cartilage and the scapula in specimens up to 3 months old. Ossification up to 9 months of age, the time when the suprascapular epiphysis fused to the scapula. The suture line remained visible in voles 9 to 12 months old, then it disappeared.

The hind limb of the Skomer vole was studied and results are summarized in Fig. 44.

The phalangeal epiphyseal cartilage started to ossify in 30 days old voles. Ossification was completed before the voles were 42 days old. The suture line was not visible in voles of 2 months and older.

The metatarsal epiphyses were very similar to the phalangeal epiphyses. They were distinct in specimens less than 30 days old and fusing in voles 30 days old. The suture line was absent in voles of 2 months and older.

The distal epiphyses of the tibia and fibula were distinct in voles less than one month old, then fused to the diaphyses. The suture line was visible in voles 42 to 60 days old and absent in voles aged more than 72 days.

The proximal epiphyses of the tibia and fibula were

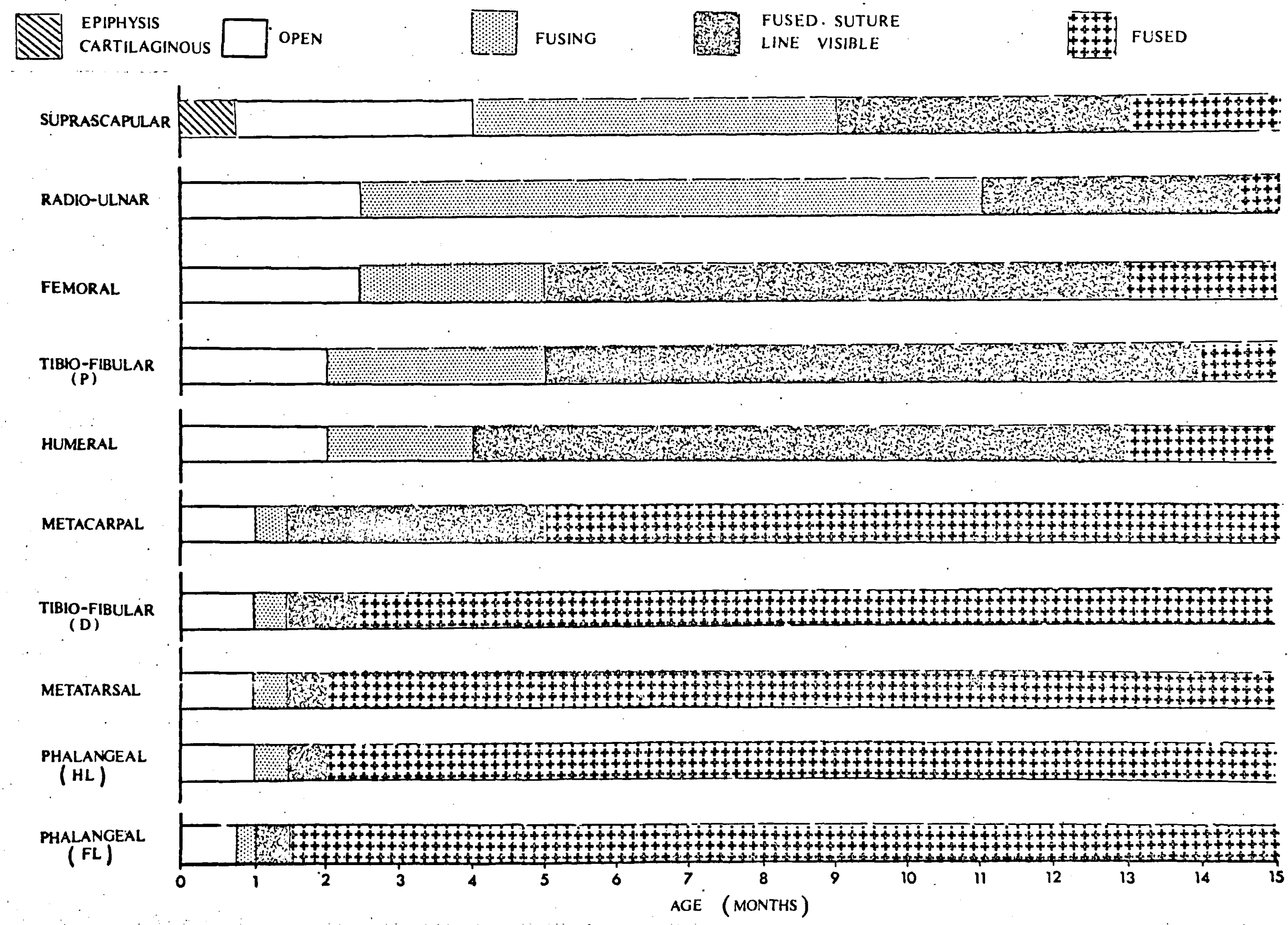


Fig. 44. Fusion of ten sets of epiphyses in the Skomer vole.

separate from the diaphyses in voles less than 60 days old. Fusion to the diaphyses was completed when the voles were 4 months old, but the suture line was visible in voles 5 to 13 months old.

The distal femoral epiphysis was distinct from the diaphysis in specimens of 2 months and younger. Gradual ossification of the epiphyseal cartilage took place in voles 72 days to 4 months old. Then the epiphysis fused to the diaphysis with the suture line remaining visible until the age of 12 months.

D. Conclusion and discussion:

The results of the present study confirmed that epiphyseal fusion can be used as an age criterion in *Clethrionomys*. By comparing the different ossification areas, one can estimate the approximate age of bank voles up to about 14 months of age. This result is highly reliable if compared with results of using this method on other mammals. For instance in the cotton rat, Chipman (1965), was only able to establish the approximate age up to 6 months. Rybář (1969 & 1971) used the method for the bats *Myotis myotis* & *Rhinolophus hipposideros*. He obtained a high accuracy for estimating the age of the former up to the age of 15 weeks & for the latter up to the age of 6 weeks, after which the skeleton became completely fused (Pucek & Lowe, 1975).

The epiphyseal fusion of the forefeet has been used most extensively by some authors to determine the age of different species of mammals. All agreed that it is a successful guide for this purpose.

In the European hedeghog (Erinaceus europaeus), epiphyseal fusion in the forefoot divided hedeghog into 4 age-related categories in the first year of life, and 3 other categories in adults (Morris, 1971). Sullivan and Haugen (1956) were able to separate adult foxes from young of the year in Vulpes fulva and Urocyon cinereoargenteus.

In the present study, if the forefoot alone, is used as an age device, the epiphyses of the radius and ulna prove to be the ones that should be concentrated on, because the phalangeal and metacarpal epiphyses fuse quite early to the diaphyses. Epiphyseal fusion in the forefeet allowed only four age categories to be derived for the mainland bank voles and Skomer voles. In the mainland bank vole these categories are:

1. Voles 42 days and younger, with the radio-ulnar epiphyses open, phalangeal fused, and the metacarpal fused with the suture line present.
2. Voles 2 to 6 months old, with the radio-ulnar epiphyses fusing to the diaphyses, the phalangeal and metacarpal epiphyses fused solidly.
3. Voles 7 to 13 months old, with the radio-ulnar epiphyses fused to the diaphyses and the suture line visible.
4. Voles above 14 months old, with the radio-ulnar epiphyses fused solidly and no visible suture line.

In the Skomer vole, epiphyseal fusion took longer so that the same morphologically distinguished categories represented the following ages:

1. Less than 60 days.
2. Seventy two days to 10 months.
3. Eleven to 14 months.
4. Fourteen months and more.

The distal epiphyses of the radius and ulna in the bank vole were distinctly separated from the diaphyses in young voles, but the fusing process took place while the voles were sexually adult, and the distinct line of fusion is easily found in adult voles. Therefore, the ossification of the distal epiphyseal cartilage of the radius and ulna does not coincide with the maturity of the voles, as traces of it remained in bank voles 9 months old, that is 7 months after maturation. In contrast, Petrides (1951) found that in squirrels, the fusion of these epiphyses did correspond to the attainment of sexual maturity. All squirrels, (Sciurus niger & S. carolinensis) with open epiphyses or a distinct epiphyseal line were immature. These differences between squirrels and bank voles are probably due to the differences in their habits. The squirrels being more active, and therefore activity might speed up fusion of epiphyses in the species. Similarly, epiphyses in Skomer voles fuse later than in the mainland bank voles, as the former are somewhat less active, with a home range being smaller than in the mainland bank vole (Jewell, 1965). The hedgehog (Erinaceus europaeus), which is a slow mammal, does not travel for long distances (a maximum straight-line distance of 600 meters, Morris, 1969), its epiphyses fuse at an age of up to 18 months. this is an early fusion in proportion to the hedgehog's life span (up to 7 years, Morris, loc.cit.).

The epiphyseal fusion of the humerus has also been used, as an age indicator. Thomsen & Mortensen (1946) studied the ossification of the epiphyseal cartilages in the shoulder and elbow of the cottontail rabbit (Sylvilagus floridanus meamsi). They concluded that the cartilage in the shoulder persists longer than at the elbow, and therefore can be used as a criterion of age over a longer period.

Hale (1949), in his study of the epiphyseal cartilage of the humerus in the same genus, concluded that it disappears at about 9 months of age. In contrast, the humeral epiphyseal cartilage, persists until the age of 9 months in the mainland bank vole, and until 3 to 4 months in the Skomer vole, which can be considered a better ageing result for the bank vole than for the cottontail rabbit, if the life span of each genus is taken into account. Rabbits are bigger, with a longer life span, large home range (few acres in size, Walker, 1968), and more active than bank voles, and without early fusion of epiphyses, they can not manage to perform their wide range movements and high speed.

The fusion of epiphyses including radio-ulnar, humeral, and femoral in Microtus gregalis & Lagurus lagurus, was studied by Tarasov (1966). Of the seven age classes he designated for voles up to one year old, the first three were the most reliable.

Results obtained during the present study are in some agreement with Tarasov's, especially those which show that epiphyses do not fuse until in old age. This is probably due to the limited activity of these small rodents as indicated by their small home range, (being 1970 square metres for males, and 1354 square metres for female

Clethrionomys glareolus (Crawley, 1969); and 1162 square yards (=971.6 square metres) for Microtus agrestis (Brown, 1956).

The early epiphyseal fusion of the phalanges, metacarpals, metatarsals, radio-ulnar, and distal tibio-fibular, could be attributed to the fact that these parts are the most commonly used by the voles. In contrast, the femoral, humeral, and suprascapular fuse at late stages, as voles do not rely on them during their early ages.

Hagen (1955 & 1956), studied the fusion of epiphyses of the tail vertebrae in Microtus arvalis as an age criterion, and claimed an accuracy of ageing of between 1 & 2 months. But I found some variations to occur in the epiphyseal fusion of the tail vertebrae in Clethrionomys. Moreover, Hansson found this method unsatisfactory in small rodents (Askaner & Hansson, 1967). However, tail vertebrae need further study.

In view of the results obtained on fusion of epiphyses in Clethrionomys glareolus, the method found a highly reliable index of age, and easy to apply. Although alizarin red-stained specimens were used in the present study, which needed dead voles, x-ray method can also be used, since it gave successful results on small rodents, e.g. Microtus & Lagurus (Tarasov, 1966). It therefore, can be used on live animals.

The following age-related categories are proposed to determine the age of the mainland bank vole and the Skomer vole, on the bases of the fusion of ten sets of epiphyses:

a. <u>The mainland bank vole</u>:

Category No.	Age / days	
1.	less than 21 days	All epiphyses are open; stain-free suprascapular epiphysis.
2.	21- 30	Open: Radio-ulnar; humeral; suprascapular; metatarsal; tibio-fibular(P); femoral. Fusing: Phalangeal (hand & foot); metacarpal; tibio-fibular (D). Fused, s. visible: ------- Fused : -------
3.	30- 42	Open : Radio-ulnar; suprascapular; metatarsal; tibio-fibular (P); femoral. Fusing: Humeral; tibio-fibular (D). Fused, s. visible : Phalangeal (hand & foot); metacarpal. Fused : -------
4.	42- 60	Open: Radio-ulnar; tibio-fibular (P); femoral. Fusing: Humeral; metatarsal. Fused, s. visible :Metacarpal; phalangeal (foot); tibio-fibular (D). Fused : Phalangeal (hand).
5.	60- 72	Open : Suprascapular. Fusing: Radio-ulnar; humeral; tibio-fibular (P); femoral. Fused, s. visible : Metacarpal; metatarsal; tibio-fibular (D). Fused : Phalangeal (hand & foot).

6.	72- 90	Open :	Suprascapular.
		Fusing:	Radio-ulnar; humeral; tibio-fibular (P); femoral.
		Fused,s. visible :	--------
		Fused :	Phalangeal; metacarpal; metatarsal; tibio-fibular (D).
7.	90-210	Open :	----------
		Fusing:	Radio-ulnar; humeral; suprascapular; tibio-fibular (P); femoral.
		Fused,s. visible :	--------
		Fused :	Phalangeal (hand & foot); metacarpal; metatarsal; tibio-fibular (D).
8.	210-270	Open :	----------
		Fusing:	Humeral.
		Fused,s. visible :	Radio-ulnar; suprascapular; tibio-fibular (P); femoral.
		Fused :	Phalangeal (hand & foot); metacarpal; metatarsal; tibio-fibular (D).
9.	270-420	Open :	---------
		Fusing:	---------
		Fused,s. visible :	Radio-ulnar; humeral; suprascapular; tibio-fibular (P); femoral.
		Fused :	Phalangeal (hand & foot); metacarpal; metatarsal; tibio-fibular (D).

(D): distal

(P): proximal

Fused s. visible: fused, suture line visible.

b. The Skomer vole:

Cat. No.	Age/ days	
1.	less than 21 days	All epiphyses are open.
2.	21- 30	Open : All except: Fusing: Phalangeal (hand).
3.	30- 40	Open : Radio-ulnar; humeral; suprascapular; tibio-fibular (P); femoral. Fusing: Metacarpal; phalangeal (foot); metatarsal; tibio-fibular (D). Fused, s. visible : Phalangeal (hand). Fused : ----------
4.	40- 60	Open : Radio-ulnar; humeral; suprascapular; tibio-fibular (P); femoral. Fusing: ---------- Fused, s. visible : Metacarpal; phalangeal (foot); metatarsal; tibio-fibular (D). Fused : Phalangeal (hand).
5.	60- 70	Open : Radio-ulnar; suprascapular; femoral. Fusing: Humeral; tibio-fibular (P). Fused, s. visible : Metacarpal; tibio-fibular (D). Fused : Phalangeal (hand & foot); metatarsal.
6.	70-120	Open : Suprascapular. Fusing: Radio-ulnar; humeral; tibio-fibular (P); femoral. Fused, s. visible : Metacarpal. Fused : Phalangeal (hand & foot); metatarsal; tibio-fibular (D).

7.	120-150	Open :	----------
		Fusing:	Radio-ulnar; suprascapular; tibio-fibular (P); femoral.
		Fused, s. visible :	Metacarpal; humeral.
		Fused :	Phalangeal (hand & foot); metatarsal; tibio-fibular (D).
8.	150-270	Open :	----------
		Fusing:	Suprascapular; radio-ulnar.
		Fused, s. visible :	Humeral; tibio-fibular (P); femoral.
		Fused :	Phalangeal (hand & foot); metacarpal; metatarsal; tibio-fibular (D).
9.	270-330	Open :	----------
		Fusing:	Radio-ulnar.
		Fused, s. visible :	Humeral; suprascapular; tibio-fibular (P); femoral.
		Fused :	Phalangeal (hand & foot); metacarpal; metatarsal; tibio-fibular (D).
10	330-390	Open :	-----------
		Fusing:	-----------
		Fused, s. visible :	Radio-ulnar; humeral; suprascapular; tibio-fibular (P).
		Fused :	Phalangeal (hand & foot); metacarpal; metatarsal; tibio-fibular (D); femoral.
11.	390 and over	All epiphyses are fused.	

II. 6. The Baculum

A. Introduction:

The baculum of mammals has often been used as a taxonomic character, (Thomas, 1915; Burt, 1936 & 1960; Hamilton, 1946; Callery, 1951; Dearden, 1958; and Anderson, 1960). In recent years, many authors have also used the baculum as a means to determine age. Their studies were confined to certain groups of mammals (Carnivora and Rodentia mainly) and have only rarely been extended to small mammals.

Deanesly (1935) and Wright (1947) used the weight of the baculum to distinguish between juvenile and adult *Mustela erminea* & *M. frenata*. The baculum weight, length, and shape were used by Friley (1949 a & b) in differentiating probable age classes in the otter (*Lutra canadensis*), and the beaver (*Castor canadensis michiganensis*). The weight and length of the baculum were acceptable age criteria in the grey squirrel (*Sciurus carolinensis*), (Kirkpatrick & Barnett, 1957). Walton (1968) separated juveniles from adult polcat (*Putorius putorius*) depending on the baculum. Elder (1951) used the weight and length of the baculum to distinguish between juvenile and adult minks (*Mustela vison*). Baumgartner & Bellrose (1943), differentiated between the adult and subadult muskrat males (*Ondatra zibethicus*), according to the size of the penis and the ease with which it can be pressed through the urethral papilla.

Sudies of bacula in small mammals are less numerous. Burt (1936) mentioned that there is considerable age variation in the bacula of the genera *Perognathus* and *Dipodomys*, for the baculum seemed not to be fully developed until the animal was adult. He also reported that the bacula of young individuals are smaller with less bulbous basal ends than are those of adults.

Artimo (1964 & 1969) in Finland, studied the baculum in male *Clethrionomys glareolus* & *Lemmus lemmus*, to differentiate between sexually mature and immature individuals. He found that the total length of the baculum, the length of its stalk, and the width of the proximal part of the stalk, could all be used for that purpose.

The purpose of the present study was to find whether the baculum is a useful structure from which to determine the age of male *Clethrionomys glareolus britannicus*, and *C. g. skomerensis*.

B. Methods:

Study of the baculum shape was based on alizarin red-stained specimens. Drawings were made with the aid of a camera lucida fitted on a binocular microscope. Photographs were taken showing different stages of development. Any part of the baculum was considered ossified when it accepted the alizarin red stain.

C. Results:

The shape of the baculum of the British *C. glareolus* is similar to that described by Ognev (1964) in Russia; Anderson (1960) for a specimen collected in Switzerland; and Artimo (1964) in Finland.

The stalk of the baculum is rather broad and angular at its proximal end. It narrows toward the distal end. The latter is slightly broad and rounded. The distal end attached to three digital processes, one central, and two lateral , (Fig. 45).

The ossification of the stalk of the baculum precedes that of the digital processes in the mainland bank vole. It started to accept stain when the animals were less than 7 days old. Its length was 1.36 mm in one 7 days old specimen. Its average length was 2.2 mm at the age of 14 days; 2.48 mm at 21 days; 2.8 mm at 30 days; and 2.9 mm at 42 days. The digital processes at the age of 42 days were still not ossified. Their ossification occurred during the seventh week of the vole's life. Bacula with ossified digital processes were found in voles 46 days old. Ossification of the three digital processes took place simultaneously. The baculum attains the adult shape,form, configuration after the ossification of the digital processes (Fig. 45). No size differences were found between bacula of adult voles in relation to age. The stalk length remained the same in voles 60 days to 450 days old, (its average length was 3.33 ± 0.04 mm for 15 age-group samples aged 49 to 450 days, with a standard deviation of 0.16 mm).

The digital processes also remained the same length since they first took up the stain. The central process, for instance, had an average length of 2.62 ± 0.03 mm, with a standard deviation of 0.09 mm, in voles aged 49 to 450 days.

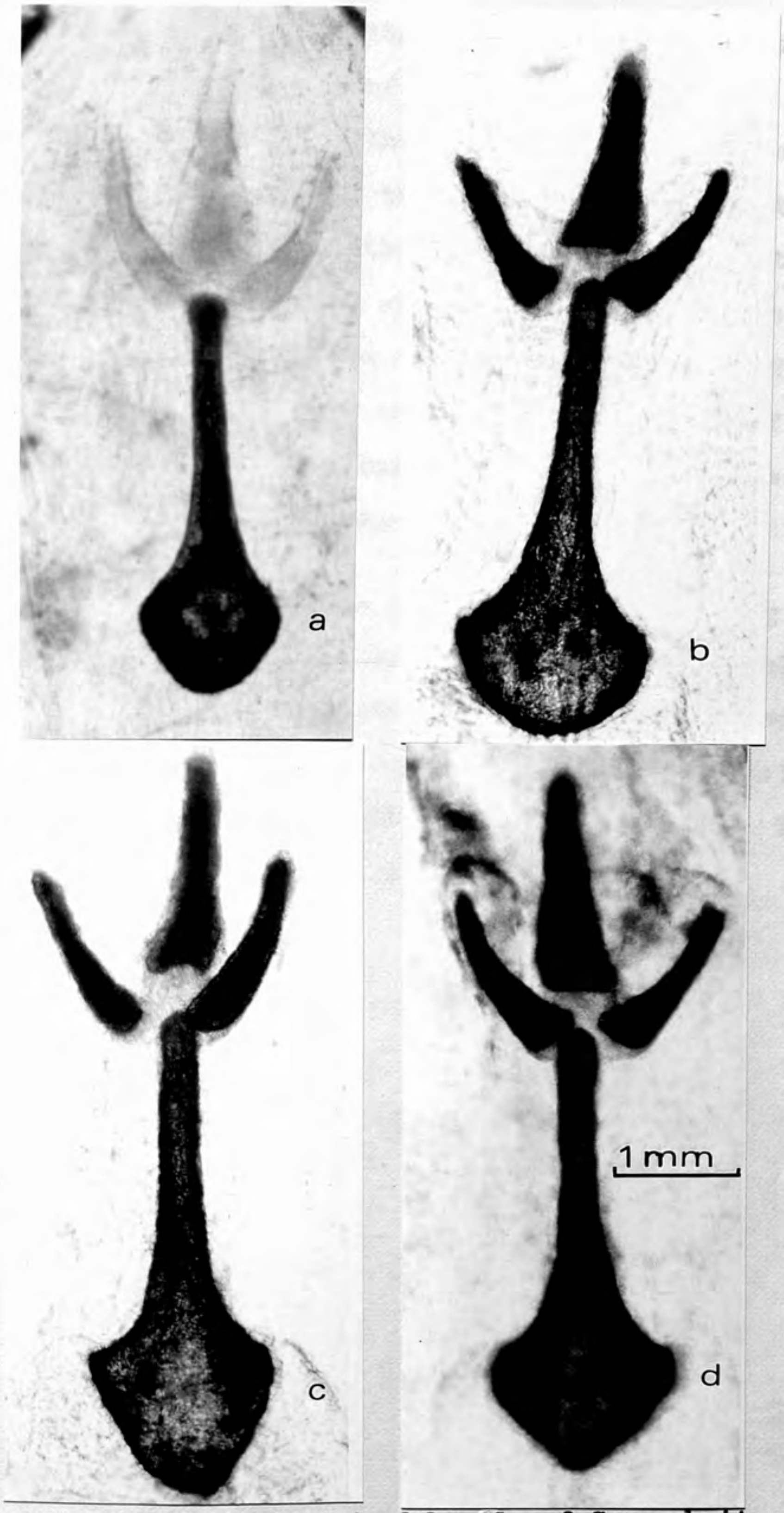


Fig. 45. Alizarin red-stained bacula of C. g. britannicus.

a. 30 days old. c. 150 days old.

b. 72 " " d. 360 " "

The ossification of the stalk of the baculum in Skomer voles also precedes that of the digital processes. It is longer than the stalk in the mainland bank vole, as a result of a bigger body size for the Skomer vole. It started showing some staining before the seventh day of age. Its length was 1.5 mm for one 7 days old specimen. Its average length was 2.8 mm at 30 days; and 3.48 mm at the age of 42 days. The stalk length remained constant above the age of 50 days. Its average length was 4.05 ± 0.03 mm in voles 60 to 360 days old, with a standard deviation of 0.09.

The digital processes started to show staining during the seventh week of the vole's life, as in the mainland bank vole, but they took longer time to complete ossification. The central process was the first to show staining, and it was the last to complete the ossification. This happened between the ages 72 and 90 days.

D. Discussion:

Based solely on the ossification of the baculum, two groups of laboratory-born *C. glareolus* could be distinguished. The first included voles less than 7 weeks old, with their baculum having only its stalk ossified, and ranging between 1.36 mm to 2.9 mm in length. The second group included voles 7 weeks and older, with their bacula having, in addition, the digital processes ossified.

Artimo (1964), working on the bacula of *C. glareolus* in Finland, stated that the development of the adult type of baculum is correlated with sexual maturation and not with age. He found that the age range for immature voles was 1.5 to 10 months, and for the mature, 1.5 to 15 months. In the present study, if we consider that the laboratory-born bank voles breed throughout the year, which they did, males became sexually mature during the seventh week of their life and the digital processes of their bacula ossified at this age. On this interpretation, the results of this study agree with that of Artimo (1964) when he stated that the bacula attain their earliest full size in breeding voles 1.5 month old.

The youngest age at which a female mainland bank vole gave birth to her first litter was 56 days , having been impregnated by her littermate. Subtracting a gestation period of 18 days gives an age at conception of 38 days. If the ossification of the digital processes corresponded to maturity in males, and males mature at the same age as females, the earliest male maturation was thus, at 38 days old. All bacula in males above the age of 42 days, in this study, had their digital processes ossified and were thus of the adult form.

Measurements of the stalk length in C. g. britannicus, and C. g. skomerensis, are higher than in the Finnish subspecies, (probably C. g. suecicus, Ellerman & Morrison-Scott, 1951). The mean stalk length for the mature Finnish subspecies was 2.45 ± 0.12 mm. It was 3.33 ± 0.04 mm for C. g. britannicus, and 4.04 ± 0.03 mm for C. g. skomerensis. The size difference of the bacula between these three subspecies might be a reflection of the size of the body and the skeleton of each of them.

In spite of the baculum having been used successfully by many authors as an age criterion for several species of mammals, it is not as satisfactory in C. glareolus. It is only useful to distinguish voles less than 7 weeks from those above this age. Beyond the age of 7 weeks, the shape and size of the baculum is fixed and no longer dependent on the age.

In voles less than 7 weeks old, with the digital processes being not ossified, the stalk length is the only means to distinguish between voles with different ages.

II. 7. The dry weight of the eye lens

A. Introduction:

Using the dry weight of the eye lens to determine the age of animals is based on the principle that the growth of the eye lens does not cease with that of the body, but continues throughout life, of humans , for instance (Smith, 1883). Krause (1935) made the same statement concerning the eye lens of the domestic rabbit. Norrby in 1958, working on rats, has also mentioned that the weight and volume of the lens and eyeball increased along an asymptotic curve .

Using this method as an age criterion for wildlife species, is a quite recent development. Lord in 1959 was the first to suggest it for determining the age of the cottontail rabbit (*Sylvilagus floridanus*). In his method, Lord depended on the fact mentioned by Lansing (1952) that "new lens fibers are continuously being proliferated by the growth and elongation of the epithelial cells at the lens equater. The lens fibers at the centre of the lens are laid down during intra-uterine life and because of the avascular nature of the lens and its density, those fibers at the centre of the lens lose their cell membrane and become dense and rigid, and their cytoplasm loses water".

Lord (1961 & 1962), in addition, has applied this method to the grey fox (*Urocyon cinereoargenteus*), and the white-tailed deer (*Odocoileus virginianus*).

Since then many research workers have followed Lord in using this method with other species of wild mammals.

The lens technique was reviewd by Friend in 1965, 1967 & 1967a. The method appears most suitable for medium-sized mammals, and relatively few attempts have been made to apply the technique to small mammals. Chipman (1965) established 5 age classes for the cotton rat (Sigmodon hispidus), depending on the dry weight of the eye lens only; Martinet (1966) obtained satisfactory results with the common vole (Microtus arvalis); Ostbye & Semb-Johansson (1970) studied lens growth of known-age Norwegian lemmings (Lemmus lemmus); Fisher & Perry (1970) mentioned the lens weight method is sufficient ageing criterion for separation of juveniles and adults, and for estimating year classes of adult grey squirrels (Sciurus carolinensis); Degn (1973) managed to differentiate juveniles from adult Sciurus vulgaris depending on the eye lens weight; Adamczewska-Andrzejewska (1973 a & b) found that increase in eye lens weight is closely parallel with the age in Microtus arvalis & Apodemus agrarius; and Gourley & Jannett (1975) found lens weights a satisfactory basis for estimating ages of Microtus pinetorum and M. montanus..

Nothing has previously been recorded concerning the use of the eye lens weight as an age indicator for Clethrionomys spp. except that of Askaner & Hansson (1967), and Le louarn (1971). The former authors found that the dry weight of the eye lens in Clethrionomys rufocanus and C. rutilus, collected in Norway, Sweden, and Finland gave greater accuracy for ageing than the molar roots. Le louarn applied the technique on C. glareolus in France and established monthly differences in eye lens weight.

B. Methods:

The method which was applied to all the laboratory-bred and enclosure populations, followed the techniques of Lord (1959), and Friend (1967a).

Two minutes after the voles were killed, the eyeballs were extracted and preserved, for 3 to 5 days, in vials containing 5% formalin. The eye lenses were dissected out, rolled on blotting paper to remove excess moisture, put in uncapped vials and placed in an oven at 60 to 70°C for another 3 to 5 days.

The right and left lenses were put together for drying, because Lord (loc. cit.), and Degn (1973), found no significant differences in weight between them in *Sylvilagus floridanus* and *Sciurus vulgaris* respectively. To confirm that Lord & Degn's observations also applied to *Clethrionomys*, the dry weight of both vole lenses was obtained separately to the nearest 0.005 mg. Weight was taken using an Oertling balance within 20 minutes of removing the eye lenses from the oven. The values of the two lenses of each vole were averaged in order to represent one animal's lens weight.

The effect of formalin on the eye lens:

Two experiments were carried out in order to find out:

1. The effect of two formalin concentrations on the eye lens weight.
2. The effect of fixation time on the eye lens weight, using one concentration of formalin, to ascertain that there

will not be any differences between eyeballs kept for 3 days in the fixative than those which kept for 5 days.

Two litters from different parents, were used. The first litter, born on 27 March 1974, comprised 2 females and 2 males, 30 days old. The second litter, born on 12 March 1974, comprised 2 females and 2 males, 42 days old. One female and one male from each litter, 4 animals in total, were used for each experiment:

a. Two formalin concentrations were used, 5% & 10%. The 4 left eyeballs, after they were extracted, were kept in 5% formalin for 3 days; the 4 right eyeballs were kept in 10% formalin also for 3 days. All the 8 lenses were subsequently put in the oven (60 to 70°C) for 3 days to dry. The weight of each lens was taken, 20 minutes after it was removed from the oven.

b. The eyeballs from the remaining voles were all fixed in 5% formalin. The 4 left eyeballs were kept in the fixative for 3 days, and the 4 right eyeballs were kept for 15 days. Then all the 8 lenses, after they have been dissected, were dried in the oven for 3 days.

The results of the experiments are presented in table 47. Neither the different concentrations of formalin, nor the duration of fixation, up to 15 days, had any significant effect on the eye lens weight. This result is similar to that of Friend (1967a), in his work on the effect of fixation time on lens weight of white rats. He showed that significant differences between fresh and fixed lenses appeared only after keeping the lenses in formalin from 4 weeks onward.

Table 47. Data showing the non-effect of two formalin concentrations, and fixation time on the dry weight of the eye lens of _C. g. britannicus_:

Sex	Age/ days	Eye lens	Concent-ration of formalin	Fixation time/days	Eye lens weight/mg
F	30	left	5%	3	1.540
"	30	right	10%	3	1.540
M	30	left	5%	3	1.540
"	30	right	10%	3	1.560
F	42	left	5%	3	1.860
"	42	right	10%	3	1.900
M	42	left	5%	3	1.880
"	42	right	10%	3	1.880
		- - - - - - - - - -			
F	30	left	5%	3	1.430
"	30	right	5%	15	1.440
M	30	left	5%	3	1.550
"	30	right	5%	15	1.600
F	42	left	5%	3	1.860
"	42	right	5%	15	1.860
M	42	left	5%	3	1.870
"	42	right	5%	15	1.860

C. Results:

a. The mainland bank vole:

a.1. Growth curve of the eye lens:

Data for the growth of the eye lens are presented in Fig.46 and Appendix 42. Differences between the two sexes were not signficant, (t_{64}=0.118, $P > 0.9$), and the data were combined.

The dry weight of the eye lens is highly correlated with age, (r for the whole sample was 0.85). The variation between individuals of similar age was very low ($\bar{v}$=5.28). The growth of the eye lens was very fast during the first four months of life (r=0.96 up to the age of 60 days). The average weight of the eye lens at the age of 14 days was 0.8388 mg. It was 1.4285 mg at the age of 30 days; 2.1088 mg at 60 days; and 2.6233 mg at 120 days. The growth of the eye lens slowed down afterwards, but it never ceased. The lowest rate of growth occurred between the age 6 to 9 months.

Differences between the weights of the two eye lenses of 238 specimens of the mainland bank vole were computed for each individual. Ninety three specimens out of the whole sample had no difference in weight between the two eye lenses. The difference was very low in the other 145 specimens. It ranged between 0.010 to 0.10 mg, and averaged 0.081±0.008 mg which was equal to 0.67% of the dry weight of the eye lenses. This result is less than that obtained by Lord (1959), for the cottontail rabbit. The mean percentage difference for the latter was 0.87±1.21.

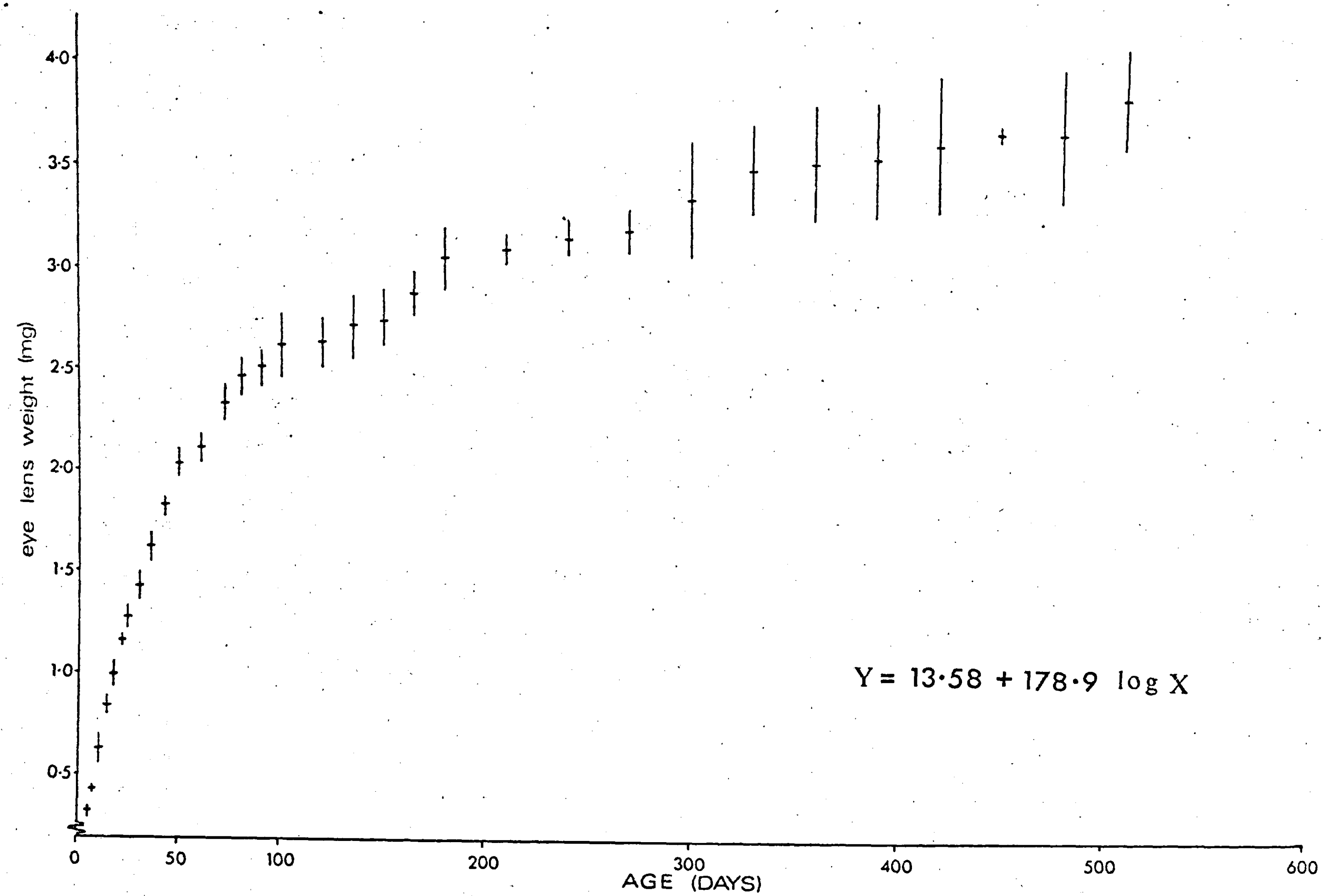


Fig. 46. Growth curve for the dry weight of the cye lens of the mainland bank vole. (see Fig. 19 for explanation).

a.2. Estimating the age from the dry weight of the eye lens:

The whole sample was divided into 29 groups according to the dry weight of the eye lens. The frequency distribution, mean age, standard deviation, standard error, and coefficient of variation, for each group were computed and 95% confidence limits were attached to the mean age of each size-group (Table 48).

The dispersion of the values within each size-group was regular ($\bar{v}$=11.98 for the whole sample).

The accuracy for estimating the age was very high up to a mean age of 104.6 days, and an eye lens weight of 2.5 to 2.595 mg (groups 1 to 19). The accuracy extended from ±0.0 (groups 1 to 5, 9, 11, and 12) to ±14.7 days (group 19). The variability increased above a mean age of 183 days (group 23) onward, due to the slowing in the growth of the eye lenses, which in turn decreased the accuracy for ageing bank voles with eye lens weights of more than 2.90 mg. The highest variability (v=34.16) was in voles with eye lens weights of 3.2 to 3.395 mg and a mean age of 313.9 days. The accuracy for estimating the age of voles with this eye lens weight was ±64.8 days (group 25).

The low accuracy for ageing voles with 3.4 to 3.495 mg eye lens weight (being 330±103.1 days), was mainly due to the small sample size (group 26), as the variability was low (v=19.64).

The high accuracy for estimating the age, the low variability ($\bar{v}$=11.98), along with the high correlation coefficient, render the use of the dry weight of the eye lens a highly reliable criterion for ageing the mainland bank vole.

Table 48. Numerical data for estimating the age of the mainland bank vole from the dry weight of the eye lens:

G. No	EL W/ mg	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.3-0.395	4	5 days	5.0± -	-	-	5.0 days
2	0.4-0.495	5	7 days	7.0± -	-	-	7.0 days
3	0.5-0.795	6	10 days	10.0± -	-	-	10.0 days
4	0.8-0.895	4	14 days	14.0± -	-	-	14.0 days
5	0.9-0.995	4	17 days	17.0± -	-	-	17.0 days
6	1.0-1.095	3	17- 21	18.3± 1.34	2.31	12.60	12.7- 24.1
7	1.1-1.195	10	17- 24	20.9± 0.53	1.66	7.96	19.7- 22.1
8	1.2-1.395	9	24- 30	26.7± 1.05	3.16	11.86	24.2- 29.1
9	1.4-1.495	5	30 days	30.0± -	-	-	30.0 days
10	1.5-1.595	5	30- 35	31.0± 1.00	2.24	7.21	28.2- 33.8
11	1.6-1.695	4	35 days	35.0± -	-	-	35.0 days
12	1.7-1.795	2	42 days	42.0± -	-	-	42.0 days
13	1.8-1.895	11	42- 60	45.9± 2.19	7.27	15.84	41.0- 50.8
14	1.9-2.095	12	49- 60	53.6± 1.64	5.66	10.57	50.0- 57.2
15	2.1-2.195	9	49- 72	58.9± 2.28	6.85	11.62	53.6- 64.2
16	2.2-2.295	9	49- 72	60.1± 1.92	5.75	9.57	55.7- 64.6
17	2.3-2.395	9	60-100	77.6± 3.91	11.74	15.13	68.5- 86.6
18	2.4-2.495	10	72-120	95.2± 5.92	18.72	19.66	81.8-108.6
19	2.5-2.595	13	80-150	104.6± 6.73	24.28	23.21	90.0-119.3
20	2.6-2.695	4	100-165	133.8±14.63	29.26	21.88	87.8-179.7
21	2.7-2.795	10	100-165	140.5± 6.35	20.05	14.28	126.2-154.9
22	2.8-2.895	9	100-180	145.6±10.22	30.66	21.07	122.0-169.2
23	2.9-2.995	10	120-270	183.0±13.94	44.05	24.07	151.5-214.5
24	3.0-3.195	28	165-360	238.9± 9.16	48.46	20.28	220.2-257.7
25	3.2-3.395	13	180-540	313.9±29.70	107.20	34.16	249.1-378.6
26	3.4-3.495	4	270-420	330.0±32.41	64.81	19.64	226.9-433.1
27	3.5-3.595	10	300-540	393.0±22.58	71.34	18.15	342.0-444.0
28	3.6-3.795	11	330-510	433.6±18.68	62.01	14.30	392.0-475.3
29	3.8-4.040	5	360-540	474.0±30.54	68.41	14.43	389.1-558.9

b. The Skomer vole:

b.1. Growth curve of the eye lens:

Data for the growth of the eye lens of the Skomer vole are presented in Fig. 47 and Appendix 43. Differences between the two sexes were not significant, ($t_{64}=0.08$, $P > 0.9$), and the data were combined.

The growth of the eye lens in Skomer voles was regular and highly correlated with age, ($r=0.85$). Variation between individuals of the same age was very low ($\bar{v}=3.63$).

The mean difference between the two eye lenses was 0.085±0.0065 mg or 0.7% of the dry weight of the lenses.

The eye lens grew very quickly during the first four months of the vole's life. Its weight averaged 0.8388 mg at the age of 14 days; 1.4115 mg at the age of 30 days; 2.1554 mg at 60 days; and 2.6788 mg at 120 days. Growth decreased afterwards but it never ceased.

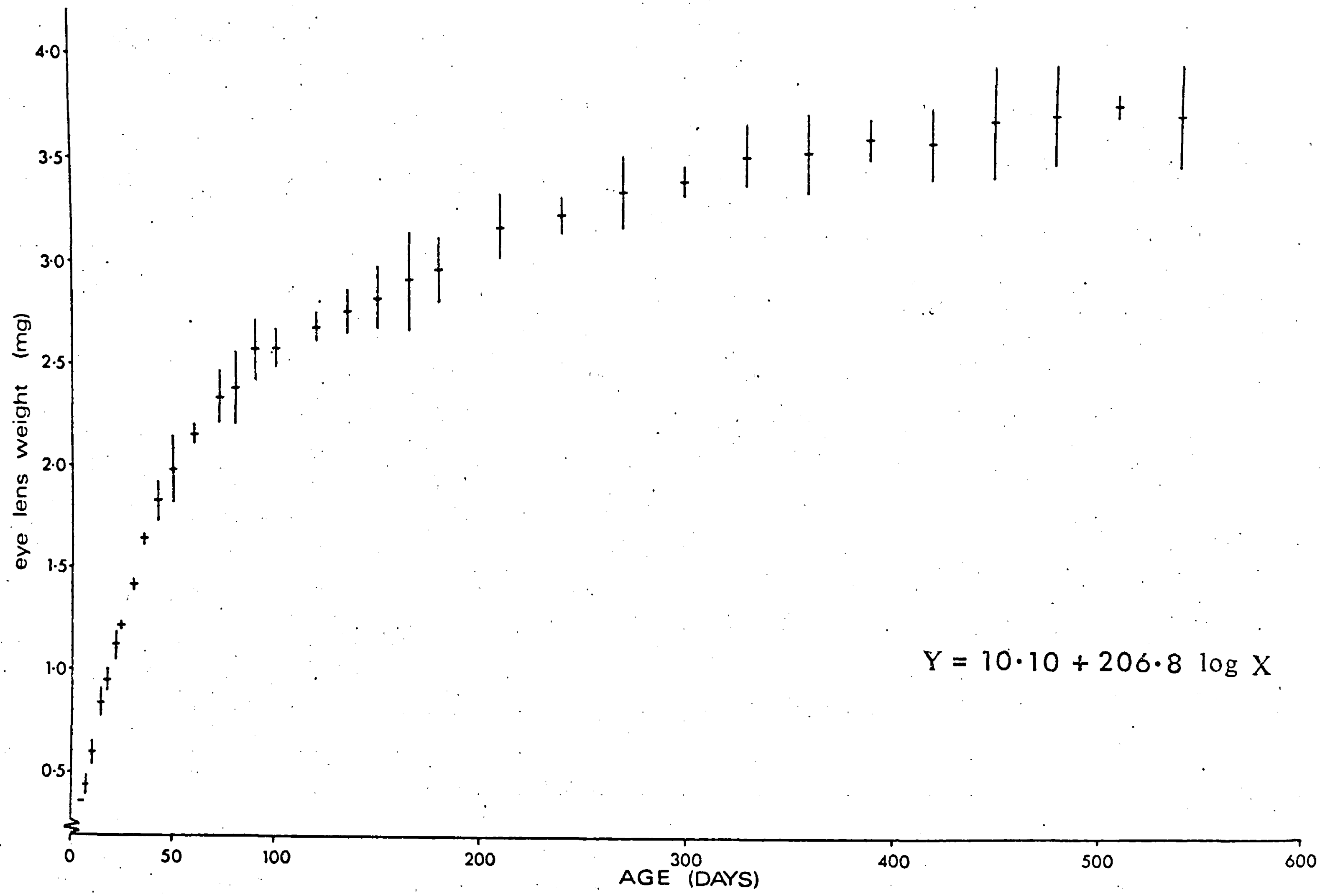


Fig. 47. Growth curve for the dry weight of the eye lens of the Skomer vole. (see Fig. 19 for explanation).

b.2. Estimating the age from the dry weight of the eye lens:

The whole sample was divided into 29 groups according to the dry weight of the eye lens (Table 49).

The distribution of the material within each group was regular and the variability was low, ($\bar{v}$=8.27). The accuracy for estimating the age was high throughout life. It extended from ±0.0 (groups 1 to 9, & 11), up to ±65.3 days (group 26).

The most variable eye lens weight value was 2.70 to 2.795 mg (v=21.6), corresponding to a mean age of 130.6 days and an accuracy for estimating the age of ±23.6 days. This accuracy is high in proportion to the mean age, (group 18). The low accuracy for estimating the age of voles with 3.8 to 3.895 mg eye lens weight (being ±113.9 days) was due to the small sample size (group 29).

The low variability, and the high accuracy for estimating the age from the dry weight of the eye lens, along with the high correlation coefficient make this character a highly reliable index.

Table 49. numerical data for estimating the age of the Skomer vole from the dry weight of the eye lens:

G. No	EL W/ mg	F.	O.Range/ days	Mean±S.E.	S.D.	V.	Estimated age range/95%c.l.
1	0.36-0.395	2	5 days	5.0± -	-	-	5.0 days
2	0.4-0.495	4	7 "	7.0± -	-	-	7.0 "
3	0.5-0.695	5	10 "	10.0± -	-	-	10.0 "
4	0.7-0.895	4	14 "	14.0± -	-	-	14.0 "
5	0.9-0.995	4	17 "	17.0± -	-	-	17.0 "
6	1.0-1.195	4	21 "	21.0± -	-	-	21.0 "
7	1.2-1.295	4	24 "	24.0± -	-	-	24.0 "
8	1.3-1.495	10	30 "	30.0± -	-	-	30.0 "
9	1.5-1.695	8	35 "	35.0± -	-	-	35.0 "
10	1.7-1.895	5	42- 49	43.4± 1.40	3.13	7.21	39.5- 47.3
11	1.9-1.995	2	49 days	49.0± -	-	-	49.0 days
12	2.0-2.195	9	49- 60	58.8± 1.22	3.67	6.24	56.0- 61.6
13	2.2-2.295	6	60- 80	65.3± 3.53	8.64	13.23	56.3- 74.4
14	2.3-2.395	3	72- 80	74.7± 2.67	4.62	6.19	63.2- 86.2
15	2.4-2.495	7	72-100	84.6± 3.51	9.29	10.98	76.0- 93.2
16	2.5-2.595	5	90-100	98.0± 2.00	4.47	4.56	92.4-103.6
17	2.6-2.695	8	90-165	125.0± 8.71	24.64	19.71	104.4-145.6
18	2.7-2.795	8	90-180	130.6± 9.97	28.21	21.60	107.0-154.3
19	2.8-2.895	4	135-180	157.5± 9.68	19.36	12.30	126.7-188.3
20	2.9-2.995	4	150-210	168.8±14.20	28.39	16.83	123.6-213.9
21	3.0-3.095	6	165-210	180.0± 6.71	16.43	9.13	162.8-197.2
22	3.1-3.195	4	210-270	240.0±12.25	24.49	10.21	201.0-279.0
23	3.2-3.295	7	210-300	244.3±12.10	32.07	13.13	214.6-273.9
24	3.3-3.395	10	210-360	297.0±13.01	41.11	13.84	267.6-326.4
25	3.4-3.495	8	300-450	371.3±20.38	57.68	15.54	323.0-419.6
26	3.5-3.595	9	270-540	400.0±28.28	84.85	21.21	334.7-465.3
27	3.6-3.695	10	330-540	450.0±22.82	72.11	16.02	398.4-501.6
28	3.7-3.795	6	360-510	470.0±24.08	58.99	12.55	408.1-531.9
29	3.8-3.895	3	450-540	490.0±26.49	45.83	9.35	376.1-603.9

D. Discussion:

The lens weight technique for determining age in the mainland bank vole and the Skomer vole in the present study proved to be of very high value. It was highly correlated with age (r=0.85 from the age of 5 days up to the age of 18 months, in the two subspecies). The correlation coefficient was higher during the first two months of life (r=0.96 & 0.98 for the mainland bank vole, and the Skomer vole respectively). Variation in eye lens weight between the voles of the same age was very low, ($\bar{v}$=5.28 for the mainland bank vole, and $\bar{v}$=3.63 for the Skomer vole). Individual voles can be assigned, each to its age group, by this technique, with high accuracy. Voles until the age of 3 months can be aged to within 1 to 2 weeks interval, and in older voles, to within 1 to 3 months (Tables 48 & 49).

The dry weight of the eye lens has proved to be a reliable character to determine the age of different species of wild mammals as well as laboratory-raised ones.

Pucek & Lowe (1975) mentioned that the standard deviation is far smaller with this method than any other using body or skull measurements and it can be recommended as the best method for determining the age of voles, lemmings, mice, dormice, squirrels, and bats. But Berry & Truslove (1968) showed that the eye lens weight was not a reliable indicator of age in a laboratory-raised population of laboratory mice (Mus musculus). They suggested that genetical differences between populations may increase the lens weight variability. The results of the present study were dissimilar to those of the above authors. The mainland bank voles which were used in this study were collected in different localities and therefore, had different genetical factors. The samples of each age-group were derived from different parents, and still, these genetical differences did not have any significant evident major notable effect on the growth curve of the eye lens, and variability was found to be very low ($\bar{v}$=5.28).

Östbye & Semb-Johansson (1970) found that the lens weight of a laboratory population of Lemmus lemmus was more likely to be of value as age criterion in young than in old animals. They found that lenses grew very quickly in voles up to about 30 to 40 days old, followed by a period of reduced increase in weight and a resumed greater increase in weight in individuals more than about 6 months old,(their sample comprised lemmings of up to 200 days old only).

The growth of eye lenses in C. glareolus differs from that in Lemmus lemmus. Eye lenses grew quickly during the first 6 months of life, after which growth slowed down, but only up to the age of 9 months, increase then resumed up to the age of 18 months. Therefore, the use of eye lens weight to determine the age of C. glareolus has application over a greater age range than in Lemmus lemmus.

Adamczewska-Andrzejewska (1973a) mentioned the difference in the growth rate of the eye lens between spring and autumn-born individuals of Microtus arvalis. She did not consider the difference in drawing the growth curve, as she added that this difference was statistically not significant. No differences, regarding seasons, were found in the eye lens weight of laboratory-born bank voles, simply because environmental factors were minimised under laboratory conditions, (see chapter IV).

Values for the dry weight of the eye lens of C. rutilus and C. rufocanus studied by Askaner & Hansson (1967) in Scandinavia, had almost the same range as the British species. One to 1.45 mg were the lowest weights in their sample and increased to 4.5, 4.95 mg in overwintered C. rutilus, and to 5.5, 5.95 mg in overwintered C. rufocanus.

In the British subspecies C. g. britannicus and C. g. skomerensis, the average dry weight of the eye lens for one month old voles, (animals of this age are easily found in the field), was 1.4 mg. The highest lens weight recorded in the present study was 4.04 mg for a male C. g. britannicus, and 3.89 mg for a male C. g. skomerensis, (7.78 mg for both eye lenses). Both voles were aged 18 months.

Le louarn (1971) used the weight of the eye lens to determine the age of C. glareolus in France. The weight values which she gave were almost the same as values obtained in the present work. Table 50 shows the results of her study and the result of the corresponding ages of the present work.

Table 50. Comparison between the dry weight of the eye lens of C. glareolus in France (obtained by Le louarn, 1971), and C. glareolus in Britain (obtained in the present study):

Age	Dry weight of the eye lenses/mg of C. glareolus in France, (Le louarn, 1971)		Mean dry weight of the two eye lenses presented combined /mg	
	Male	Female	C. g. britannicus	C. g. skomerensis
3 weeks	2.3	2.2	2.3112	2.2426
1 month	-	3.0	2.8570	2.8230
2 "	4.1	4.2	4.2176	4.3108
3 "	5.0	4.7	5.0028	5.1280
4 "	5.7	5.5	5.2466	5.3576
5 "	5.8	-	5.4714	5.6340
6 "	6.2	5.4	6.0814	5.9060
7 "	6.6	-	6.1634	6.3184
9 "	-	6.3	6.3290	6.6420
13 "	-	7.3	7.0100	7.1380

The dry weight values of the eye lens of other species of Clethrionomys from Scandinavia (Askaner & Hansson, 1967) look similar to those of C. glareolus in France (Le louarn, 1971), and Britain (the present study), though they are a little heavier in C. rutilus and C. rufocanus.

This result shows that the eye lens weight is a specific character, having the same weight in the different subspecies of a mammal, a result which has been shown in the present study regarding C. g. britannicus & C. g. skomerensis. This result is not in agreement with Adamczewska-Andrzejewska (1973a) in her suggestion that an eye lens weight differential exists between two subspecies of Microtus arvalis in Poland and France.

The effect of the nutritional status on the eye lens weight, was discussed by some authors, mainly in large mammals, e.g. Lord (1962) on deer (Odocoileus); Edwards (1962) on the cottontail rabbit (Sylvilagus floridanus); Lueth (1963), and Friend & Severinghaus (1967) on the white-tailed deer (Odocoileus virginianus); Friend & Linhart (1964) on the red fox (Vulpes fulva); and Friend (1967b) on laboratory rats.

Lueth (1963) found that the eye lens weight technique for ageing deer apparantly is not accurate beyond the ½ year age class. It may be a good indication of nutrition. Lord (1962), found an apparant difference in the growth rate of the lens between deer raised in pens and wild deer. The former had heavier eye lenses than the latter. He attributed the difference to the superior nutritional status of the penned deer. Friend (1967b), on one hand, showed no effect of different nutritional levels on the eye lens weight of laboratory rats. On the other hand, Friend & Severinghaus (1967) recorded that nutritional deficiencies (starvation) in wild deer would retard eye lens growth in fawns during their foetal period or prior to weaning.

Matschke (1963), in his work on the effect of nutrition on the weight of eye lens of wild hogs (Sus scrofa), concluded that nutrition affects the body weight which in turn affects the eye lens weight. Matschke, in his experiment used two different concentrations of protein in the diet which he gave to the hogs. It is most likely that body weight and eye lens weight were mainly affected by starvation.

In the present study, the body weight was found not to have any effect on the eye lens weight of normal voles. If the body weight affects the eye lens weight, then the two characters should have the same correlation coefficient with age. But results of the present study showed differences between these two characters with age. In addition, variability in the dispersion of the values within each age-group sample was very low in eye lens weight, while the body weight was highly variable.

II. 8. Moult and the sequence of pelages

A. Introduction:

It is known that the pelage of any individual rodent varies according to age, season, and sexual stage, as a result of growing and moulting.

Collins (1923) distinguished three pelages in the life cycle of the genus *Peromyscus*, namely, the juvenile, the postjuvenile, and the adult. Four pelages were distinguished by other authors for many rodents. These are, the juvenile, the postjuvenile, the preadult, and the adult. Moreover, Koponen (1964) mentioned that "if an individual survives long enough, it may have several successive hair growths of the adult type".

Thus, the sequence of hair growth and the progression of moult could be used as criteria to determine the age of small rodents.

Moult progression has been used for ageing different species of rodents such as, the meadow mouse (*Microtus californicus*), Ecke & Kinney (1956); the deer mouse (*Peromyscus leucopus noveboracensis*), Gottschang, (1956); the Norwegian lemming (*Lemmus lemmus*), Koponen, (1964 & 1970); the cotton rat (*Sigmodon hispidus*), Chipman, (1965); and the golden mouse (*Ochrotomys nuttalli*), Linzey and Linzey, (1967).

The moult is usually studied using the dried skin, the inside of which shows deeply pigmented areas where melanin has accumulated prior to being incorporated into the hairs.

As a new hair develops, a heavy concentration of pigment is deposited at the follicular site. Thus, the skin in the area of new hair growth takes on a dark bluish hue which can be detected from both, the fur side and underside of the skin, (Ecke & Kinney, 1956).

Regarding the genus Clethrionomys, Kryltzov (1963), in his study of the moult topography of some rodents and lagomorphs, mentioned the juvenile and seasonal moultings which occur in C. glareolus, C. rufocanus, & C. rutilus.

Manning (1956), in his work on C. rutilus in Canada, mentioned the presence of a single juvenile moult, the autumn, and the spring moults.

Apart from that of Manning and Kryltzov, I have found nothing in the literature about hair growth, moult, and sequence of pelages in Clethrionomys, except for a few taxonomic descriptions of the adult pelage (Southern, 1964).

The present work was carried out with the purpose of:

1. Following the course of pelage changes, and
2. Finding out the degree of correlation between moult and age.

B. Methods:

Two hundred dried skins of the mainland bank vole and 160 of the Skomer vole were examined in this study. The skins were prepared as follows:

After the vole was killed, the skin was removed by making a longitudinal incision on the underside from the anus to the chin and from the central incision along the hind limbs. After removal from the carcass, excess fat was peeled off and the skin was rubbed with Borax. Then it was streched and pinned flat on a cork board to be dried for at least 7 days.

C. Results:

a. The mainland bank vole:

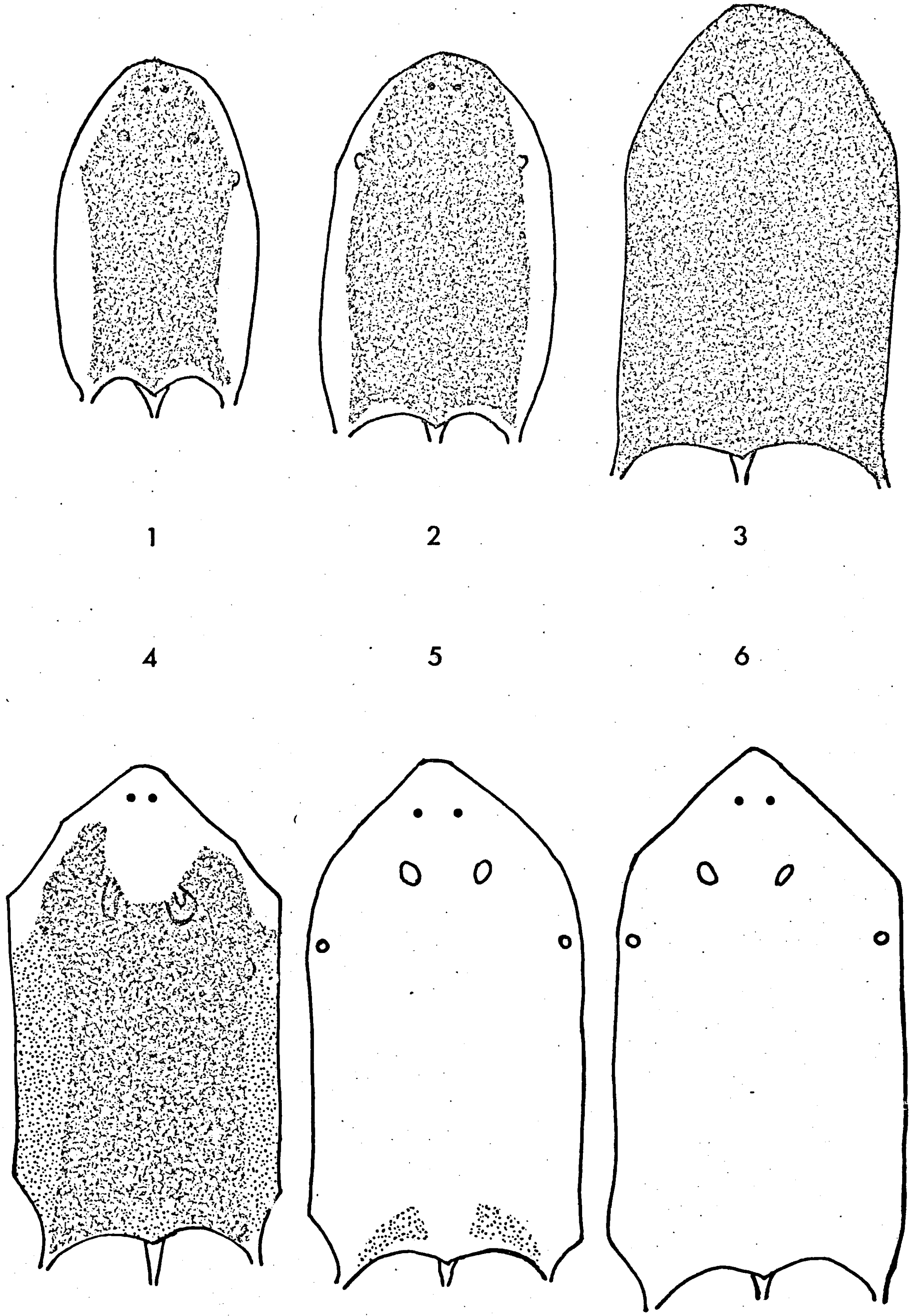
Two regular moults were found to take place during the first 3 months of life, and after the development of the young pelage. These will be discussed separately.

1. Young pelage (Fig 48):

Newborn voles are copletely naked. The skin is semi-transparent and unpigmented. Pigment starts to appear on the head, and extends backward to the dorsum on the second day indicating that the hair develops first on these parts. On the third day, the pigment spreads backwards to the rump region, tail, and the hind limbs. It covers the wrists on the fourth day. The melanophores and xanthophylls are obvious when the skin is examined at its inner or outer surfaces. At the same time the belly is still transparent except for a few scattered white hairs and there is no trace of any pigment.

Hairs of two different colours are found on the upper parts, black, and yellow. The latter, increase in number and become longer and darker by the seventh day of life, which gives the pelage its shiny colour.

The pigmentation spreads very quickly and covers the whole underparts by the tenth day. In this stage, the hairs elongate and the grey bases develop throughout the body; the hairs having white tips on the belly, pale yellow tips on the flanks, and brown on the upper parts.



1. 5 DAYS OLD
2. 7 = =
3. 10 = =
4. 14 DAYS OLD
5. 17 = =
6. 21-25 =

Fig. 48. Development of young pelage in the mainland bank vole.

At the age of 13 to 14 days, the pigment begins to disappear from the underside of the skin, first from the head, then from the belly and dorsum. By the 17th day, the whole pigmentation disappears, and the voles now have the young pelage (Fig. 48).

This pelage is very fine, mostly grey with very short white tips on the abdomen, pale yellow on the flanks, and brown on the upper parts. There is no pigmentation on the flesh side of the skin once pelage growth has been completed. The vole keeps this pelage until the age of 25 days, the time when the first moult occurs.

2. <u>The first moult (Fig. 49):</u>

The young vole begins the moult, that will take it through the juvenile to the subadult stage, at the age of 26 to 27 days. The pigment patterns at this stage are seen first along the belly and the thoracic region. They extend upward to the flanks and continue until they meet the pigment patterns of the other side on the mid-dorsum. The pigment then, spreads very quickly backward to the rump and forward to the head and cheeks. At the same time, the pigment starts to disappear, first at the belly, then at the flanks, dorsum, and rump. The last area from which the pigment vanishes is the top of the head. This type of moult is called sublateral by Kryltzov (1963).

The moult lasts until the age of 50 to 65 days, and the vole after completing this moult is sexually mature. It was immature while the above moult took place.

The moult occurs by the development of a new hair under the old one. These two types of hair can easily be

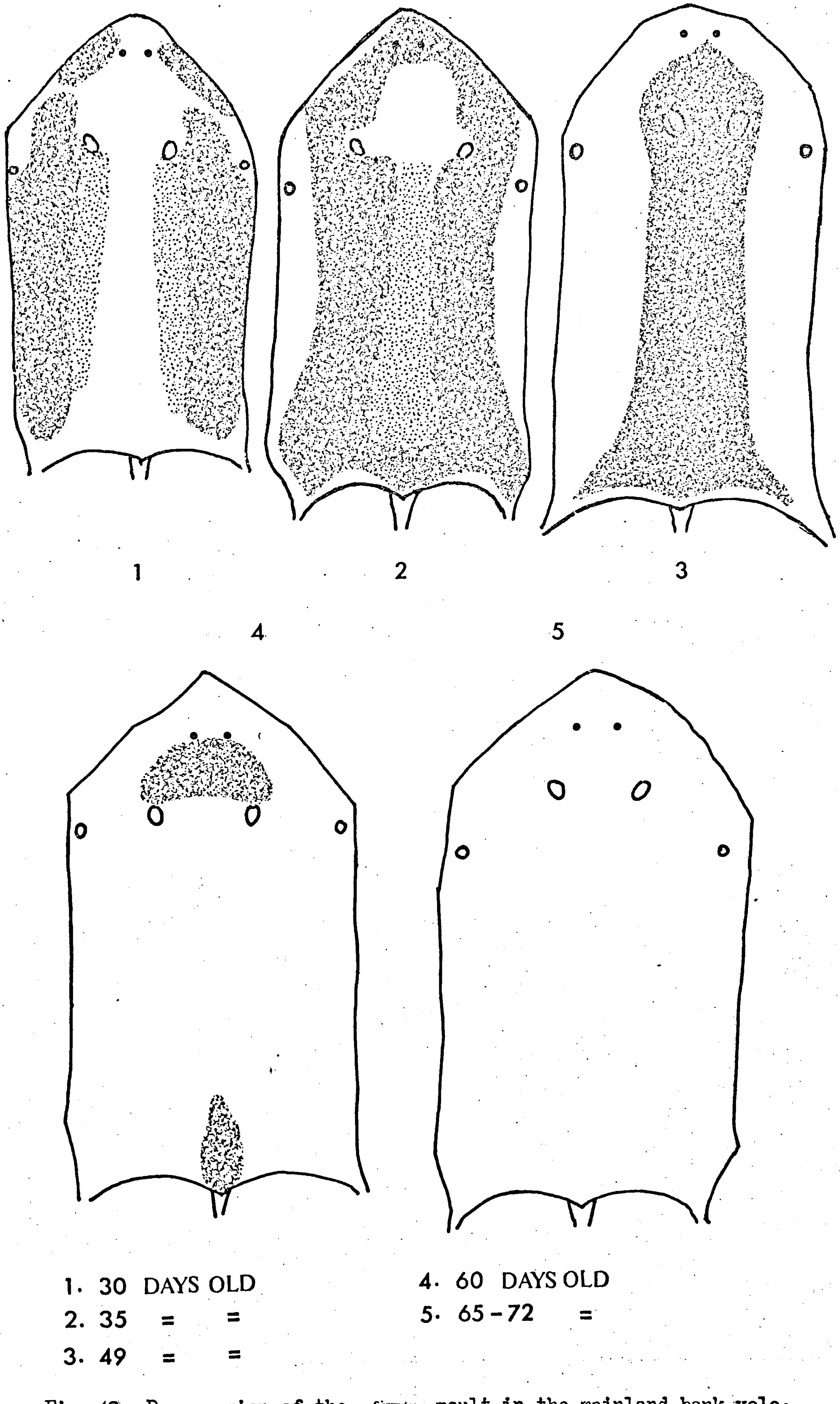


Fig. 49. Progression of the first moult in the mainland bank vole.

seen if the hair is parted transversely using a needle.

The new pelage is like the youngs' in colour, except that it is coarser and becomes longer. The vole retains this pelage till the age of 80 to 90 days, the time for the next moult to take place.

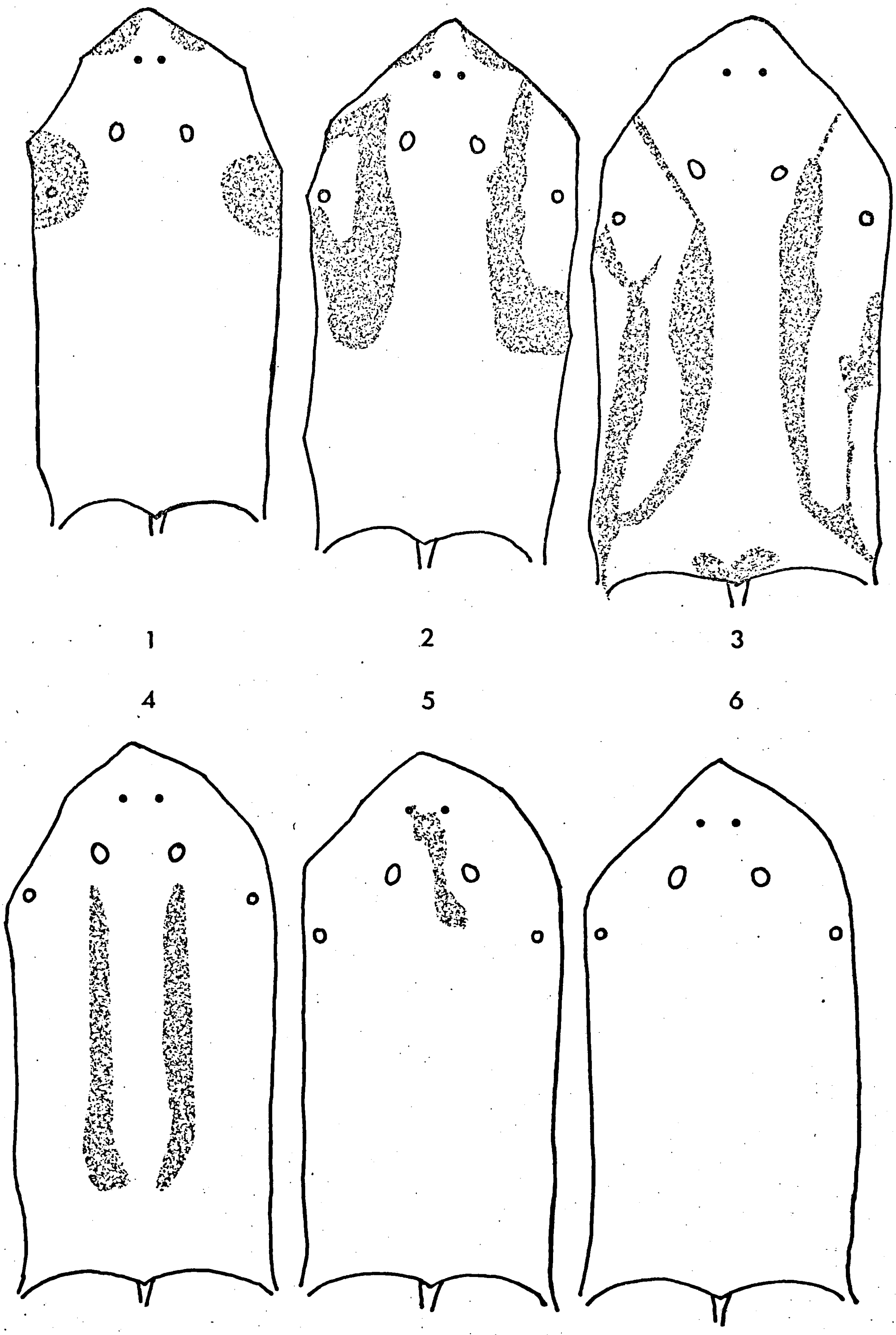
3. The second moult (Fig.50):

This moult takes place when the animal is 80 to 90 days old. The pigment is first seen in the forelimbs. It spreads from there making a continuous ring-shape around each forelimb. It then enlarges and extends backwards to cover the flanks and upward to the dorsum to meet the contralateral side and proceeds forwards over the head. At that time the pigment starts to disappear from the flanks, then from the dorsum. The last area to moult is the top of the head, (Fig. 50).

This moult takes a long time. It ends at the age of 120 to 140 days, and the voles now possess the adult pelage. The hair is coarse, with long grey bases, long brown tips at the back, yellow tips on the flanks, and pale yellow on the underparts.

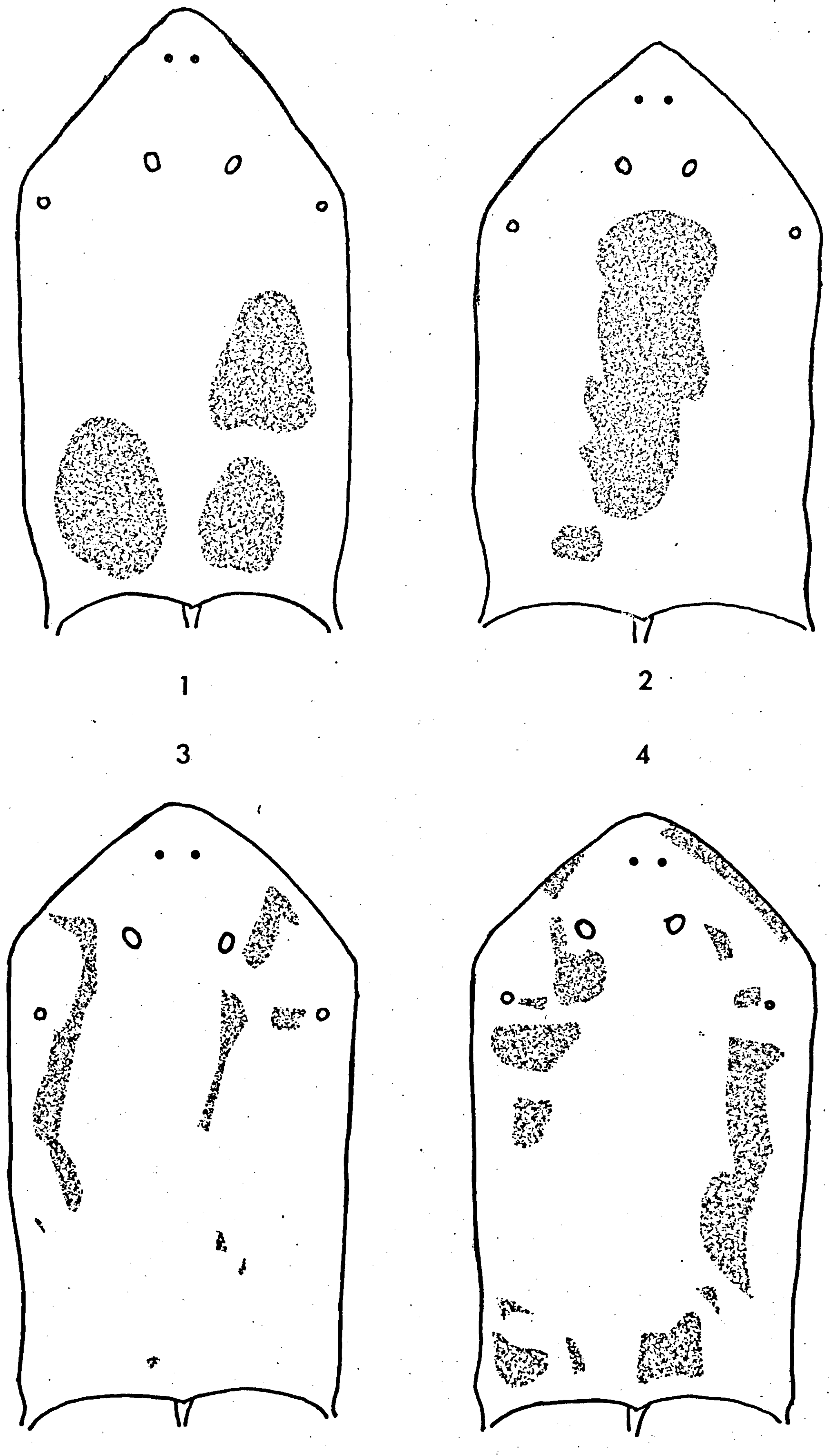
Several other irregular moults occur during the adult stage and throughout the rest of the vole's life. They take place in the form of patches anywhere on the skin. And it is not unusual to see these patches on the skins of voles having different ages, (Fig. 51).

It is not clear whether these irregular moults have something to do with age or whether they are seasonal moults. This needs further study. For instance factors other than



1. 80 DAYS OLD
2. 90 = =
3. 100 = =
4. 120 DAYS OLD
5. 135 = =
6. 150 = =

Fig. 50. Progression of the second moult in the mainland bank vole.



1· 180 DAYS OLD   3· 300 DAYS OLD

2· 240 = =   4· 360 = =

Fig. 51. Moulting patches in adult mainland bank vole.

age, such as physiological factors might stimulate this type of moult and ecological factors are not to be neglected in such studies.

b. <u>The Skomer vole:</u>

Two regular moults were observed in the Skomer vole, after the development of the hair in the young.

The young pelage develops at the age of 3 days, and is completed at the age of 18 to 19 days. It is fine, grey with brown tips on the dorsal surface, grey with yellow tips on the flanks, and grey with pale yellow or white tips on the ventral surface.

The first moult, into the subadult stage, starts by the 24th to the 25th day of life, on the belly, proceeds forward to the chest, and up on the flanks to meet the contralateral side on the dorsal midline. Then it proceeds backwards to the rump, and forwards to cover the head. At that time the ventral surface has completed its moult and grown the preadult pelage.

This moult lasts until the vole is 50 to 60 days old. The second moult begins at the age of 65 to 80 days, and progresses to completion at 90 to 100 days of age. This moult starts at the forelimbs in the form of a ring. It proceeds over the flanks and the belly and then up to the dorsum, forward to the cheeks and head, and backward to the rump.

After these two regular moults which led to the adult pelage, many other irregular moults were found to take place during the rest of the adult's life. These moults take place in the form of patches over the whole body, and black pigment is usually found on the flesh side of the vole skins throughout their lives.

D. Discussion:

The results of studying the sequence of pelages, in the present study, indicate a parallel between age and moult pattern from birth until the age of 4 months in the mainland bank vole, and from birth until the age of 3 months in the Skomer vole (Fig. 52).

young	pelt	first moult	pelt	second moult	adult irregular moults

0 17 26-27 50-65 80-90 120-140

Age/days

Clethrionomys glareolus britannicus

young	pelt	first moult	pelt	second moult	adult irregular moults

0 18-19 24-25 50-60 65-80 90-100

Age/days

Clethrionomys glareolus skomerensis

Fig. 52. Summary of the cycle of pelage development in the mainland bank vole and the Skomer vole.

Differences were found between results of the present study and those obtained by Manning (1956), in his work on a field population of C. rutilus in Canada. For instance, he found the voles to moult only once, and that was the juvenile moult (which sometimes was replaced by an autumn moult into winter pelage), but no second subsdult moult, while two regular moults were found to take place in C. glareolus. He added that there was a cosiderable variation in the size and probably the age at which the juvenile moult occurred. This did not occur in my sample, as all voles moulted at the same time.

Manning mentioned the autumn moult and an irregular spring moult which sometimes took the form of patches.

Seasonal moults have not been discussed in the present study. But the moult which occurred in adult voles in the form of patches might be comparable to the spring moult which he mentioned.

Hair growth in the young bank vole agrees with that described for Lemmus lemmus (Koponen, 1964 & 1970), except that the pigment patterns in L. lemmus can be seen in the flesh side immediately after birth, while that in the bank vole can not be seen until the second day of its life. The pigment disappears in L. lemmus at the age of 18 days, at 17 days in the mainland bank vole, and at 18 to 19 days in the Skomer vole.

Bank voles differ from L. lemmus in the onset and the pattern of the postjuvenile moult (the first moult). Post-juvenile moulting began in L. lemmus at the age of 20 to 23 days, at the age of 26 to 27 days in the mainland bank vole, and at the age of 24 to 25 days in the Skomer vole.

It is complete at 38 to 42 days in L. lemmus, at 50 to 65 in the mainland bank vole, and 50 to 60 days in the Skomer vole.

While the postjuvenile moult pattern in the bank vole differs from that in L. lemmus, it resembles the preadult moult in this genus, but again not in the time of onset. The preadult moult in L. lemmus starts at the age of 6 to 7 weeks, and completes at 2½ months.

The postjuvenile moult in the bank vole, also agrees with that described for Ochrotomys nuttalli (Linzey & Linzey, 1967), in its progression, but not in the time at which the animal starts moulting. Ochrotomys begins the postjuvenile moult at an average age of 36 days in males and 38 days in females, while the bank voles begin their first moult at the age of 25 days. The duration of this moult is the same for both of them, 25 to 29 days.

Ecke & Kinney (1956), in their study of the age-moult correlation in Microtus californicus, found that ages could be estimated to within 4 days between the 20th and 60th days of age. In the present study ageing could be estimated to within 2 to 3 days until the age of 25 days, 5 to 6 days until the age of 60 days, and to within one week until the age of 3 to 4 months.

Chipman (1965) discussed moulting as an age indicator in the cotton rat (Sigmodon hispidus). He described the postjuvenile and adult moults which differ in pattern and duration from those in the bank vole. Chipman mentioned the occurence of irregular moults which took the form of patches all over the flesh side of the skin in the adult stage. These moult patches resembled those in the bank vole.

Kryltzov (1963), in his review of moult in rodents and lagomorphs, mentioned that the juvenile and seasonal moults in C. glareolus, C. rufocanus, and C. rutilus, proceed by the sublateral type, while old animals moult diffusely. The same result has been obtained in the present study, in addition to the adult moult which proceeds by the sublateral type.

The effect of environmental factors on moult have not been discussed in the present study, but since the first two moults were maturational, i.e. voles moult at the same age irrespective of season, therefore, environmental factors have no effect on these moults, and age seemed the only factor associated with their occurence. Diffuse extra moulting was found to take place in captive adult voles throughout their life. Therefore environmental conditions might still not stimulate this type of moult in adult voles suggesting that moult is a physiological process affected by internal factors.

CHAPTER III. Experimental mainland bank voles which were kept on a low-calcium diet.

Experimental mainland bank voles which were kept on a low-calcium diet:

Food was assumed to be a factor which might affect the criteria of age determination. Two major criteria being studied (teeth & bones) were most likely to be affected by the calcium content of the diet. So, of the various dietary manipulations that were possible, low-calcium was the one selected for experimentation. Availability of calcium is something that may affect real-life vole populations, e.g. those living on different soil types. So this study could be relevant when considering the validity of age criteria derived from one population being applied to others.

Voles raised on this diet (see page 22), lived normally and bred, so it was not fatally deficient in any factor. They were killed and processed in the same manner as the control sample. Data for the growth of these voles were analysed and treated as before. Student's t test was applied to compare the means of the control and experimental groups (Table 51).

The growth and development of the molar roots were not affected by feeding on the low-calcium diet, neither was tooth wear, as no significant differences were detected between the control and the experimental samples. The ten sets of epiphyses fused to their diaphyses at the same time in the two samples. The bacula grew at the same rate. No significant differences were found in skull measurements. Moreover, when the results of body weight, body measurements, and dry weight of the eye lenses were compared, no significant differences were noticed. These results demonstrate

Table 51. Results of applying the t test between the means of the control and the experimental samples:

Character	t value	Probability
Whole body weight	t40=0.80	$P > 0.4$
Head-body length	t40=0.51	$P > 0.6$
Tail length	t38=1.19	$P > 0.2$
Ear pinna length	t40=1.24	$P > 0.2$
Hind foot length	t40=1.07	$P > 0.3$
Skull length	t40=0.39	$P > 0.7$
Zygomatic breadth	t40=0.34	$P > 0.7$
Lower jaw length	t40=0.396	$P > 0.6$
RM_1 length	t36=0.232	$P > 0.8$
RM_2 length	t36=0.27	$P > 0.7$
RM_3 length	t36=0.41	$P > 0.6$
RM^1 length	t34=0.15	$P > 0.8$
RM^2 length	t34=0.20	$P > 0.8$
RM^3 length	t34=0.09	$P > 0.9$
CM_1 height	t40=0.38	$P > 0.7$
CM_2 height	t40=0.45	$P > 0.6$
CM_3 height	t40=0.61	$P > 0.5$
CM^1 height	t40=0.17	$P > 0.8$
CM^2 height	t40=0.29	$P > 0.7$
CM^3 height	t40=0.62	$P > 0.5$
Dry weight of eye lens	t40=0.08	$P > 0.9$

that the particular low-calcium diet selected had no effect on the growth of the mainland bank voles.

Discussion:

The lack of any effect of the low-calcium diet on the age determination criteria of the mainland bank voles had not been expected, as calcium is supposed to be an important element for the growth of bones, and any deficit in this element might be expected to result in a retardation of bone growth (Le Gros Clark, 1971). But results in the present study showed that bones and teeth developed and grew normally. Molar roots developed at the same time as in normal voles.

The low-calcium diet which is supposed to be softer than the normal-calcium diet, might retard tooth wear. But again teeth were found to wear at the same rate as in normal voles.

Bones of voles kept on low-calcium diet were expected to grow slower, but results showed that they grew at the same rate as in normal voles, and epiphyseal cartilages disappeared at the same time also.

It is possible that the voles were not affected by the low-calcium diet because the 0.45% gm Ca amount given in the food might be sufficient for the needs of the bank vole, and the 1.10% gm Ca amount in the standard food might be more than the voles need.

This speculation is confirmed by data available on the calcium content of the food eaten by the Skomer vole at Skomer Island (T.D.Healing, personal communication). It was found that out of the four common plants found within the vole's area, they eat the red campion (Silene dioica) and sometimes the sorrel (Rumex sp.). These two plants contain 0.62% and 0.58% gm Ca respectively, a percentage which is not much more than the 0.45% gm calcium content of the present food. The voles never eat wood sage (Teucrium scorodonia) which contains 0.97% gm Ca, and they may eat sea campion (Silene maritima) which contains 0.91% gm Ca.

Bell et al (1941) found that variation of the Ca intake between 0.075% to 1.39% gm Ca did not affect the appetite or the general condition of rats and bones grew normally. Moreover, Orr et al (1935) and Gaunt et al (1938) showed that a diet containing 0.248% gm Ca dry matter is adequate for growth and reproduction in the rat.

Boelter & Greenberg (1941), on the other hand, found that giving rats food containing 0.01% gm Ca resulted in retardation of growth and activity, paralysis of the hind quarters, uncalcified skull, and a striking difference between the bones of normal and low-calcium rats. The control rats in their experiment, had been given food which contained 0.546% gm Ca.

From what has been mentioned above, it is obvious that the special food (contained 0.45% gm Ca), which has been given to the mainland bank vole was adequate and enough for their growth.

CHAPTER IV. Field study

Field study

The last phase of the present study was to obtain growth data from a field population, and compare it with the data from laboratory-raised mainland bank voles. But a real field population of known-age animals would have required a large scale mark-capture programme for which neither time nor facilities were available. As a compromise, a population living in natural weather conditions was used in an outdoor enclosure. Animals were supplied from the laboratory at age 21 to 28 days and left to live as members of a 'field' population for varying lengths of time.

The advantage of this arrangement was that exactly known-age animals were made available, without a totally disproportional expenditure of time and effort. While the disadvantage was that the first 3 weeks of the voles' lives were spent in the laboratory, although for half that time the voles were being suckled just as they would be in the wild.

The small enclosures (see page 23) were built in the grounds of the Zoology Department. The area where the pens were established is unmanaged rough grassland. The soil is a clay with a compact texture. Many bank voles were trapped in the surrounding area indicating that it is suitable bank vole habitat.

Each laboratory-born vole to be released was toe-clipped for identification. A total of 73 known-age (21 to 28 days) laboratory-born voles were released from September 1973 to March 1975. Thirty six were males, and 37 females.

Unfortunately, 55 voles out of the whole sample, (75.3%), disappeared from the enclosures, for different reasons. Many of them managed to escape by digging underneath the walling. Some others were found partly eaten by their co-habitants. Only 18 voles (24.7%), 7 males and 11 females, were recaptured and killed. Their age ranged from 42 to 210 days (Table 1). One of the males (210 days old) was trapped outside the enclosure.

Each retrapped vole was processed in the same way as the laboratory voles.

Student's t test was not applied on the field sample, because the sample size was thought to be too small. The mean values were used to compare the two samples.

Results:

1. Body weight:

The mean body weight, up to the age of 5 months was lower in the field sample than in the laboratory-raised one. In voles 6 and 7 months old, it was above 20 gm (22.03 & 21.2 gm), which is the same as that of the laboratory sample.

The difference between field and laboratory samples during the first 5 months of life is probably due to the first group needing time to adapt to the field conditions, and also to the increase in their activity, such as digging, and fighting.

Seasonal variations were not obvious in the field sample. Voles born in spring or autumn, having spent the same period of time in the field, have the same weight. In other wards, voles born in spring are not heavier than the autumn born individuals.

2. Body measurements:

Data for body measurements of the field sample were found not to differ from those of laboratory-raised voles, especially above the age of 4 months. Body measurements in voles younger than 4 months were somewhat lesser than the corresponding ages of the laboratory sample.

3. Skull measurements:

There were no obvious differences between the means of the field and laboratory samples, regarding the three skull measurements (Table 52).

Skull growth in the mainland bank vole is the same in field and laboratory-raised individuals. Data from the latter are useful and apparently valid when used as criteria for estimation of age in wild animals.

Table 52. Means of skull measurements of the laboratory-raised and field samples of the mainland bank vole:

Age/ days	Skull length mm		Zygomatic breadth mm		Lower jaw length mm	
	field s.	lab. s.	field s.	lab. s.	field s.	lab. s.
42	21.63	21.39	12.50	12.30	12.28	12.12
60	21.70	21.89	12.69	12.76	12.38	12.37
72	22.50*	22.43	12.23*	12.83	12.50*	12.44
90	22.14	22.53	12.66	12.80	12.58	12.49
120	21.85*	22.98	12.58*	13.35	12.60*	12.97
150	22.93	23.14	13.35	13.65	13.09	13.35
180	23.21	22.81	13.59	13.31	13.36	13.24
210	22.87	23.19	13.39	13.42	13.15	13.09

* one specimen cnly.

4. Root development:

Although the roots of the molar teeth of the field sample started to develop at the same time as in the laboratory sample, they started to grow faster above the age of 4 months, (Table 53). The average monthly increase above the age of 90 days, and up to the age of 210 days, was 0.27; 0.20; 0.22; 0.23; 0.15; and 0.19 mm for, M_1; M_2; M_3; M^1; M^2; and M^3 respectively.

Using laboratory root development rates as a criterion of age will result in estimates which average 1.3 ± 0.1 month younger than the actual age in voles between 3 to 7 months old.

Table 53. mean length of the molar roots of the corresponding ages of field and laboratory-raised bank voles/mm:

Age/	RM_1		RM_2		RM_3		RM^1		RM^2		RM^3	
days	F	L	F	L	F	L	F	L	F	L	F	L
42	0.16	0.07	0.18	0.07	0.13	0.08	0.13	0.06	0.13	0.03	0.07	0.06
60	0.36	0.26	0.28	0.20	0.17	0.11	0.36	0.21	0.23	0.19	0.19	0.15
72	0.38*	0.40	0.31*	0.31	0.16*	0.17	0.38*	0.32	0.20*	0.26	0.24*	0.20
90	0.53	0.52	0.47	0.42	0.14	0.26	0.50	0.56	0.44	0.45	0.29	0.31
120	0.80*	0.71	0.58*	0.63	0.28*	0.36	0.76*	0.68	0.42*	0.53	0.46*	0.47
150	1.25	0.93	0.99	0.86	0.61	0.51	1.11	0.90	1.02	0.71	0.80	0.66
180	1.34	1.01	1.05	0.81	0.80	0.50	1.14	0.98	0.91	0.76	0.80	0.63
210	1.62	1.19	1.27	1.01	1.03	0.64	1.40	1.15	1.17	0.88	1.05	0.76

* one specimen only F: Field sample L: Laboratory sample

5. Tooth wear:

As expected, teeth of the released voles wore down more quickly than those of laboratory-raised voles, probably as a result of using them for eating different types of natural food, their use in digging and for chewing, rather than using them only to eat one uniform type of food in the laboratory (Table 54). The average monthly decrease in crown height, between the ages 60 to 210 days, was, 0.26; 0.25; 0.22; 0.27; 0.22; 0.16 mm for M_1; M_2; M_3; M^1; M^2; and M^3 respectively, which was comparable to the growth rate of the molar roots.

Using the molar crown height of laboratory-raised voles as a criterion of age produces estimates with averages of 4.38 ± 0.37 months younger than the actual age in voles, 2 to 7 months old, with a molar crown height which differs according to each molar (Table 54).

Table 54. The mean height of molar crowns of the corresponding ages of field and laboratory-raised mainland bank voles / mm :

Age/ days	CM_1 F	CM_1 L	CM_2 F	CM_2 L	CM_3 F	CM_3 L	CM^1 F	CM^1 L	CM^2 F	CM^2 L	CM^3 F	CM^3 L
42	3.21	3.30	2.86	2.98	2.47	2.61	3.77	3.92	3.04	3.21	2.23	2.38
60	2.65	3.06	2.51	2.84	2.16	2.49	3.34	3.74	2.73	3.09	1.99	2.22
72	2.70*	2.88	2.49*	2.69	2.22*	2.27	3.43*	3.48	3.78*	2.83	2.08*	2.04
90	2.55	2.78	2.26	2.59	2.07	2.13	3.19	3.38	2.60	2.77	1.95	2.04
120	2.20*	2.51	2.00*	2.36	1.75*	2.11	2.60*	3.02	2.30*	2.53	1.70*	1.86
150	1.77	2.28	1.64	2.08	1.39	1.83	2.24	2.85	1.89	2.39	1.40	1.72
180	1.77	2.26	1.61	2.14	1.19	1.83	2.21	2.72	1.65	2.35	1.33	1.71
210	1.32	2.06	1.14	1.97	0.85	1.73	1.79	2.42	1.45	2.12	1.05	1.58

* one specimen only F: Field sample L: Laboratory sample

6. <u>Dry weight of the eye lens</u>:

A difference was found between the dry weight of the eye lenses of the two samples. The laboratory-raised voles' eye lens weight being slightly greater. This difference was statistically not significant, $t_{14}=1.47$, $P > 0.1$ (Table 55).

Laboratory data for the dry weight of the eye lens appear to be a useful method for age determination and can be validly applied to field animals.

Table 55. Mean dry weight of the eye lens of the corresponding ages, for the released and laboratory-raised bank voles:

Age/ days	mean eye lens weight/mg, for field sample	mean eye lens weight/mg for lab-sample
42	1.77	1.82
60	2.03	2.11
72	2.27	2.33
90	2.30	2.50
120	2.56	2.62
150	2.64	2.73
180	2.85	3.04
210	2.86	3.08

7. Epiphyseal fusion:

The fusion of epiphyses of the field sample were found to be in agreement with the laboratory-raised voles. The phalangeal, metacarpal, and metatarsal epiphyses, the distal epiphyses of the radius and ulna, tibio-fibula, humerus, and femur, and the proximal epiphyses of the femur, all appear to be consistent with the laboratory data .

8. Baculum:

Digital proccesses in the bacula of the males were ossified in males 60 days old and older. Males under that age were not available in the sample. It seems that captive and'wild' males are comparable, regarding the ossification of their bacula.

9. Moult:

Data for moulting of the released bank voles coinside with the data obtained from laboratory animals.

Discussion:

Although the information on released voles was limited, the results were enough to give an idea about the growth of the bank vole in its natural habitat.

Some authors who have worked on the age determination of small mammals, obtained satisfactory results from rearing animals in the field and laboratory.

Lidicker &MacLean (1969), in their study on ageing the California vole (Microtus californicus), concluded that data on body and skull measurements from the laboratory could be applied to field populations. Their results on field animals were obtained from 24 voles ranging in age from 40 to 412 days, which were released in outdoor enclosures.

Chipman (1965) compared age criteria between laboratory-raised and released cotton rats. My results are in agreement with Chipman's findings regarding epiphyseal fusion, moulting, body and skull measurements, and the dry weight of the eye lens. The only difference was our comparisons of body weight. Chipman found that weight increase, in cotton rats, was much slower in the field than in the laboratory, throughout life, whereas I found that the weight of the bank voles was lower in the field in voles less than 5 months old, but not in older voles.

Growth of the molar roots in voles raised in the enclosure was faster than in the laboratory animals, so was tooth wear. As teeth wear quickly, roots grow faster and penetrate deep in the alveolus to support the worn crowns. The ratio of root length/crown height at a certain age is constant in both populations, but the measurements themselves were higher in pen population than in voles of the same age, raised in the laboratory regarding the root length, and lower regarding the crown height .

The rapid wear of teeth might explain why field animals have a shorter life span than laboratory animals. The life span for the former was said to be 12 to 14 months (Schwarz, et al, 1964); 17 to 21 months (Pucek, et al, 1969), and up to 24 months (one record by Lowe, 1971). While laboratory voles, in the present study, lived up to more than two years, (two voles lived up to 27 months).

Regarding the Skomer vole, no field work on known age animals has been done in the present study. Seventeen skulls of unknown age voles, collected on Skomer Island and kindly provided by T.D.Healing, were examined to be compared with skulls of laboratory-raised voles.

One of these skulls belonged to a nearly known age female which was obtained by the CMR method. This female is known to be more than one year old. It had first been trapped on 4 October 1972, and killed on 23 September 1973. It is most probable that this female was born during the summer of 1972, and the earliest would be the end of April of that year. Therefore its maximum age at the date of death would most likely be 17 months.

Data on the skull measurements and molar teeth of this female were taken and are presented in table 56.

The age of this female is presented separately according to each character, and on the basis of the results which were obtained from laboratory-raised voles.

These results indicate that the age of this female according to the skull length, for instance, is probably at least of 410 days. In the laboratory-raised sample, the highest value of a female skull length was 25.26 mm for a 450 days old female. Another 480 days old female had a skull length of 25.12 mm.

The results for estimating the age of this female according to the zygomatic breadth, lower jaw length, and the molar root length are almost the same. The mean age

Table 56: Skull and molar teeth measurements, the mean estimated age and range under a probability level of 0.05, of a female Skomer vole collected at Skomer Island:

Character	measurement/ mm	mean age/ days	age range/ days/95% c.l.
Skull length	25.40	410.0	-
Zygomatic breadth	14.60	420.0	361.7-478.3
Lower jaw length	14.78	407.1	345.3-469.0
RM_1 length	2.20	415.0	378.2-451.8
RM_2 length	2.05	462.0	419.5-504.5
RM_3 length	1.44	453.0	403.0-503.0
RM^1 length	2.00	462.9	427.5-498.2
RM^2 length	2.11	472.5	374.0-570.9
RM^3 length	1.72	510.0	478.0-542.0
CM_1 height	1.21	482.5	460.3-504.7
CM_2 height	1.00	474.0	447.7-500.4
CM_3 height	0.66	514.0	-
CM^1 height	1.28	505.0	468.2-541.5
CM^2 height	0.76	530.0	487.0-573.0
CM^3 height	0.66	510.0	-

extended from 407.1 to 510 days. The maximum age ranged between 451.8 to 570.9 days, and the minimum age ranged between 345.3 to 478.0 days.

The age of this female according to the crown height is higher than according to the other measurements mentioned above, simply because experiments with a'field population' of mainland bank voles showed that voles in natural habitats suffer increased wear of their teeth when compared with laboratory stock.

We see that estimating the age of laboratory-raised Skomer voles by crown height gives a younger age if applied directly on field animals.

CHAPTER V. General comparison and discussion

General comparison and discussion

The present study was based mainly upon the interpretation of characters from dead animals. The main purpose of this study was to ascertain by the use of laboratory animals of known-age which of various age determination criteria would give the most accurate and reliable estimates of age, and to investigate whether environmental factors might influence the reliability of these criteria.

A summary of the data for each character is presented in tables 57 & 58 for the mainland bank vole and the Skomer vole respectively.

Among the characters, the one which was felt to give the best picture of age changes was the dry weight of the eye lens. It proved to be the best method for determining the age of bank voles. Its growth continued throughout life. Lens weight attained 30.46% of the maximum recorded, at the age of 21 days; 61.44% at the age of 72 days; 91.96% at 12 months; and 95.73% of the maximum weight at the age of 15 months (Appendix 44).

Laboratory data on the growth of eye lenses can be applied to wild bank voles. Variation between individuals in a given age category were very low, and the dispersion of individuals around the estimated age was low. Thus, using the dry weight of the eye lens alone to determine the age of bank voles will give results of high accuracy.

Table 57. Correlation coefficient, mean of coefficient of variation, and mean age of all the characters which were used in the present study to determine the age of the mainland bank vole:

Character	r1	r2	r	mean age1	$\bar{v}1$	mean age2	$\bar{v}2$
B. weight	0.99	-	0.74	173.7	12.28	62.1	29.47
HB length	0.91	-	0.66	178.9	4.01	100.5	37.10
T length	0.92	-	0.56	"	6.80	82.6	45.41
E length	0.85	-	0.57	"	5.53	102.0	35.62
HF length	0.82	-	0.43	"	3.59	60.5	39.30
SK length	0.86	-	0.62	"	2.54	99.4	29.02
Zyg.breadth	0.84	-	0.62	"	3.00	92.8	33.86
LJ length	0.80	-	0.64	"	3.04	140.3	37.64
RM_1 length	-	-	0.96	231.1	16.46	215.3	14.29
RM_2 "	-	-	0.96	"	13.40	201.4	11.62
RM_3 "	-	-	0.95	"	21.11	253.7	16.79
RM^1 "	-	-	0.96	"	17.61	207.5	14.86
RM^2 "	-	-	0.95	"	18.4	226.7	15.72
RM^3 "	-	-	0.95	"	18.41	222.6	15.22
CM_1 height	0.80	-0.90	-	178.9	11.03	195.3	17.05
CM_2 "	0.79	-0.90	-	"	10.76	214.5	17.36
CM_3 "	0.87	-0.93	-	"	9.98	221.0	19.69
CM^1 "	0.86	-0.93	-	"	12.50	193.3	20.05
CM^2 "	0.86	-0.93	-	"	11.49	232.0	18.51
CM^3 "	0.85	-0.91	-	"	12.29	192.5	23.82
Eye lens W	0.98	-	0.85	"	5.28	122.0	11.98

r1: correlation coefficient up to the age of 35 days.
r2: " " , from 42 to 540 days.
r : " " for the whole sample, 5 to 540 d.
$\bar{v}1$: mean of coefficient of variation for the age group samples.
v2: " " " " " " " size-groups.
mean age1 for the age group samples.
" age2 for the size-groups.

Table 58.* Correlation coefficient, mean of coefficient of variation, and mean age of all the characters which were used to determine the age of the Skomer vole:

Character	r1	r2	r	mean age1	$\bar{V}1$	mean age2	$\bar{V}2$
B. weight F	0.98	-	0.75	178.9	8.66	87.8	23.90
B. " M	0.98	-	0.74	"	8.65	79.7	25.27
HB length	0.95	-	0.71	"	3.61	143.7	29.96
T "	0.96	-	0.60	"	5.38	93.9	32.78
E "	0.90	-	0.52	"	4.25	66.7	30.16
HF "	0.90	-	0.42	"	2.46	75.6	41.80
SK length	o.93	-	0.61	"	1.74	100.4	18.80
Zyg. breadth	0.93	-	0.67	"	2.36	94.8	24.25
L. jaw l.	0.92	-	0.64	"	2.15	111.5	25.17
RM_1 length	-	-	0.98	231.1	14.69	232.2	10.95
RM_2 "	-	-	0.98	"	11.97	259.7	10.07
RM_3 "	-	-	0.96	"	19.96	251.8	16.08
RM^1 "	-	-	0.95	"	15.50	223.4	12.41
RM^2 "	-	-	0.97	"	16.35	242.1	14.60
RM^3 "	-	-	0.96	"	20.04	231.9	16.33
CM_1 height	0.89	-0.96	-	178.9	7.54	225.6	13.30
CM_2 "	0.88	-0.96	-	"	7.78	241.1	16.81
CM_3 "	0.86	-0.94	-	"	8.83	206.6	20.19
CM^1 "	0.93	-0.95	-	"	7.60	240.0	20.87
CM^2 "	0.92	-0.94	-	"	7.45	240.9	16.53
CM^3 "	0.91	-0.94	-	"	7.72	248.1	18.57
Eye lens W.	0.98	-	0.85	"	3.63	150.4	8.27

* see table 57 for explanation.

The length of the molar roots is also one of the characters best correlated with age in bank voles. The root growth curve, which appeared as a straight line, is derived from points with greater scatter than the curve for the dry weight of the eye lens. Variation in the several age categories was higher. The lowest ($\bar{v}$ being 13.4) was for RM_2 in the mainland bank vole, and for RM_2 in the Skomer vole ($\bar{v}$=11.97). The highest ($\bar{v}$=21.11) was for RM_3 in the mainland bank vole, and for RM^3 in the Skomer vole ($\bar{v}$=20.04).

Roots grow continuously throughout life. Growth of RM_1 achieved 10.48% of the maximum root length recorded, at the age of 60 days; 28.63% at the age of 120 days; 60.08% at 240 days; 91.94% at 420 days; and 95.56% at the age of 480 days. The same result was obtained for the other 5 molars (Appendix 44).

The crown height of the molar teeth in Clethrionomys is highly correlated with age, and it can be a highly reliable criterion of age throughout the vole's life, but also it can be a highly variable character as it is affected by food eaten by voles (see chapter IV). Tooth wear in bank voles needs an extensive field study in order to see the different factors affecting it, such as, the type and variety of food eaten, the type of soil the voles live on, and the seasonal variations which affect the growth and wear of molars. In addition, the hardness of the teeth should be studied as the hardness of the crowns is one of the basic factors affecting the wear of the teeth during the animal's life and is therefore of considerable importance when the degree of wear of the teeth is used as a measure of age (Adamczewska-Andrzejwska, 1966). This authoress found that the hardness of dentine is subject to significant variations in different years and causes differences in the rate of wear of the teeth of Sorex araneus, which in practice makes it necessary to correct the estimate of age on the basis of the wear of the teeth.

Growth curves for root length and crown height of laboratory-raised voles cannot be applied directly on field populations, as data on these two characters were found to differ between the laboratory and 'field' samples. The mean difference was 1.3±0.1 month for the root length, in voles 60 days to 7 months old, and 4.38±0.37 months for the crown height in voles 4 to 7 months old (Tables 53 & 54).

The three skull measurements which were studied here, were not very highly correlated with age, because their growth slowed down after the voles attained maturity. But their growth curves exhibit lesser dispersion than any other measurement. Growth in skull length achieved 86.05% of the maximum size recorded at the age of 30 days ; 91.78% at the age of 60 days; 97.23% at 210 days; 100% at the age of 330 days. Not much difference was found in growth rate between skull length, zygomatic breadth, and lower jaw length. The same result was obtained by Zimmerman (1972) for the growth rate of the skull measurements of the thirteen-lined ground squirrel (Spermophilus tridecemlineatus).

According to Pucek & Lowe (1975), although the skull in most small mammals continues to grow throughout life, its growth tends to be seasonal. Results of the present study are not in agreement with the last part of their statment, as no differences in skull measurements were found between the 'field' and laboratory animals. My results were in agreement with Lidicker & MacLean (1969), working on Microtus californicus.

Although skull length is less correlated with age (r=0.65), than the two other skull measurements, its growth exhibits the lesser scatter. And when the material was divided into skull-length groups, the distribution of the voles around each group had the lowest variability. But its slow growth in adults might make it difficult to determine the age of adult animals based upon skull length. Many other authors came to the same conclusion, among them Adamczewska-Andrzejewska (1973b) in her work on Apodemus agrarius.

The growth in zygomatic breadth was regular. Its correlation with age was as high as that of the skull length and the lower jaw length in both the mainland bank vole and the Skomer vole. Its growth curve exhibits lesser dispersion than the lower jaw length.

The growth curve of the lower jaw exhibits more dispersion than that of the skull length in the Skomer vole, and the skull & zygomatic breadth in the mainland bank vole. When the material was divided into size-groups, the dispersion of the vole ages within each size-group was high when the lower jaw length was the factor, on the basis of which the material was divided. But the lower jaw length might still be a satisfactory criterion for determining the age of bank voles, especially when the skull is broken, as the longest undamaged part of it is often the lower jaw.

Body weight is a quick and simple guide to approximate age, often used successfully by many investigators, especially with small and short-life span mammals. For example, Michielson (1966), applied it successfully to shrews (Sorex araneus).

Different factors, apart from age, affect body weight in mammals, such as diet, health of the animal, season, and sexual status. Thus, body weight must be treated with caution, if it is to be used as an age indicator.

Although diet and health were fairly uniform, the results of the present study for body weight of the bank vole in relation to age were not satisfactory. Variation between individuals in a given age category was high above the age of 30 days. In spite of the correlation coefficient with age being high, and despite the small difference in weight between laboratory and 'field' voles, body weight data from the former could not be used reliably to age the latter owing to the uncertainties caused by a high level of individual variation.

Brambell & Rowlands (1936) found the body weight to vary in adult voles, extending between 12.5 to 32 gm in the females (excluding pregnancies), and to vary a lot in the males especially during the winter months, (Rowlands,1936). Jewell (1966) depended mainly on the sexual status of each vole to differentiate between juvenile, preadult, and adult animals in a sample of Skomer voles. He then related the body weight to these categories. But he never depended on the body weight alone to divide the material into the above categories.

Some of the linear body measurements are good enough to be used as age criteria. The head-body length is the most adequate, but it is difficult to measure in live voles unless they are anaesthetized. The ear pinna length is also a satisfactory criterion, but voles can be assigned, according to their ear pinna length, to wide range age groups as the ear pinna growth is very slow.

Tail and hind foot are not reliable age indicators above the age of 6 weeks for the former and 3 weeks for the latter. Layne (1960) has also found that the hind foot and tail of Ochrotomys nuttalli grew very quickly in early age.

Adamczewska-Andrzejewska (1973b), was successful in using tail length to assess the age in Apodemus agrarius. But the tail of Apodemus is approximately twice the length of the tail of Clethrionomys. It needs more time to grow, and therefore its growth continues longer.

The same result was found to occur in the Skomer vole. The tail of this subspecies is longer than that of the mainland bank vole. It took a longer time, 3 months, to complete its growth, while the tail of the mainland bank vole took only 6 weeks to attained the adult size. This result might explain the higher correlation coefficient with age for the tail of the Skomer vole.

If body measurements are to be used for assessing age in bank voles, attention should be concentrated on head-body length and ear pinna length.

In spite of the baculum being used successfully to determine the age of several mammals, it was of limited use for this purpose in bank voles. The baculum has been used as an age indicator for medium size and big mammals, which have longer life spans, and which attain maturity when they are, at least, one year old.

The baculum has not been used for ageing small mammals which attain maturity very quickly. Laboratory bank voles attain maturity during and soon after the seventh week of their life, and the baculum reaches the adult size by then. Therefore it is not useful to use the baculum as an age indicator above the age of seven weeks.

Epiphyseal fusion can be studied on both dead and live animals. Alizarin stained specimens may be examined in the former, and radiography used on the latter. By studying several ossification areas in the fore and hind limbs, one can estimate the approximate age of the bank vole up to 14 months of age (Figs. 43 & 44).

Epiphyseal fusion is not affected by field conditions, and results obtained in the present study can be applied on field populations. Watson & Tyndale-Biscoe (1953) also found that the conditions of captivity did not affect the bone development of Oryctolagus cuniculus.

Succession of moult has recently been used as an age indicator, mainly in small mammals, and can be used as a guide to age, thereafter moulting appears to be somewhat haphazard and not related to age.

There are several published works which adopted biochemical methods to determine the age of different small mammals. Biochemical changes in the eye lens have been used recently for this purpose. For example, Dische et al (1956), in their work on the eye lenses of laboratory rats, found that the relative amounts of water soluble and insoluble proteins changed with age. These changes result from the oxidation of cysteine in the soluble protein into cystine in the insoluble protein.

Dapson et al (1968) used a colorimetric procedure to analyze the protein contents of eye lenses of white mice, and suggested that the technique looked promissing for determining the age of small mammals.

Later work on laboratory-reared old-field mice, Peromyscus polionotus, (Dapson & Irland, 1972) demonstrated the value of the insoluble fraction of protein which they found to vary curvilinearly with age to at least 750 days. They rejected the use of the soluble fraction for ageing as it was an unreliable indicator of age.

Although this method proved to be a useful way to determine the age of mammals, for instance, in Peromyscus polionotus, the 95% confidence limits about a predicted age of 100 days were 96 to 107 days for a mean prediction, it should be remembered that this method requires complicated apparatus and analyses (Otero & Dapson, 1972), which are not practical in field studies.

The biochemical analysis of eye lenses was investigated in the present study, using white mice. The technique was found to take a disproportionate amount of time, and because the sample of bank voles was limited, and their eye lenses were used for another purpose, the technique was not investigated further.

Fedyk (1974c), in her work on the bank vole in Poland, found a significant correlation between age and the total water and total protein content in the body. The correlation for the latter was affected by the season when the voles were born. She added that water contents could be used to determine the age of bank voles until 3 months.

This method is no better than any other used to age bank voles.

Comparison between growth of the mainland bank vole and the Skomer vole:

The differences between the body size of the mainland bank vole and the Skomer vole, with the latter being bigger, have long been known, (Barrett-Hamilton & Hinton, 1910-21; Matthew, 1952; Steven, 1953; Fullagar *et al*, 1963; and Jewell, 1965).

The skull of the Skomer vole is bigger than that of the mainland bank vole. But the differenceis statistically not significant except for the lower jaw length ($t_{64}=1.32$, $P>0.1$, for the skull length; $t_{64}=1.74$, $P>0.05$, for the zygomatic breadth; and $t_{64}=2.53$, $P<0.02$, for the lower jaw length)

Molar roots developed similarly in the two subspecies. They continued to grow throughout life with almost the same average monthly increase. Differences did not occur between root length in the corresponding ages in the two subspecies.

The molar crowns are bigger in Skomer voles. This is probably due to the jaws being bigger in this subspecies. Tooth crowns wore at the same rate in both races. However, because molar crowns of the Skomer vole are bigger, differences occurred between the crown height of the corresponding ages of the two races. These differences were statistically not significant except for CM^3 ($t64=1.56$, $P>0.1$, for CM_1; $t64=1.59$, $P>0.1$, for CM_2; $t60=1.96$, $P>0.05$, for CM_3; $t64=1.53$, $P>0.1$, for CM^1; $t64=1.93$, $P>0.05$, for CM^2; and $t60=3.59$, $P<0.001$, for CM^3).

Epiphyses fused earlier in the mainland bank vole. This is possibly due to the latter being smaller in size and more active as a result of competition with other small mammals. This result might in addition demonstrate a possible longer life span for the Island vole as it needs longer time to grow.

The stalk of the baculum in the Skomer vole is longer, which is a reflection of a bigger body and skeleton. Digital processes of the baculum ossified at the same time in both races, which means that they reach maturity at the same time.

No differences existed between the dry weight of the eye lenses of the two subspecies, ($t64=0.05$, $P>0.9$). The lack of these differences is a further evidence to prove that the dry weight of the eye lenses is not correlated with body size and weight.

No differences occurred in the moult in the two races.

Growth in the Skomer vole was more regular than in the mainland bank vole. Data for each character exhibited lesser dispersion. This result confirms the belief that the Skomer vole was derived from ordinary mainland stock, introduced to the island by man (Corbet, 1961). The original stock was presumably composed of small numbers of the ordinary mainland bank vole, which after continuous inbreeding, gave rise to the Skomer vole population which is less genotypically variable, as it originated from only few voles with fixed genotype. Therefore growth can be expected to be regular, as heredity plays an important part in the growth and formation of animals.

Application of ageing techniques to field studies:

The problem which faces the investigator is how to apply ageing data derived from laboratory-raised voles on wild animals, since these data were obtained from voles kept under ideal laboratory conditions, and therefore take no account of seasonal changes.

It is important to know the biology of the mammal under investigation, and its breeding season in particular. This is helpful in determining the probable date of birth, and the longevity of the mammal.

The breeding season of the British mainland bank vole is known, from the studies of Baker (1930); Brambell & Rowlands (1936); Rowlands (1936); and Smyth (1966), and of the Skomer vole, from studies made by Jewell (1965 & 1966); and Coutts & Rowlands (1969). All agreed that the breeding season of the mainland bank vole, extends between March and October inclusive, and if food is available, it extends up to December (Smyth, 1966). The breeding season in the Skomer vole extends, between April and September, and they do not breed during winter (Jewell, 1965). The situation on the continent of Europe is similar to that of the British bank vole (Zejda, 1962 & Gliwicz *et al*, 1968).

Gliwicz *et al* (loc.cit.) studied the dynamics of cohorts of an Island population of *Clethrionomys glareolus* in Poland using the CMR method (Catch-Mark-Release). They found 5 cohorts to occur during the whole year (Fig. 53). One of them was the overwintered (Ko), one was the spring (K1), 2 were the summer (K2 & K3), and one was the autumn-born generation (K4). Since the breeding habits in *C. glareolus* are similar in both Britain and the continent of Europe (Jewell, 1965), the division made by Gliwicz *et al* can be applied to British bank voles.

According to them, Ko comprised voles not less than 6 months old. K1 comprised voles born between 23 April to 26 May (mean 5 May). K2 comprised voles born between 27 May to 10 July (mean 19 June). K3 comprised voles born between 11 July to 28 August (mean 2 August), and K4 comprised voles born from 29 August to 1 October (mean 10 September).

The question which now faces the investigator is how to estimate the age of voles belonging to any of the above cohorts, caught at any time during the year?

If we have a sample of 50 voles caught during, for instance, October. How are we going to assign them to their right cohorts ?

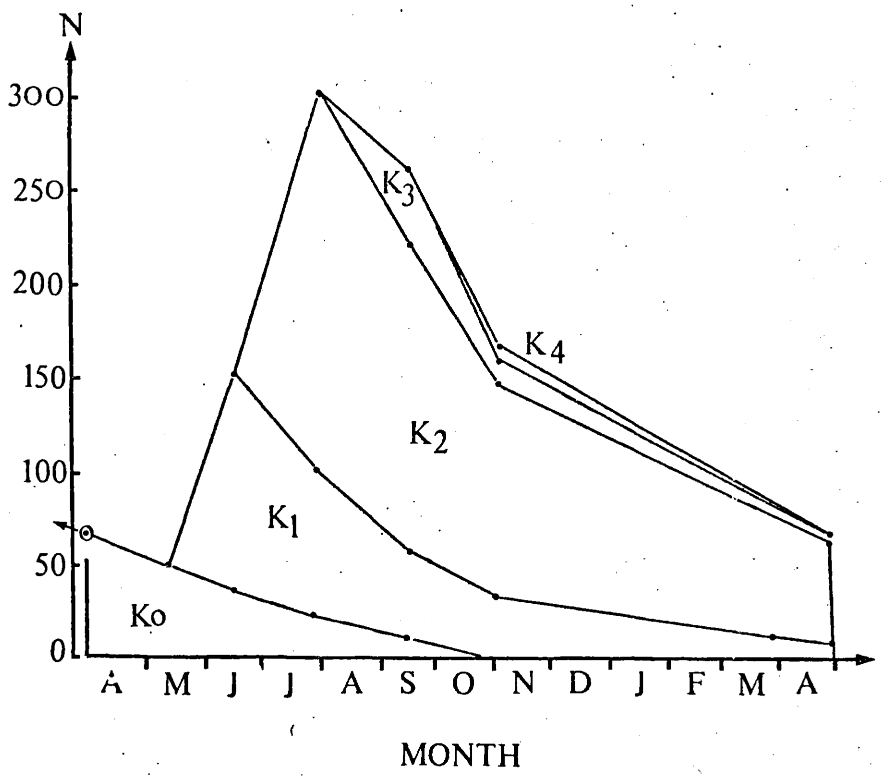


Fig. 53. Dynamics of different cohorts of Clethrionomys glareolus in Poland. (redrawn from Gliwicz et al, 1968).

If a vole is caught at any time during the year, what are the probable ageing techniques which can be used to estimate its age ?

The degree of accuracy for estimating the age of these bank voles, depends mainly upon the ageing method used. Ageing methods can be applied to both, a sample or any single individual. Before applying any method to estimate the age of the individual, the vole should be classified under one of two categories according to the method which can be used. These are live voles, and dead ones.

A summary for the maximum age, at which various criteria taken on live and dead voles cease to be reliable, is presented in Figs. 54 & 55 (measurements given are not maxima, but merely indicate measurement beyond which, that method is no longer useful).

I. Live voles:

1. Body weight:

The body weight is not reliable as age indicator above 14 gm in the mainland bank vole and above 18 gm in the Skomer vole, corresponding to a maximum age of one month. Therefore the body weight alone cannot be used for ageing bank voles above the stated weight.

2. Body measurements:

Body measurements may be used as an age criterion on live bank voles. The tail and hind foot lengths have earlier been excluded for use as age criteria since they completed their growth in early age. Ear pinna length divides voles into wide age-related categories above the age of 2 months.

The results were still overlapping in few of these categories. The head-body length is a more reliable age index than any other body measurement. But it is less reliable in adult voles than younger voles (above a head-body length of 86 mm in the mainland bank vole and above 90 mm in the Skomer vole).

3. Fusion of epiphyses:

The most reliable ageing method which can be used on live bank voles is studying the fusion of their epiphyses.

The X-ray method can be used as it gave successful results when used with small rodents (Tarasov, 1966). Fusion of epiphyses is not affected by seasonal variations and therefore data from laboratory populations can be applied successfully on field animals (Figs 43 & 44).

Since the fusion of epiphyses is not correlated with seasonal variations, Gliwicz _et al_ cohorts were not discussed under this topic.

4. Moulting:

Moulting can give more satisfactory data on dead voles which involves the pattern of the coloured areas on the inside of the skin (Figs 48, 49, & 50).

II. _Dead voles_:

In dead voles, the problem of ageing becomes easier, as more reliable methods can be used.

1. Dry weight of the eye lens:

This is the easiest and most accurate method. The weight of the eye lens is not affected by seasonal variations, sexual maturity, date of birth, or body weight (chapters II. 7. & IV). The eye lens growth is a reflection of increasing age and can be successfully applied to voles caught during any time of the year (Tables 48 & 49).

2. Molar root development:

Another highly reliable age criterion which can be applied to dead voles only, is molar root length. The onset of root development was at 35 to 42 days. A vole caught at any time of the year with its molars having a root (neck) would be less than 38.5±3.5 days old. Voles with rooted molars would be older than this .

The growth of roots has been recorded by many authors. But Lowe (1971) and Viitala (1971) mentioned the occurence of seasonal variation in root growth of C. g. britannicus and C. rufocanus respectively. It ranged between 0.05 to 0.55 mm / month in the former, and 0.16 to 0.29 mm for males, 0.39 mm for females in the latter.

In the present study, and since the bank voles were kept under laboratory conditions, the growth was regular. This result was supported by Mazak (1963) on laboratory population. The growth under laboratory conditions was somewhat, slower than in field animals, but the difference was not big (a mean of 1.3±0.1 month between the ages 60 to 210 days). If this difference is added to the estimated age, the result would be reliable with high accuracy. But there are still the possible seasonal influences which should be taken into account when working on field animals.

When root development is considered in relation to the Gliwicz et al cohorts, the molar teeth of voles belonging to the autumn cohort (K4) are expected to develop root (neck) at the end of October or beginning of November depending upon the birth date of the vole. The molar roots of these voles (RM_1) grow slowly during winter according to Lowe (1971) and Viitala (1971). (The lowest rate was recorded by Lowe to be 0.05 to 0.11 mm / month for RM_1, and by Viitala to be 0.16 mm / month for RM_2 during winter months). The growth then increases during the next spring and continues with a higher spring-summer rate. From Lowe's findings, autumn bank voles would have RM_1 length (excluding the neck), of up to 0.1 mm at the end of March (when they are 5 months old). Five months old mainland bank voles in the present study have RM_1 mean length of 0.93 mm (including the neck).

The overwintered animals (Ko), if caught in spring would have longer root length depending on the date of birth. According to Lowe, those born in spring of the last year would have a root length of 1.77 mm for males and 1.66 mm for females (excluding the neck). The root length of 12 months old laboratory-raised mainland bank vole was 2.17 mm (including the neck), which is similar to the root length of Lowe's material. The seasonal influences were not obvious in Lowe's voles because I think the slow growth during winter has been compensated for, during spring and summer and therefore, the molar roots of one year old voles in both samples have grown the same amount during that year.

3. Molar crown height:

The molar crown height is another reliable age criterion, but results derived from laboratory-raised voles cannot be directly applied to field animals, because as it has been mentioned, tooth wear is highly affected by food eaten by voles (chapter IV).

A difference of 4.38±0.37 months in age was found between laboratory-raised and 'field' voles between the ages 4 to 7 months.

An extensive study is needed to determine factors affecting tooth wear before applying laboratory data to field animals.

4. Baculum:

The baculum is a reliable age indicator until sexual maturity. Maturity took place during the seventh week of life under laboratory conditions. While it differs in the field. Artimo (1964) mentioned it to take place between 1.5 to 10 months in Finland. Since most of the voles which born in spring join the breeding adults and themselves contribute offspring to the late summer expansion of the population (Jewell, 1965), and since the ossification of the baculum is related to sexual maturity and not to age, the baculum is no longer useful as an age index in field animals. It can be used to differentiate sexually mature and immature voles. Any male vole with ossified digital processes would be more than 6 weeks old and considered as sexually mature.

Following Gliwicz _et al_ (1968), bacula of male voles belonging to K4 cohort (autumn generation), would have unossified digital processes as they were born at the end of the breeding season (mean 10 September), and would not join the breeding voles. Thus, the baculum of a vole with a non-ossified digital processes caught during the winter months would indicate a September or October birth.

Voles belong to K1 cohort (born between 23 April to 26 May), would have a baculum with ossified digital processes during the seventh week of life, as they join the breeding adults (Ko & K4) by then.

The other 2 summer cohorts (K2 & K3) would have ossified digital processes during their second month of life. Ko voles (the overwintered), have already had ossified digital processes, since they passed through the breeding season.

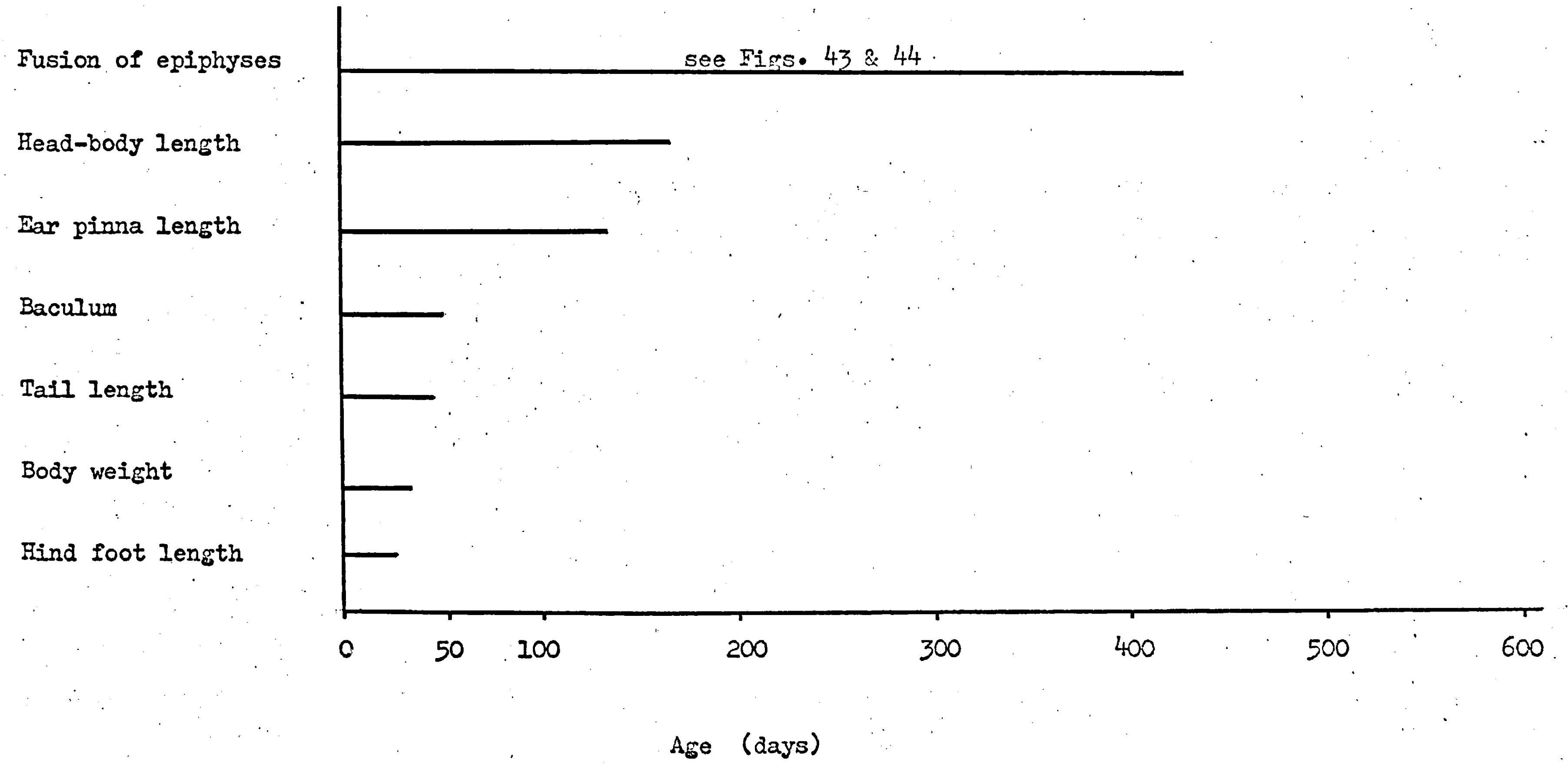


Fig. 54. Maximum age at which various criteria, on live voles, cease to be reliable

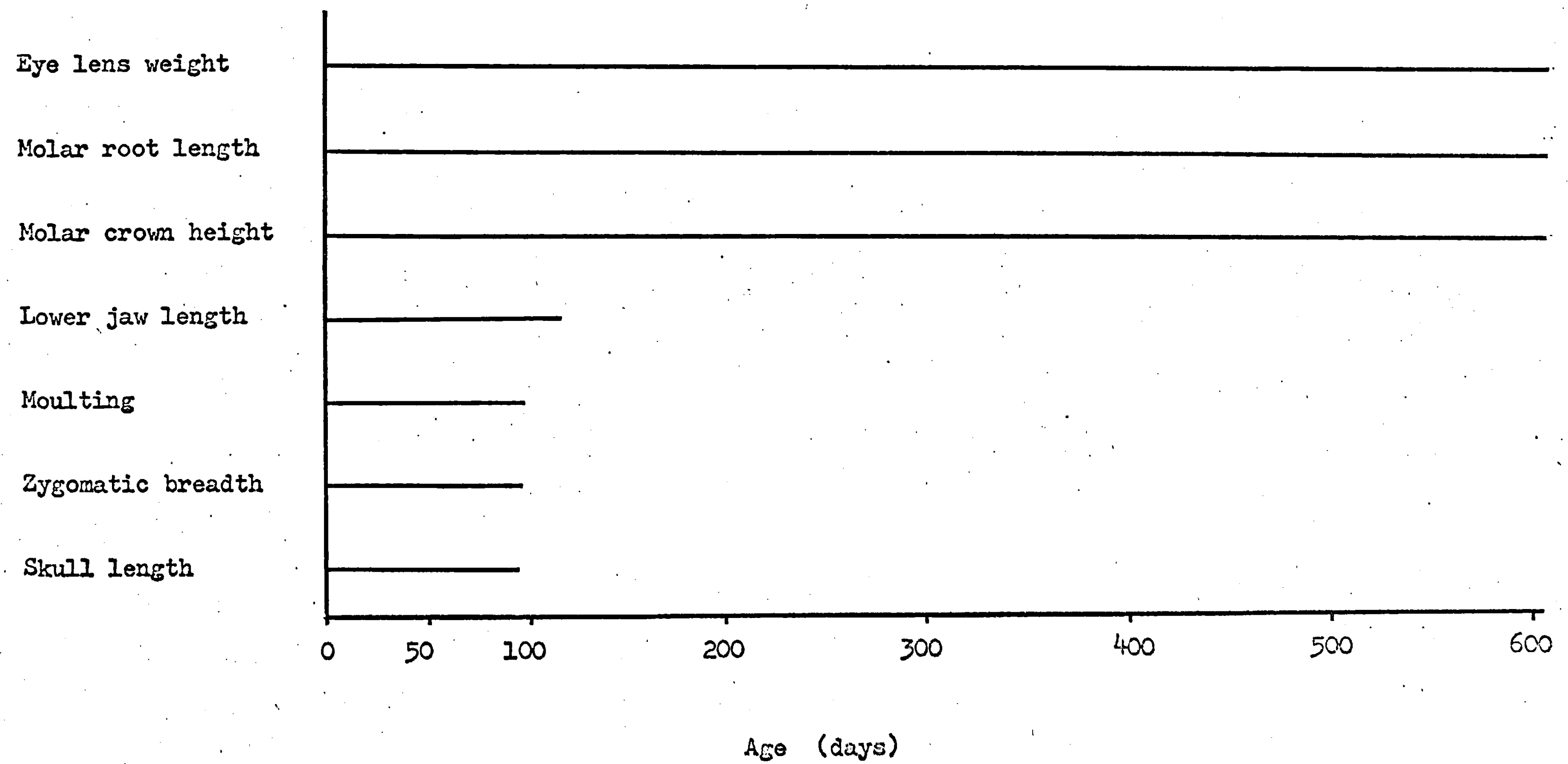


Fig. 55. Maximum age at which various criteria, on dead bank voles, cease to be reliable.

Conclusion

From the preceeding text, it is clear that accuracy for ageing is connected with the growth and developmental changes of every character used. If the growth is rapid in early age, the accuracy tends to be low among adults, since the growth of the organ has been completed very early, as, for example happened with the hind foot and tail in bank voles.

If the ageing character changes continuously throughout life (e.g. eye lens weight and molar root length), accurate ageing of older animals is easier.

Further studies are needed to determine factors other than age which might affect age criteria, such as, physiological, ecological, and genetic factors.

Although information on growth rates of known- age bank voles released in enclosures, showed close agreement with the laboratory data in the present study, extensive field studies on known age animals released in natural habitats are still needed.

CHAPTER VI. References

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APPENDICES

Appendix 1. Numerical data for the increase in body weight of the mainland bank vole:

Age/ days	Sample size	Range	Mean±S.E.	S.D.	V.	95%c.l.
0	9	1.50- 1.85	1.64±0.03	0.10	6.09	1.56- 1.72
5	14	3.20- 4.60	3.60±0.09	0.33	9.16	3.41- 3.79
7	18	4.00- 5.40	4.40±0.72	0.31	7.04	4.24- 4.56
10	31	5.00- 7.60	5.74±0.13	0.70	12.16	5.48- 6.00
14	14	5.50- 8.70	6.80±0.19	0.70	10.29	6.40- 7.20
17	21	7.10-12.80	9.00±0.26	1.20	13.30	8.45- 9.55
21	22	8.00-13.00	10.68±0.29	1.34	12.54	10.08-11.28
24	13	9.90-14.30	11.24±0.36	1.30	11.56	10.45-12.03
30	22	10.30-16.75	13.90±0.44	2.05	14.74	13.00-14.80
35	13	13.00-18.50	15.70±0.43	1.56	9.90	14.76-16.64
42	15	14.00-22.00	16.46±0.56	2.16	13.12	15.27-17.65
49	10	13.00-19.50	16.50±0.61	1.90	11.50	15.12-17.88
60	21	12.55-23.90	17.20±0.72	3.30	19.18	15.70-18.70
72	4	19.00-22.00	20.30±0.54	1.08	5.32	18.57-22.03
80	9	14.20-21.20	17.73±0.79	2.37	13.36	15.93-19.53
90	7	15.16-21.40	18.14±0.76	2.00	11.02	16.28-20.00
100	5	14.10-29.10	20.16±2.20	4.90	24.30	14.04-26.28
120	6	17.70-26.15	20.50±1.09	2.67	13.02	17.70-23.30
135	4	16.40-22.60	18.99±1.23	2.45	12.90	15.09-22.89
150	6	15.60-22.00	19.56±1.06	2.60	13.29	16.82-22.30
165	6	16.65-27.60	21.50±1.38	3.40	15.80	17.92-25.08
180	12	14.20-22.70	18.80±0.72	2.50	13.29	17.20-20.40
210	13	19.00-35.80	24.80±1.55	5.58	22.50	19.45-30.15
240	8	18.00-23.40	20.50±0.66	1.87	9.12	18.93-22.07
270	11	16.50-34.00	24.40±1.65	5.45	22.40	20.72-28.08
300	4	21.00-27.30	24.98±1.25	2.50	10.00	20.98-28.98
330	6	22.70-35.90	26.40±1.95	4.79	18.14	21.37-31.43
360	6	21.90-31.60	25.74±1.24	3.05	11.85	22.54-28.94
390	4	23.15-28.80	25.49±1.08	2.15	8.43	22.09-28.89
420	3	21.30-28.25	24.72±1.60	2.80	11.32	17.67-31.77
450	3	26.00-29.90	27.57±o.97	1.68	6.08	23.39-31.75
480	4	20.50-26.60	22.73±1.17	2.34	10.29	19.03-26.43
510	3	25.00-27.90	26.03±0.75	1.30	4.99	22.75-29.31
540	3	19.50-24.20	21.98±1.20	2.10	9.55	16.75-27.21

S.D.: standard deviation

S.E.: standard error

95% c.l.: 95% confidence limits

Appendix 2. Numerical data for the increase in body weight of the female Skomer vole:

Age/ days	Sample size	Range/ gm.	Mean±S.E.	S.D.	V.
5	6	4.30- 5.20	4.71±0.13	0.31	6.58
7	3	4.85- 5.90	5.44±0.31	0.54	9.90
10	5	6.40- 7.90	6.88±0.27	0.60	8.70
14	5	8.20- 9.50	8.94±0.25	0.56	6.26
17	6	9.20-12.00	10.82±0.40	0.99	9.15
21	2	12.20-15.10	13.65±1.45	2.05	15.00
24	2	14.80-18.00	16.40±1.60	2.26	13.78
30	4	16.35-18.70	17.59±0.65	1.29	7.33
35	4	17.10-22.00	19.63±1.01	2.02	10.29
42	2	19.00-20.15	19.58±0.57	0.81	4.14
49	2	19.72-21.00	20.36±0.64	0.91	4.47
60	5	18.60-23.10	21.12±0.84	1.89	8.95
72	1	20.80gm	20.80± -	-	-
80	2	20.30-21.70	21.00±0.70	0.99	4.70
90	3	18.00-19.10	18.53±0.32	0.55	2.97
100	1	18.15gm	18.15± -	-	-
120	2	21.50-22.70	22.10±0.60	0.85	3.85
135	3	19.50-24.45	22.48±1.52	2.63	11.70
150	2	19.70-20.60	20.15±0.45	0.64	3.18
165	3	19.50-27.40	23.03±2.32	4.02	17.45
180	1	19.8gm	19.80± -	-	-
210	2	21.50-29.95	25.73±4.23	5.98	23.24
240	2	21.94-22.00	21.97±0.03	0.04	0.18
270	2	21.50-21.50	21.50± -	-	-
300	4	20.50-30.30	24.48±2.13	4.25	17.36
330	2	25.20-29.50	27.35±2.15	3.04	11.12
360	3	22.35-28.10	24.72±1.74	3.01	12.18
390	2	21.60-24.80	23.20±1.60	2.26	9.74
420	2	23.20-25.70	24.45±1.25	1.77	7.24
450	1	30.30gm	30.30± -	-	-
480	2	26.10-29.70	27.90±1.80	2.55	9.14
510	2	26.00-27.50	26.75±0.75	1.06	3.96
540	1	27.00gm	27.00± -	-	-

Appendix 3. Numerical data for the increase in the body weight of male Skomer vole:

Age/ days	Sample size	Range/ gm.	Mean±S.E.	S.D.	V.
5	3	4.32- 4.88	4.53±0.17	0.30	6.60
7	5	5.11- 6.00	5.44±0.16	0.35	6.40
10	3	6.12- 6.80	6.52±0.21	0.36	5.50
14	2	8.30- 9.20	8.75±0.45	0.64	7.30
17	3	9.70-11.50	10.47±0.53	0.93	8.88
21	2	12.50-13.40	12.95±0.45	0.64	4.95
24	2	14.20-14.75	14.45±0.25	0.35	2.42
30	4	16.20-19.70	18.33±0.78	1.55	8.46
35	3	19.20-21.00	20.37±0.58	1.01	4.96
42	2	22.80-22.90	22.85±0.05	0.07	0.30
49	2	23.00-23.85	23.43±0.42	0.60	2.56
60	6	19.40-27.95	23.96±1.52	3.72	15.50
72	2	23.90-25.30	24.60±0.70	0.99	4.02
80	3	20.80-28.00	24.83±2.12	3.68	14.82
90	2	27.60-29.65	28.63±1.03	1.45	5.06
100	5	20.50-31.50	25.66±2.05	4.59	17.89
120	2	23.60-26.00	24.80±1.20	1.70	6.85
135	2	21.60-22.00	21.80±0.20	0.28	1.28
150	3	23.80-28.50	26.00±1.36	2.36	9.08
165	2	22.20-27.10	24.65±2.45	3.46	14.04
180	3	27.70-34.00	30.50±1.85	3.21	10.52
210	4	25.40-32.30	29.53±1.49	2.98	10.09
240	3	28.80-33.50	31.63±1.44	2.49	7.87
270	3	26.20-31.10	27.93±1.59	2.75	9.85
300	3	25.70-31.60	28.13±1.78	3.08	10.95
330	3	26.10-33.20	29.80±2.06	3.56	11.95
360	2	31.00-36.40	33.70±2.70	3.82	11.34
390	3	28.50-33.80	30.40±1.70	2.95	9.70
420	2	27.10-36.40	31.75±4.65	6.58	20.72
450	3	25.60-35.20	31.60±3.02	5.23	16.55
480	2	32.60-35.70	34.15±1.55	2.19	6.41
510	3	29.50-31.00	30.40±0.46	0.79	2.60
540	3	30.90-37.90	34.60±2.03	3.52	10.17

Appendix 4. Numerical data for the increase in head-body length of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	4	43- 47	45.00±0.91	1.83	4.07	42.10- 47.90
7	4	47- 54	49.75±1.55	3.10	6.23	44.82- 54.68
10	4	55- 60	57.50±1.04	2.08	3.62	54.19- 60.81
14	4	55- 65	61.75±2.36	4.72	7.64	54.24- 69.26
17	4	66- 73	68.25±1.65	3.30	4.84	63.00- 73.50
21	6	70- 76	73.67±0.99	2.42	3.28	71.12- 76.22
24	5	70- 80	74.80±1.62	3.63	4.85	70.30- 79.30
30	8	71- 81	77.00±1.41	4.00	5.15	73.67- 80.33
35	5	78- 85	81.20±1.31	3.11	3.83	77.34- 85.06
42	6	75- 88	82.50±1.84	4.51	5.47	77.77- 87.23
49	10	82- 91	87.80±0.99	3.12	3.55	85.56- 90.04
60	17	78- 95	87.12±1.19	4.90	5.62	84.60-89.64
72	7	80- 94	87.57±1.61	4.28	4.89	83.63- 91.51
80	10	85- 95	90.80±0.93	2.94	3.24	88.70- 92.90
90	6	87- 95	90.17±1.19	2.93	3.25	87.11- 93.23
100	8	85- 96	90.31±1.17	3.31	3.67	87.54- 93.08
120	8	85- 99	93.13±1.59	4.49	4.82	89.37- 96.89
135	5	86- 95	91.20±1.82	4.09	4.48	86.15- 96.25
150	5	87- 97	93.20±1.85	4.15	4.45	88.06- 98.34
165	5	92- 98	95.00±1.00	2.24	2.36	92.22- 97.78
180	12	88-100	93.00±1.07	3.72	4.00	90.64- 95.36
210	12	88-103	95.83±1.44	4.97	5.15	92.66- 99.00
240	8	92-100	95.13±0.97	2.75	2.89	92.84- 97.42
270	11	90-109	97.82±1.43	4.73	4.84	92.98-102.66
300	4	97-102	98.25±1.25	2.50	2.54	94.27-102.23
330	7	96-106	98.43±1.38	3.64	3.69	95.05-101.81
360	6	93-102	97.00±1.57	3.85	3.97	92.96-101.04
390	4	97-100	98.00±0.71	1.41	1.44	95.75-100.25
420	3	93-103	99.60±3.33	5.77	5.79	85.27-113.93
450	4	96-102	99.25±2.75	2.75	2.77	94.86-103.64
480	5	96-102	98.40±1.12	2.51	2.55	95.29-101.51
510	3	100-102	101.33±0.67	1.15	1.13	98.45-104.21
540	3	96-100	97.67±1.20	2.08	2.13	92.51-102.83

Appendix 5. Numerical data for the increase in tail length of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	8	10-13	10.96±0.44	1.24	11.31	9.92-12.00
7	9	13-15	14.17±0.20	0.61	4.30	13.71-14.63
10	16	15-24	17.97±0.60	2.38	13.24	16.69-19.25
14	8	19-26	22.15±0.93	2.63	11.87	19.95-24.35
17	13	24-32	27.58±0.78	2.83	10.26	25.88-29.28
21	9	26-36	32.17±1.18	3.54	11.00	29.45-34.89
24	5	34-38	35.60±0.75	1.67	4.69	33.52-37.68
30	8	31-39	35.63±1.06	2.99	8.39	33.12-38.14
35	8	36-41	37.63±0.63	1.77	4.70	36.14-39.12
42	10	35-42	38.90±0.77	2.42	6.22	37.16-40.64
49	10	40-47	43.10±0.71	2.23	5.17	41.49-44.71
60	22	34-49	40.55±0.78	3.66	9.03	38.94-42.17
72	7	39-48	42.00±1.20	3.16	7.52	39.06-44.94
80	14	36-46	41.50±0.72	2.68	6.46	39.94-43.06
90	8	37-45	41.00±0.96	2.73	6.66	38.73-43.27
100	8	38-49	43.38±1.19	3.38	7.79	40.56-46.19
120	7	42-51	45.29±1.25	3.30	7.29	42.23-48.35
135	9	38-46	43.00±0.87	2.60	6.05	40.99-45.01
150	5	41-45	43.00±0.71	1.58	3.67	41.03-44.97
165	5	42-47	43.90±0.81	1.82	4.15	41.65-46.15
180	12	39-48	43.25±0.81	2.80	6.47	41.47-45.03
210	14	40-49	43.93±0.68	2.56	5.83	42.46-45.40
240	8	38-54	46.19±1.55	4.37	9.46	42.52-49.86
270	10	40-47	43.85±0.64	2.03	4.63	42.40-45.30
300	4	41-47	43.50±1.26	2.52	5.79	39.49-47.51
330	8	43-49	45.38±0.75	2.13	4.69	43.61-47.15
360	6	41-50	45.00±1.32	3.22	7.16	41.61-48.39
390	5	41-45	44.20±0.80	1.79	4.05	41.98-46.42
420	3	42-47	44.33±1.45	2.52	5.68	38.09-50.57
450	4	43-45	43.75±0.48	0.96	2.19	42.22-45.28
480	4	44-48	45.75±0.85	1.71	3.74	43.05-48.45
510	3	40-45	43.33±1.67	2.89	6.67	36.14-50.52
540	2	40-45	42.50±2.50	3.54	8.33	*

* The 95% confidence limits were not attached to the mean because the sample size was very small.

Appendix. 6. Numerical data for the increase in the ear pinna length of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	4	2.8- 3.8	3.15±0.22	0.44	13.97	2.45- 3.85
7	6	3.0-3. 8	3.33±0.13	0.32	9.61	3.00- 3.66
10	8	4.5- 6.0	5.20±0.16	0.44	8.46	4.82- 5.58
17	6	8.0-10.3	9.07±0.43	1.05	11.58	7.96-10.18
21	6	10.0-11.0	10.60±0.19	0.47	4.43	10.11-11.09
24	5	9.5-11.0	10.50±0.32	0.71	6.76	9.61-11.39
30	8	9.3-12.2	10.90±0.35	1.00	9.17	10.07-11.73
35	5	10.0-11.0	10.74±0.31	0.70	6.52	9.88-11.60
42	6	10.0-12.3	11.07±0.33	0.80	7.23	10.22-11.92
49	10	11.0-12.0	11.62±0.12	0.36	3.10	11.35-11.89
60	16	10.0-12.9	11.37±0.18	0.74	6.51	10.99-11.75
72	7	11.0-12.0	11.46±0.16	0.42	3.66	11.07-11.85
80	10	11.0-12.1	11.46±0.16	0.51	4.45	11.10-11.82
90	6	11.4-13.0	12.10±0.21	0.52	4.30	11.56-12.64
100	8	11.0-12.5	11.71±0.19	0.52	4.44	11.26-12.16
120	8	11.0-13.0	12.19±0.23	0.65	5.33	11.64-12.74
135	5	12.0-14.0	12.60±0.36	0.80	6.35	11.60-13.60
150	5	11.6-12.5	12.12±0.17	0.38	3.14	11.65-12.59
165	5	12.0-12.5	12.18±0.09	0.20	1.64	11.93-12.43
180	8	12.1-13.2	12.66±0.15	0.43	3.40	12.30-13.02
210	11	11.0-14.0	12.33±0.24	0.81	6.57	10.52-14.14
240	7	11.5-13.8	12.83±0.31	0.81	6.31	12.07-13.59
270	11	11.0-13.0	12.41±0.20	0.66	5.32	11.96-12.86
300	4	12.1-13.0	12.75±0.25	0.50	3.92	11.95-13.55
330	6	12.3-13.5	12.97±0.16	0.38	2.97	12.56-13.38
360	6	12.2-13.0	12.72±0.14	0.34	2.67	12.36-13.08
390	4	12.0-13.7	13.03±0.38	0.76	5.83	11.82-14.24
420	3	13.0-13.5	13.20±0.15	0.26	1.97	12.55-13.85
450	4	12.5-13.8	13.13±0.27	0.54	4.11	12.27-13.99
480	5	12.2-13.3	13.00±0.21	0.46	3.54	12.42-13.58
510	3	12.8-13.6	13.23±0.23	0.40	3.02	12.24-14.22
540	3	12.5-13.0	12.83±0.17	0.29	2.26	12.11-13.55

Appendix 7. Numerical data for the increase in the hind foot length of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	7	7.2- 9.0	8.00±0.24	0.63	7.88	7.41- 8.59
7	8	9.0-11.0	9.98±0.21	0.60	6.01	9.48-10.48
10	16	11.0-14.0	11.79±0.26	1.03	8.74	11.24-12.34
14	8	13.0-15.0	13.81±0.31	0.88	6.37	13.08-14.54
17	11	14.0-16.5	14.77±0.26	0.86	5.82	14.19-15.35
21	9	15.0-17.0	15.92±0.23	0.70	4.40	15.39-16.45
24	5	15.6-17.0	16.32±0.29	0.64	3.92	15.51-17.13
30	8	15.0-17.0	16.19±0.28	0.78	4.82	15.53-16.85
35	5	15.5-17.0	16.42±0.26	0.58	3.53	15.70-17.14
42	6	15.0-17.0	16.55±0.32	0.78	4.71	15.73-17.37
49	10	16.3-18.0	17.13±0.19	0.61	3.57	16.70-17.56
60	17	15.5-17.5	16.54±0.14	0.58	3.51	16.24-16.84
72	7	16.0-17.0	16.51±0.15	0.39	2.36	16.14-16.88
80	10	15.5-17.0	16.23±0.15	0.48	2.96	15.89-16.57
90	6	15.5-17.4	16.43±0.29	0.72	4.38	15.68-17.18
100	8	16.0-17.3	16.68±0.17	0.47	2.82	16.28-17.08
120	8	16.0-17.5	16.73±0.18	0.51	3.05	16.30-17.16
135	5	16.0-17.0	16.66±0.21	0.48	2.88	16.08-17.24
150	5	16.0-17.0	16.48±0.22	0.50	3.03	15.87-17.09
165	4	16.2-17.4	16.90±0.25	0.50	2.96	16.10-17.70
180	8	16.2-17.4	16.80±0.14	0.40	2.38	16.47-17.13
210	10	16.0-18.0	16.77±0.21	0.68	4.05	16.30-17.24
240	8	16.8-17.8	17.16±0.12	0.33	1.92	16.88-17.44
270	11	16.0-17.8	16.66±0.16	0.54	3.24	16.30-17.02
300	4	16.5-17.0	16.63±0.13	0.25	1.50	16.22-17.04
330	7	16.5-18.0	17.01±0.21	0.56	3.29	16.50-17.52
360	6	16.2-17.0	16.55±0.12	0.29	1.75	16.24-16.86
390	4	16.3-17.0	16.65±0.16	0.31	1.86	16.14-17.16
420	3	16.0-17.3	16.70±0.38	0.66	3.95	15.07-18.33
450	4	16.3-17.0	16.60±0.15	0.29	1.75	16.12-17.08
480	5	16.0-17.1	16.76±0.20	0.45	2.68	16.20-17.32
510	3	16.8-17.2	16.93±0.13	0.23	1.36	16.37-17.49
540	3	16.0-16.2	16.07±0.07	0.12	0.75	15.78-16.36

Appendix 8. Numerical data for the increase in head-body length of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	2	47- 50	48.50±1.50	2.12	4.37	*
7	4	50- 52	51.00±0.41	0.82	1.61	49.70- 52.30
10	3	57- 58	57.67±0.33	0.58	1.01	56.27- 59.07
14	4	64- 67	65.00±0.71	1.41	2.17	62.74- 67.26
17	4	67- 70	68.88±0.52	1.03	1.50	67.23- 70.53
21	4	73- 79	67.75±1.32	2.63	3.43	72.55- 80.95
24	4	75- 85	80.25±2.06	4.11	5.12	73.70- 86.80
30	9	71- 88	82.44±1.86	5.59	6.76	78.14-86.74
35	8	83- 89	86.75±0.65	1.83	2.11	85.21- 88.29
42	4	87- 95	91.00±1.64	3.27	3.59	85.78- 96.22
49	4	91- 98	95.25±1.70	3.40	3.57	89.84-100.66
60	13	85- 99	94.23±1.09	3.95	4.20	91.85- 96.61
72	4	86-102	95.25±3.40	6.80	7.14	84.44-106.06
80	5	93-100	97.00±1.48	3.32	3.42	92.89-101.11
90	5	92-103	98.00±1.82	4.06	4.14	92.94-103.06
100	7	92-102	97.14±1.47	3.89	4.00	93.54-100.74
120	4	96-100	98.00±0.92	1.83	1.87	95.07-100.93
135	5	95-102	98.20±1.39	3.11	3.17	94.34-102.06
150	5	96-100	98.40±0.75	1.67	1.70	96.31-100.49
165	5	95-104	98.00±1.67	3.74	3.82	93.36-102.64
180	5	90-111	101.00±3.62	8.09	8.01	90.94-111.06
210	6	92-106	101.00±2.07	5.06	5.01	95.68-106.32
240	5	95-108	103.00±2.43	5.43	5.27	96.24-109.76
270	5	96-110	100.50±1.48	3.32	3.30	96.39-104.61
300	7	97-109	102.71±1.44	3.82	3.72	99.18-106.24
330	5	105-112	108.60±1.50	3.36	3.09	104.43-112.77
360	5	103-111	106.60±1.69	3.78	3.55	101.90-111.30
390	5	102-110	105.40±1.54	3.44	3.26	101.12-109.68
420	4	104-115	107.50±2.54	5.07	4.72	99.42-115.58
450	4	105-113	110.25±1.80	3.59	3.26	104.53-115.97
480	4	106-111	108.75±1.11	2.22	2.04	105.22-112.28
510	5	105-110	108.00±0.95	2.12	1.96	105.36-110.64
540	4	105-113	108.25±1.70	3.40	3.14	102.84-113.66

Appendix 9. Numerical data for the increase in tail length of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	4	13-14	13.55±0.43	0.87	6.39	12.18-14.92
7	5	15-16	15.50±0.32	0.71	4.57	14.61-16.39
10	9	16-22	20.23±0.75	2.24	11.07	18.50-21.96
14	7	23-26	24.43±0.52	1.37	5.60	23.16-25.70
17	8	28-31	29.81±0.38	1.07	3.58	28.91-30.71
21	7	34-38	35.93±0.71	1.88	5.23	34.19-37.67
24	4	37-41	38.75±0.85	1.71	4.41	36.05-41.45
30	10	37-43	40.20±0.57	1.81	4.51	38.91-41.49
35	8	41-47	43.38±0.84	2.37	5.46	41.39-45.37
42	4	45-53	47.88±1.74	3.47	7.25	42.35-53.41
49	4	45-52	48.50±1.44	2.89	5.96	43.92-53.08
60	13	47-59	50.00±0.87	3.14	6.28	48.10-51.90
72	4	45-54	50.50±2.02	4.04	8.00	44.08-56.92
80	5	46-51	48.20±0.68	1.92	3.98	46.31-50.09
90	5	47-58	52.40±1.89	4.22	8.05	47.15-57.65
100	7	43-51	47.57±1.00	2.64	5.55	45.12-50.02
120	4	48-50	48.75±0.48	0.96	1.97	47.22-50.28
135	5	45-51	48.60±1.03	2.30	4.73	45.74-51.46
150	5	47-52	49.60±0.87	1.95	3.93	47.18-52.02
165	5	46-53	48.40±1.21	2.70	5.58	45.04-51.76
180	5	44-55	50.00±1.98	4.42	8.83	44.50-55.50
210	6	47-55	49.67±1.18	2.88	5.80	46.64-52.70
240	5	47-54	51.00±1.45	3.24	6.35	46.97-55.03
270	5	49-56	51.80±1.35	3.03	5.85	48.05-55.55
300	8	49-55	52.19±0.69	1.96	3.76	50.55-53.83
330	4	54-58	56.25±0.85	1.71	3.04	53.55-58.95
360	5	50-55	53.40±0.92	2.07	3.88	50.83-55.96
390	5	51-55	53.00±0.71	1.58	2.98	51.03-54.97
420	4	49-61	53.25±2.66	5.32	9.98	44.79-61.71
450	4	51-56	54.50±1.19	2.38	4.37	50.72-58.28
480	4	52-58	54.50±1.26	2.52	4.62	50.49-58.51
510	5	51-53	51.80±0.49	1.10	2.11	50.44-53.16
540	4	50-54	52.25±1.03	2.06	3.95	48.97-55.53

Appendix 10. Numerical data for the increase in the ear pinna length of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	5	2.5- 3.7	3.04±0.19	0.43	14.07	2.51- 3.57
7	4	3.3- 3.5	3.43±0.05	0.10	2.79	3.27- 3.59
10	9	3,8- 5.8	4.68±0.22	0.65	13.92	4.17- 5.19
14	7	6.3- 8.0	7.47±0.26	0.70	9.36	6.83- 8.11
17	5	8.1- 9.0	8.50±0.14	0.32	3.81	8.11- 8.89
21	7	10.0-11.0	10.21±0.14	0.38	3.68	9.87-10.55
24	4	10.0-11.3	10.83±0.29	0.57	5.24	9.91-11.75
30	10	9.5-12.0	10.76±0.25	0.80	7.40	10.19-11.33
35	8	10.8-12.5	11.49±0.21	0.58	5.02	10.99-11.99
42	4	10.8-12.0	11.33±0.27	0.54	4.75	10.47-12.19
49	4	11.2-12.0	11.70±0.19	0.38	3.27	11.10-12.30
60	13	11.4-13.0	12.16±0.11	0.38	3.09	11.92-12.40
72	4	11.3-13.0	12.08±0.35	0.70	5.79	10.97-13.19
80	5	11.5-13.0	12.00±0.27	0.61	5.10	11.25-12.75
90	5	12.0-13.0	12.52±0.21	0.48	3.81	11.94-13.10
100	7	11.3-13.0	12.16±0.20	0.53	4.32	11.67-12.65
120	4	12.2-13.4	12.53±0.17	0.34	2.72	11.99-13.07
135	5	11.8-13.4	12.26±0.22	0.49	3.98	11.65-12.87
150	5	12.0-12.5	12.30±0.12	0.27	2.23	11.97-12.63
165	5	12.0-12.3	12.12±0.06	0.13	1.08	11.95-12.29
180	5	12.0-13.0	12.46±0.19	0.42	3.34	11.93-12.99
210	6	12.0-13.1	12.48±0.19	0.47	3.77	11.99-12.97
240	5	12.3-13.0	12.54±0.12	0.27	2.15	12.21-12.87
270	5	12.4-13.5	12.82±0.22	0.50	3.88	12.21-13.43
300	7	12.6-13.0	12.94±0.06	0.15	1.17	12.79-13.09
330	5	12.7-13.5	13.10±0.13	0.29	2.23	12.74-13.46
360	5	12.2-13.3	12.80±0.20	0.44	3.45	12.24-13.36
390	5	12.4-13.5	13.02±0.18	0.40	3.09	12.52-13.52
420	4	12.7-13.3	12.98±0.14	0.28	2.12	12.53-13.43
450	4	12.4-13.6	13.00±0.25	0.49	3.77	12.20-13.80
480	4	13.0-13.2	13.05±0.05	0.10	0.77	12.89-13.21
510	5	13.0-13.3	13.14±0.07	0.15	1.15	12.95-13.33
540	4	12.6-13.8	13.10±0.25	0.50	3.84	12.30-13.90

Appendix 11. Numerical data for the increase in the hind foot length of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	6	8.0- 9.5	8.92±0.20	0.49	5.51	8.41- 9.43
7	5	10.0-10.5	10.20±0.12	0.27	2.68	9.87-10.53
10	10	12.2-13.7	12.88±0.15	0.48	3.75	12.54-13.22
14	7	14.8-15.2	15.00±0.05	0.12	0.77	14.88-15.12
17	9	15.0-16.5	15.70±0.17	0.52	3.32	15.31-16.09
21	6	16.0-17.0	16.42±0.16	0.40	2.42	16.01-16.83
24	4	16.5-17.3	16.88±0.18	0.35	2.07	16.31-17.45
30	10	16.5-18.0	17.30±0.13	0.42	2.44	17.01-17.59
35	8	16.5-18.0	17.29±0.19	0.55	3.19	16.84-17.74
42	4	17.5-18.0	17.75±0.15	0.29	1.63	17.27-18.23
49	4	18.0-18.1	18.03±0.03	0.05	0.28	17.93-18.13
60	13	17.1-19.0	17.81±0.15	0.53	2.95	17.48-18.14
72	4	17.2-18.1	17.65±0.24	0.47	2.64	16.89-18.41
80	5	17.2-18.2	17.64±0.20	0.44	2.49	17.08-18.20
90	5	17.1-18.6	18.04±0.26	0.59	3.29	17.32-18.76
100	7	17.0-18.5	17.67±0.23	0.60	3.38	17.11-18.23
120	4	17.0-18.0	17.38±0.22	0.43	2.50	16.68-18.08
135	5	17.2-18.0	17.64±0.16	0.35	1.99	17.20-18.08
150	5	17.5-18.3	17.96±0.13	0.29	1.60	17.60-18.32
165	5	16.8-18.3	17.72±0.26	0.59	3.32	17.00-18.44
180	5	17.4-18.3	17.76±0.20	0.45	2.54	17.12-18.40
210	6	17.8-19.0	18.33±0.18	0.43	2.33	17.87-18.79
240	5	17.0-18.5	17.76±0.25	0.57	3.22	17.06-18.46
270	5	17.2-18.5	17.58±0.24	0.54	3.05	16.91-18.25
300	7	17.6-18.5	18.01±0.10	0.26	1.45	17.76-18.26
330	5	18.0-18.18	18.04±0.04	0.08	0.45	17.93-18.15
360	5	17.4-18.5	17.88±0.20	0.44	2.48	17.32-18.44
390	5	17.5-18.15	17.75±0.13	0.30	1.71	17.39-18.11
420	4	18.0-18.5	18.13±0.13	0.25	1.38	17.72-18.54
450	4	17.4-18.2	17.70±0.18	0.36	2.01	17.13-18.27
480	4	17.2-18.4	17.83±0.29	0.57	3.19	16.91-18.75
510	5	16.6-18.0	17.26±0.24	0.53	3.05	16.59-17.93
540	4	17.2-18.0	17.48±0.18	0.36	2.06	16.91-18.05

Appendix 12. Numerical data for the increase in skull length of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	4	13.16-14.40	13.56±0.29	0.57	4.21	12.64-14.48
7	4	14.30-15.89	14.86±0.35	0.70	4.74	13.75-15.97
10	4	17.20-17.97	17.50±0.17	0.33	1.89	16.96-18.04
14	4	16.75-18.80	18.04±0.45	0.90	4.97	16.61-19.47
17	7	18.10-19.74	18.81±0.19	0.50	2.68	18.34-19.28
21	7	19.30-21.30	19.97±0.26	0.69	3.46	19.33-20.61
24	7	18.95-20.50	19.91±0.19	0.49	2.44	19.44-20.38
30	9	18.95-21.42	20.24±0.28	0.85	4.22	19.59-20.89
35	5	20.10-21.11	20.81±0.19	0.43	2.08	20.28-21.34
42	6	20.80-21.75	21.39±0.13	0.33	1.54	21.06-21.72
49	10	21.09-22.50	21.96±0.15	0.48	2.19	21.62-22.30
60	17	20.52-22.95	21.89±0.18	0.76	3.47	21.51-22.27
72	7	21.20-23.07	22.43±0.25	0.67	2.98	21.82-23.04
80	10	21.80-23.20	22.63±0.15	0.47	2.08	22.29-22.97
90	6	22.00-23.15	22.53±0.16	0.39	1.74	22.12-22.94
100	7	22.15-23.26	22.72±0.14	0.38	1.69	22.38-23.06
120	8	22.21-23.70	22.98±0.16	0.44	1.91	22.60-23.36
135	5	22.11-23.41	22.88±0.23	0.52	2.28	22.24-23.52
150	7	22.00-23.79	23.14±0.25	0.66	2.84	22.53-23.75
165	6	22.50-23.35	22.92±0.16	0.39	1.69	22.51-23.33
180	11	22.00-23.85	22.81±0.16	0.53	2.32	22.45-23.17
210	12	22.40-23.90	23.19±0.16	0.56	2.40	22.84-23.54
240	12	22.28-24.16	23.25±0.16	0.55	2.36	22.90-23.60
270	11	22.10-24.00	23.22±0.17	0.55	2.36	22.84-23.60
300	4	23.13-24.64	23.52±0.38	0.75	3.18	22.31-24.73
330	7	23.35-24.60	23.85±0.18	0.48	2.02	23.41-24.29
360	6	22.65-24.40	23.43±0.29	0.71	3.01	22.68-24.18
390	4	22.86-24.10	23.57±0.30	0.59	2.50	22.62-24.52
420	3	23.25-24.34	23.85±0.32	0.55	2.32	22.47-25.23
450	4	23.23-24.45	23.70±0.26	0.52	2.21	22.87-24.53
480	5	22.95-23.60	23.39±0.12	0.26	1.09	23.06-23.72
510	3	23.53-23.94	23.78±0.13	0.22	0.93	23.22-24.34
540	3	22.80-23.72	23.31±0.27	0.47	2.01	22.15-24.47

Appendix 13. Numerical data for the increase in the zygomatic breadth of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	4	7.76- 8.95	8.13±0.28	0.55	6.83	7.24- 9.02
7	4	8.16- 9.45	8.75±0.27	0.53	6.11	7.89- 9.61
10	4	10.05-10.92	10.53±0.18	0.36	3.40	9.96-11.10
14	4	9.60-11.20	10.52±0.33	0.67	6.35	9.47-11.57
17	4	10.80-11.82	11.21±0.22	0.44	3.94	10.51-11.91
21	6	11.08-12.00	11.55±0.15	0.36	3.09	11.16-11.94
24	5	11.15-11.91	11.67±0.14	0.32	2.72	11.28-12.06
30	8	11.20-12.35	11.97±0.13	0.38	3.17	11.66-12.28
35	5	11.80-12.85	12.19±0.17	0.39	3.22	11.72-12.66
42	6	11.40-12.68	12.30±0.20	0.49	3.96	11.79-12.81
49	10	12.00-13.10	12.68±0.12	0.37	2.91	12.41-12.95
60	17	12.00-13.94	12.76±0.12	0.49	3.83	12.51-13.01
72	7	12.50-13.24	12.83±0.11	0.30	2.31	12.56-13.10
80	10	12.20-13.56	12.88±0.14	0.44	3.43	12.56-13.20
90	7	12.10-13.00	12.80±0.12	0.32	2.50	12.51-13.09
100	6	12.60-13.95	13.04±0.20	0.48	3.64	12.53-13.55
120	8	12.93-13.70	13.35±0.10	0.29	2.18	13.11-13.59
135	5	12.80-13.64	13.22±0.16	0.36	2.72	12.78-13.66
150	6	13.26-14.10	13.65±0.15	0.36	2.64	13.17-14.04
165	5	12.76-13.84	13.40±0.18	0.40	3.00	12.90-13.90
180	11	12.90-13.65	13.31±0.08	0.27	2.05	13.13-13.49
210	12	12.90-13.90	13.42±0.10	0.33	2.47	13.20-13.64
240	8	13.10-13.75	13.43±0.09	0.25	1.83	13.22-13.64
270	11	13.10-14.00	13.50±0.09	0.30	2.26	13.30-13.70
300	4	13.34-14.16	13.61±0.19	0.38	2.76	13.01-14.21
330	7	13.21-14.36	13.81±0.14	0.37	2.70	13.47-14.15
360	6	13.06-14.10	13.55±0.18	0.43	3.15	13.09-14.01
390	4	13.18-14.42	13.70±0.27	0.53	3.89	12.84-14.56
420	3	13.52-14.01	13.82±0.16	0.27	1.92	13.13-14.51
450	4	13.73-14.24	13.91±0.12	0.23	1.62	13.53-14.29
480	5	13.63-14.00	13.76±0.05	0.11	0.81	13.62-13.90
510	3	13.71-13.90	13.81±0.06	0.10	0.69	13.55-14.07
540	3	13.30-13.44	13.38±0.06	0.10	0.75	13.12-13.64

Appendix 14. Numerical data for the increase in the lower jaw length of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm ; 95% c.l.
5	4	7.30- 9.03	8.27±0.36	0.72	8.71	7.13- 9.41
7	4	8.83- 9.60	9.15±0.17	0.33	3.61	8.61- 9.69
10	6	10.00-10.50	10.31±0.08	0.19	1.84	10.10-10.52
14	4	10.15-11.50	10.82±0.29	0.57	5.29	9.90-11.74
17	4	11.00-11.90	11.38±0.19	0.39	3.39	10.78-11.98
21	6	11.14-12.14	11.73±0.14	0.35	3.02	11.37-12.09
24	8	11.10-12.04	11.55±0.13	0.36	3.14	11.24-11.86
30	10	11.00-12.70	11.83±0.16	0.52	4.36	11.47-12.19
35	5	11.40-12.12	11.81±0.12	0.26	2.23	11.48-12.14
42	6	11.50-12.50	12.12±0.15	0.36	2.98	11.73-12.51
49	12	11.70-12.50	12.12±0.07	0.25	2.07	11.97-12.27
60	23	11.60-13.28	12.37±0.10	0.46	3.72	12.16-12.58
72	7	11.80-12.90	12.44±0.14	0.38	3.09	12.10-12.78
80	10	12.10-13.10	12.71±0.11	0.35	2.73	12.46-12.96
90	7	12.00-12.80	12.49±0.12	0.31	2.46	12.20-12.78
100	8	12.10-13.30	12.51±0.14	0.39	3.13	12.18-12.84
120	10	12.25-13.65	12.97±0.12	0.39	2.99	12.70-13.24
135	6	12.50-13.27	12.83±0.13	0.31	2.41	12.50-13.16
150	7	13.00-13.80	13.35±0.13	0.34	2.56	13.03-13.67
165	6	12.74-13.28	13.02±0.07	0.17	1.33	12.84-13.20
180	11	12.70-13.80	13.24±0.11	0.36	2.70	12.99-13.49
210	13	12.75-13.75	13.09±0.10	0.35	2.68	12.87-13.31
240	8	12.90-13.85	13.29±0.14	0.40	3.00	12.96-13.62
270	11	12.87-13.93	13.33±0.09	0.30	2.28	13.13-13.53
300	4	12.76-13.44	13.04±0.15	0.29	2.25	12.56-13.52
330	7	12.90-14.14	13.57±0.15	0.39	2.85	13.20-13.94
360	6	12.75-14.27	13.35±0.25	0.61	4.58	12.71-13.99
390	4	12.89-13.76	13.39±0.20	0.40	2.95	12.75-14.03
420	3	13.41-13.95	13.67±0.16	0.27	1.98	13.03-14.31
450	4	13.00-14.24	13.39±0.29	0.57	4.26	12.47-14.31
480	5	13.16-13.80	13.53±0.12	0.26	1.95	13.20-13.86
510	3	13.35-14.00	13.62±0.20	0.34	2.48	12.76-14.48
540	3	12.90-13.25	13.05±0.10	0.18	1.38	12.62-13.48

Appendix 15. Numerical data for the increase in skull length of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	2	14.25-14.45	14.35±0.10	0.14	0.99	13.09-15.61
7	4	14.85-15.70	15.28±0.18	0.35	2.27	14.71-15.85
10	3	16.77-17.70	17.31±0.28	0.48	2.78	16.11-18.51
14	4	18.50-19.00	18.75±0.13	0.26	1.37	18.34-19.16
17	4	19.30-19.55	19.40±0.06	0.12	0.62	19.21-19.59
21	4	20.22-20.60	20.37±0.09	0.17	0.86	20.08-20.66
24	4	20.60-21.40	20.91±0.19	0.37	1.77	20.31-21.51
30	10	20.72-21.90	21.37±0.11	0.35	1.62	21.12-21.62
35	8	21.75-22.60	22.04±0.10	0.30	1.36	21.80-22.28
42	4	22.20-22.75	22.55±0.12	0.24	1.07	22.17-22.93
49	4	22.58-23.45	23.03±0.18	0.36	1.55	22.46-23.60
60	13	22.75-23.70	23.25±0.07	0.27	1.17	23.10-23.40
72	4	22.73-23.60	23.37±0.22	0.43	1.84	22.67-24.07
80	5	23.30-24.02	23.60±0.19	0.43	1.82	23.07-24.13
90	5	23.30-24.50	23.87±0.21	0.48	2.00	23.29-24.45
100	7	22.85-24.00	23.44±0.15	0.39	1.66	23.07-23.81
120	4	23.58-23.95	23.74±0.08	0.15	0.65	23.49-23.99
135	5	23.17-24.00	23.69±0.14	0.31	1.32	23.30-24.08
150	5	23.46-24.20	23.71±0.14	0.31	1.29	23.32-24.10
165	5	23.21-24.55	23.82±0.24	0.53	2.22	23.15-24.49
180	5	22.34-24.70	23.81±0.44	0.99	4.16	22.59-25.03
210	6	23.00-24.88	24.12±0.29	0.70	2.92	23.37-24.87
240	5	23.14-24.91	24.28±0.31	0.69	2.86	23.42-25.14
270	5	23.70-24.95	24.16±0.23	0.52	2.13	23.52-24.80
300	7	24.00-24.50	24.27±0.08	0.22	0.89	24.07-24.47
330	5	24.24-25.30	24.75±0.21	0.46	1.87	24.17-25.33
360	5	23.67-24.90	24.43±0.24	0.54	2.20	23.76-25.10
390	5	23.82-24.78	24.31±0.18	0.41	1.67	23.81-24.81
420	4	23.87-25.34	24.47±0.31	0.62	2.54	23.48-25.46
450	4	23.88-25.26	24.69±0.30	0.60	2.45	23.74-25.64
480	4	24.35-25.12	24.84±0.17	0.34	1.35	24.30-25.38
510	5	24.15-24.68	24.36±0.09	0.20	0.83	24.11-24.61
540	4	24.00-24.65	24.34±0.16	0.31	1.26	23.83-24.85

Appendix 16. Numerical data for the increase in the zygomatic breadth of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	2	8.90- 9.05	8.98±0.08	0.11	1.18	7.96-10.00
7	4	9.15-10.00	9.48±0.18	0.36	3.83	8.91-10.05
10	3	10.16-10.75	10.37±0.19	0.33	3.18	9.55-11.19
14	4	10.95-11.40	11.12±0.10	0.20	1.76	10.80-11.44
17	4	11.27-11.65	11.49±0.09	0.17	1.49	11.20-11.78
21	4	11.60-12.20	11.88±0.13	0.25	2.10	11.47-12.29
24	4	11.75-12.65	12.28±0.20	0.39	3.16	11.64-12.92
30	10	12.00-12.85	12.54±0.09	0.29	2.34	12.34-12.74
35	8	12.40-13.29	12.85±0.09	0.25	1.95	12.64-13.06
42	4	13.00-13.45	13.19±0.20	0.19	1.46	12.55-13.83
49	4	13.00-13.40	13.24±0.09	0.18	1.37	12.95-13.53
60	13	13.12-14.04	13.61±0.09	0.32	2.38	13.41-13.81
72	4	13.00-14.20	13.58±0.26	0.51	3.72	12.75-14.41
80	5	13.19-13.90	13.52±0.13	0.29	2.11	13.16-13.88
90	5	13.40-14.15	13.80±0.13	0.30	2.16	13.44-14.16
100	7	13.16-14.00	13.57±0.10	0.27	1.98	13.32-13.82
120	4	13.35-14.00	13.68±0.14	0.29	2.10	13.23-14.13
135	5	13.23-14.10	13.81±0.16	0.35	2.52	13.37-14.25
150	5	13.58-14.11	13.95±0.09	0.21	1.52	13.70-14.20
165	5	13.35-14.27	13.82±0.17	0.39	2.81	13.35-14.29
180	5	13.20-14.76	13.97±0.26	0.58	4.16	13.25-14.69
210	6	13.20-14.68	14.09±0.22	0.53	3.75	13.52-14.66
240	5	13.50-14.50	14.23±0.19	0.42	2.96	13.70-14.76
270	5	13.54-14.55	14.10±0.19	0.42	2.97	13.57-14.63
300	7	13.66-14.55	14.19±0.11	0.30	2.12	13.92-14.46
330	5	14.11-15.10	14.53±0.17	0.37	2.57	14.06-15.00
360	5	13.71-14.98	14.41±0.25	0.55	3.83	13.71-15.11
390	5	14.06-14.78	14.32±0.13	0.28	1.95	13.96-14.68
420	4	14.14-15.00	14.40±0.20	0.40	2.80	13.76-15.04
450	4	14.29-14.76	14.54±0.10	0.20	1.36	14.22-14.86
480	4	14.58-14.96	14.75±0.10	0.20	1.33	14.43-15.07
510	5	14.12-14.65	14.47±0.10	0.23	1.57	14.19-14.75
540	4	14.22-14.66	14.47±0.11	0.22	1.53	14.16-14.78

Appendix 17. Numerical data for the increase in the lower jaw length of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5	2	9.10- 9.45	9.28±0.18	0.25	2.67	6.99-11.57
7	4	9.57-10.05	9.79±0.10	0.20	2.08	9.47-10.11
10	3	10.30-11.12	10.67±0.23	0.40	3.79	9.68-11.66
14	4	11.20-11.70	11.44±0.11	0.21	1.80	11.09-11.79
17	4	11.60-12.00	11.77±0.08	0.17	1.43	11.52-12.02
21	4	12.25-12.50	12.33±0.06	0.12	0.95	12.14-12.52
24	4	12.00-12.75	12.45±0.16	0.33	2.62	11.94-12.96
30	10	12.30-13.00	12.57±0.08	0.26	2.08	12.39-12.75
35	8	12.70-13.15	12.88±0.05	0.15	1.17	12.76-13.00
42	4	13.18-13.60	13.32±0.10	0.19	1.45	13.00-13.64
49	4	13.00-13.63	13.18±0.15	0.30	2.29	12.70-13.66
60	13	13.26-14.00	13.53±0.06	0.21	1.58	13.40-13.66
72	4	13.16-13.80	13.41±0.14	0.28	2.10	12.96-13.86
80	5	13.25-13.90	13.56±0.13	0.28	2.04	13.20-13.92
90	5	13.30-14.35	13.73±0.19	0.42	3.06	13.20-14.26
100	7	13.00-13.78	13.49±0.10	0.26	1.96	13.24-13.74
120	4	13.70-13.96	13.79±0.06	0.12	0.89	13.60-13.98
135	5	13.31-14.05	13.65±0.12	0.27	2.01	13.32-13.98
150	5	13.35-14.15	13.76±0.17	0.37	2.67	13.29-14.23
165	5	13.32-14.45	13.83±0.20	0.44	3.20	13.27-14.39
180	5	13.05-14.27	13.80±0.22	0.49	3.54	13.19-14.41
210	6	13.35-14.32	13.89±0.13	0.31	2.25	13.56-14.22
240	5	13.45-14.33	13.94±0.16	0.36	2.56	13.50-14.38
270	5	13.70-14.15	13.92±0.08	0.17	1.20	13.70-14.14
300	7	13.75-14.37	14.11±0.09	0.24	1.71	13.89-14.33
330	5	13.90-15.00	14.40±0.18	0.41	2.84	13.90-14.90
360	5	13.85-14.70	14.28±0.14	0.31	2.20	13.89-14.67
390	5	13.75-14.20	14.03±0.08	0.18	1.25	13.81-14.25
420	4	13.76-14.55	14.04±0.18	0.35	2.52	13.47-14.61
450	4	14.00-14.84	14.24±0.20	0.41	2.85	13.60-14.88
480	4	14.24-15.00	14.53±0.17	0.33	2.30	13.99-15.07
510	5	13.85-14.43	14.18±0.10	0.22	1.56	13.91-14.45
540	4	13.73-14.45	14.06±0.16	0.31	2.24	13.55-14.57

Appendix 18. Numerical data for the increase in the neck-root length of M_1 of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35	4	0.00-0.03	0.01±0.01	0.02	150.00	0.00-0.04
42	5	0.00-0.11	0.07±0.02	0.05	64.68	0.01-0.13
49	11	0.04-0.20	0.15±0.02	0.05	31.24	0.11-0.19
60	22	0.13-0.45	0.26±0.02	0.08	30.49	0.22-0.30
72	7	0.30-0.56	0.40±0.04	0.10	25.72	0.31-0.49
80	11	0.35-0.59	0.45±0.02	0.07	16.58	0.41-0.49
90	7	0.35-0.68	0.52±0.05	0.12	22.37	0.40-0.64
100	11	0.38-0.78	0.59±0.04	0.13	22.52	0.50-0.68
120	11	0.52-0.99	0.71±0.05	0.16	21.87	0.60-0.82
135	6	0.62-0.98	0.79±0.05	0.12	15.28	0.66-0.92
150	7	0.62-1.18	0.93±0.08	0.22	23.82	0.74-1.12
165	8	0.75-1.07	0.92±0.05	0.13	14.43	0.80-1.04
180	12	0.72-1.35	1.01±0.06	0.20	19.60	0.88-1.14
210	19	0.87-1.46	1.19±0.04	0.18	14.85	1.11-1.27
240	9	1.10-1.90	1.49±0.08	0.26	17.56	1.31-1.67
270	10	1.00-2.00	1.55±0.09	0.30	19.27	1.35-1.75
300	4	1.67-2.05	1.83±0.08	0.16	8.81	1.58-2.08
330	7	1.75-2.27	2.04±0.06	0.17	8.30	1.89-2.19
360	7	1.94-2.35	2.17±0.06	0.17	7.88	2.02-2.32
390	4	2.00-2.44	2.19±0.10	0.20	9.00	1.87-2.51
420	4	2.12-2.40	2.28±0.07	0.13	5.86	2.06-2.50
450	5	2.04-2.56	2.31±0.09	0.20	8.76	2.06-2.56
480	5	2.17-2.79	2.37±0.11	0.25	10.46	2.06-2.68
510	3	2.20-2.70	2.48±0.15	0.26	10.30	1.83-3.13
540	3	2.20-2.80	2.42±0.19	0.33	13.56	1.60-3.24

Appendix 19. Numerical data for the increase in the neck-root length of M_2 of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35	4	0.00-0.04	0.01±0.01	0.02	200.00	0.00-0.04
42	6	0.00-0.14	0.07±0.02	0.05	72.09	0.02-0.12
49	8	0.12-0.19	0.14±0.01	0.03	19.07	0.12-0.16
60	17	0.10-0.31	0.20±0.01	0.06	30.54	0.18-0.22
72	7	0.25-0.38	0.31±0.02	0.05	15.29	0.26-0.36
80	10	0.33-0.53	0.39±0.02	0.07	17.65	0.35-0.43
90	6	0.34-0.54	0.42±0.03	0.07	17.28	0.34-0.50
100	11	0.40-0.67	0.51±0.03	0.09	17.39	0.44-0.58
120	9	0.51-0.75	0.63±0.03	0.08	13.31	0.56-0.70
135	6	0.62-0.95	0.70±0.05	0.13	18.79	0.57-0.83
150	5	0.80-0.98	0.86±0.03	0.07	7.69	0.78-0.94
165	6	0.70-0.96	0.84±0.04	0.11	13.27	0.74-0.94
180	12	0.70-0.94	0.81±0.03	0.09	10.77	0.74-0.88
210	18	0.82-1.29	1.01±0.03	0.13	12.64	0.95-1.07
240	9	1.00-1.59	1.19±0.07	0.20	16.40	1.03-1.35
270	11	1.00-1.59	1.23±0.05	0.18	14.52	1.12-1.34
300	4	1.38-1.62	1.50±0.07	0.13	8.33	1.28-1.72
330	7	1.40-1.75	1.59±0.06	0.15	9.55	1.44-1.74
360	7	1.48-1.83	1.68±0.05	0.14	8.43	1.56-1.80
390	4	1.62-2.05	1.80±0.10	0.20	11.15	1.48-2.12
420	4	1.70-2.12	1.84±0.09	0.17	9.17	1.55-2.13
450	5	1.63-1.94	1.82±0.05	0.12	6.75	1.68-1.96
480	5	1.62-2.29	1.84±0.12	0.27	14.50	1.51-2.17
510	3	1.84-2.25	2.04±0.12	0.21	10.05	1.52-2.56
540	3	1.91-2.11	1.98±0.06	0.11	5.69	1.72-2.24

Appendix 20. Numerical data for the increase in the neck-root length of M_3 of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35	4	0.00-0.05	0.01±0.02	0.03	250.00	0.00-0.07
42	6	0.00-0.17	0.08±0.02	0.06	71.88	0.03-0.13
49	10	0.05-0.27	0.12±0.02	0.07	60.73	0.08-0.16
60	17	0.04-0.20	0.11±0.01	0.05	41.78	0.09-0.13
72	7	0.14-0.22	0.17±0.01	0.03	18.73	0.15-0.19
80	10	0.14-0.39	0.24±0.03	0.08	33.09	0.17-0.31
90	6	0.15-0.38	0.26±0.04	0.09	34.63	0.16-0.36
100	11	0.17-0.35	0.26±0.02	0.07	26.56	0.22-0.30
120	9	0.21-0.52	0.36±0.04	0.12	34.33	0.27-0.45
135	6	0.35-0.70	0.48±0.05	0.12	24.67	0.35-0.61
150	5	0.41-0.56	0.51±0.03	0.06	12.04	0.43-0.59
165	6	0.45-0.68	0.58±0.04	0.10	16.56	0.48-0.68
180	12	0.40-0.60	0.50±0.02	0.06	12.58	0.46-0.54
210	18	0.43-0.96	0.64±0.03	0.13	19.76	0.58-0.70
240	9	0.54-0.99	0.73±0.05	0.16	21.85	0.61-0.85
270	11	0.62-1.08	0.78±0.05	0.18	22.70	0.67-0.89
300	4	0.90-1.00	0.97±0.03	0.05	4.87	0.87-1.07
330	7	0.89-1.18	1.03±0.05	0.13	12.72	0.91-1.15
360	7	1.02-1.28	1.12±0.04	0.10	9.00	1.02-1.22
390	4	1.00-1.33	1.13±0.07	0.14	12.73	0.91-1.35
420	4	1.00-1.30	1.16±0.07	0.13	10.94	0.94-1.38
450	5	0.85-1.40	1.20±0.10	0.23	19.28	0.92-1.48
480	5	1.00-1.55	1.27±0.09	0.20	17.37	1.02-1.52
510	3	1.24-1.42	1.33±0.05	0.09	6.78	1.11-1.55
540	3	1.21-1.50	1.32±0.09	0.16	11.91	0.93-1.71

Appendix 21. Numerical data for the increase in the neck-root length of $_{M}1$ of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35						
42	6	0.04-0.11	0.06±0.02	0.04	68.85	0.01-0.11
49	11	0.04-0.28	0.16±0.02	0.08	51.78	0.12-0.20
60	21	0.06-0.37	0.21±0.02	0.09	41.79	0.17-0.25
72	7	0.23-0.37	0.32±0.02	0.05	17.10	0.27-0.37
80	11	0.32-0.57	0.43±0.02	0.07	16.92	0.39-0.47
90	7	0.43-0.68	0.56±0.04	0.11	19.93	0.46-0.66
100	11	0.42-0.89	0.57±0.04	0.14	24.01	0.48-0.66
120	11	0.45-0.88	0.68±0.04	0.14	20.88	0.59-0.77
135	6	0.72-1.07	0.86±0.05	0.12	13.88	0.73-0.99
150	7	0.66-1.09	0.90±0.07	0.18	19.45	0.73-1.07
165	8	0.74-1.06	0.89±0.05	0.14	15.34	0.77-1.01
180	12	0.73-1.27	0.98±0.05	0.17	17.37	0.87-1.09
210	19	0.85-1.48	1.15±0.04	0.18	15.94	1.07-1.23
240	9	1.16-1.86	1.42±0.07	0.21	14.79	1.26-1.58
270	11	1.00-1.94	1.38±0.09	0.30	21.90	1.18-1.58
300	4	1.63-2.06	1.77±0.10	0.20	11.14	1.45-2.09
330	7	1.76-2.22	1.92±0.05	0.14	7.50	1.80-2.04
360	7	1.60-2.35	2.07±0.11	0.28	13.53	1.80-2.34
390	4	1.82-2.25	2.10±0.10	0.19	9.19	1.78-2.42
420	4	2.05-2.40	2.23±0.09	0.18	7.87	1.94-2.52
450	5	2.10-2.54	2.25±0.08	0.18	7.82	2.03-2.47
480	5	2.06-2.45	2.25±0.06	0.14	6.19	2.08-2.42
510	3	2.12-2.70	2.49±0.18	0.32	12.81	1.72-3.26
540	3	2.00-2.84	2.38±0.25	0.43	17.89	1.30-3.46

Appendix 22. Numerical data for the increase in the neck-root length of $_{M}2$ Of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35	5	0.00-0.02	0.01±0.01	0.01	100.50	0.00-0.02
42	6	0.00-0.09	0.03±0.02	0.04	132.78	0.00-0.08
49	10	0.05-0.29	0.15±0.03	0.08	51.84	0.08-0.22
60	17	0.10-0.29	0.19±0.01	0.06	30.78	0.17-0.21
72	7	0.15-0.35	0.26±0.03	0.08	29.74	0.19-0.33
80	10	0.33-0.44	0.38±0.01	0.04	10.97	0.36-0.40
90	6	0.33-0.58	0.45±0.04	0.09	19.65	0.35-0.55
100	11	0.34-0.59	0.45±0.02	0.08	17.73	0.41-0.49
120	9	0.40-0.68	0.53±0.04	0.11	21.31	0.44-0.62
135	6	0.45-0.75	0.58±0.05	0.12	21.18	0.45-0.71
150	5	0.60-0.85	0.71±0.05	0.11	15.35	0.57-0.85
165	6	0.52-0.85	0.71±0.04	0.11	16.13	0.61-0.81
180	12	0.60-0.97	0.76±0.03	0.12	15.86	0.69-0.83
210	18	0.70-1.37	0.88±0.04	0.17	19.16	0.80-0.96
240	9	0.80-1.56	1.13±0.08	0.23	20.16	0.95-1.31
270	11	0.80-1.65	1.12±0.08	0.27	24.11	0.94-1.30
300	4	1.18-1.68	1.33±0.12	0.24	17.85	0.95-1.71
330	7	1.22-1.70	1.41±0.06	0.16	11.55	1.26-1.56
360	7	1.24-1.80	1.56±0.08	0.22	13.94	1.37-1.75
390	4	1.55-1.89	1.71±0.07	0.14	8.24	1.49-1.93
420	4	1.56-1.93	1.75±0.08	0.15	8.84	1.50-2.00
450	6	1.54-1.76	1.65±0.04	0.09	5.79	1.55-1.75
480	5	1.40-1.96	1.69±0.10	0.23	13.90	1.41-1.97
510	3	1.64-2.15	1.89±0.15	0.26	13.51	1.24-2.54
540	3	1.50-2.00	1.70±0.15	0.26	15.56	1.05-2.35

Appendix 23. Numerical data for the increase in the neck-root length Of $_{M}3$ of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35						
42	6	0.03-0.10	0.06±0.01	0.02	36.61	0.04-0.08
49	10	0.04-0.20	0.10±0.01	0.04	43.73	0.08-0.12
60	17	0.10-0.24	0.15±0.01	0.04	25.22	0.13-0.17
72	7	0.15-0.28	0.20±0.02	0.04	20.96	0.15-0.25
80	10	0.21-0.40	0.30±0.02	0.07	22.46	0.25-0.35
90	6	0.22-0.46	0.31±0.04	0.09	27.97	0.21-0.41
100	11	0.30-0.45	0.37±0.02	0.06	15.72	0.33-0.41
120	9	0.33-0.64	0.47±0.04	0.12	25.52	0.38-0.56
135	6	0.40-0.86	0.59±0.07	0.18	29.93	0.41-0.77
150	5	0.43-0.85	0.66±0.07	0.16	23.70	0.47-0.85
165	6	0.44-0.80	0.63±0.05	0.12	19.47	0.50-0.76
180	12	0.50-0.89	0.63±0.03	0.11	17.49	0.56-0.70
210	18	0.56-0.99	0.76±0.03	0.13	16.88	0.70-0.82
240	9	0.81-1.26	0.99±0.06	0.18	17.82	0.85-1.13
270	11	0.80-1.35	0.94±0.05	0.18	18.98	0.83-1.05
300	4	1.00-1.38	1.16±0.09	0.17	14.74	0.87-1.45
330	7	1.08-1.50	1.28±0.06	0.17	13.16	1.13-1.43
360	7	1.15-1.59	1.36±0.07	0.18	13.50	1.19-1.53
390	4	1.32-1.50	1.39±0.04	0.08	5.80	1.26-1.52
420	4	1.35-1.58	1.47±0.06	0.11	7.80	1.28-1.66
450	5	1.31-1.62	1.44±0.06	0.13	8.88	1.27-1.61
480	5	1.21-1.80	1.40±0.10	0.23	16.45	1.12-1.68
510	3	1.53-1.83	1.64±0.10	0.17	10.07	1.21-2.07
540	3	1.30-1.50	1.39±0.06	0.10	7.24	1.13-1.65

Appendix 24. Numerical data for the increase in the neck-root length of M_1 of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35	4	0.00-0.08	0.02±0.02	0.04	200.00	0.00-0.08
42	5	0.00-0.06	0.02±0.01	0.03	141.42	0.00-0.05
49	4	0.06-0.20	0.13±0.04	0.07	54.03	0.00-0.26
60	13	0.10-0.47	0.23±0.03	0.11	46.10	0.16-0.30
72	4	0.24-0.41	0.34±0.04	0.07	21.88	0.21-0.47
80	5	0.30-0.45	0.35±0.03	0.06	18.52	0.27-0.43
90	5	0.36-0.56	0.47±0.04	0.10	20.50	0.36-0.58
100	7	0.40-0.68	0.52±0.04	0.11	20.90	0.42-0.62
120	4	0.55-0.67	0.59±0.03	0.05	9.22	0.49-0.69
135	5	0.67-0.80	0.72±0.02	0.05	7.37	0.66-0.78
150	5	0.70-0.90	0.80±0.04	0.09	10.99	0.69-0.91
165	5	0.81-0.94	0.87±0.02	0.05	6.22	0.81-0.93
180	5	0.80-1.14	1.04±0.06	0.14	13.40	0.89-1.21
210	6	1.01-1.34	1.14±0.05	0.12	10.81	1.01-1.27
240	5	1.11-1.56	1.37±0.10	0.23	16.56	1.09-1.65
270	5	1.20-1.98	1.53±0.14	0.31	19.95	1.14-1.92
300	7	1.50-1.90	1.62±0.05	0.14	8.56	1.50-1.74
330	5	1.70-2.00	1.88±0.05	0.12	6.43	1.74-2.02
360	5	1.77-2.22	1.98±0.07	0.16	8.23	1.79-2.17
390	5	1.75-2.24	1.95±0.09	0.20	10.29	1.70-2.20
420	5	2.19-2.49	2.29±0.06	0.13	5.63	2.12-2.46
450	4	2.26-2.50	2.37±0.06	0.12	5.02	2.18-2.56
480	4	2.30-2.60	2.40±0.07	0.14	5.91	2.18-2.62
510	5	2.35-2.62	2.43±0.05	0.11	4.52	2.29-2.57
540	4	2.40-2.82	2.58±0.09	0.18	6.85	2.29-2.87

Appendix 25. Numerical data for the increase in the neck-root length of M_2 of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35	4	0.00-0.05	0.01±0.02	0.03	250.00	0.00-0.07
42	5	0.02-0.09	0.06±0.01	0.03	45.03	0.03-0.09
49	4	0.10-0.18	0.14±0.02	0.04	31.07	0.08-0.20
60	13	0.17-0.32	0.25±0.01	0.05	20.47	0.23-0.27
72	4	0.23-0.44	0.32±0.05	0.09	28.75	0.16-0.48
80	4	0.37-0.40	0.39±0.01	0.02	3.85	0.36-0.42
90	3	0.41-0.45	0.43±0.01	0.02	4.84	0.39-0.47
100	7	0.31-0.59	0.46±0.04	0.10	22.28	0.36-0.56
120	3	0.56-0.69	0.65±0.05	0.08	11.55	0.43-0.87
135	5	0.60-0.70	0.66±0.02	0.05	7.11	0.60-0.72
150	5	0.53-0.88	0.72±0.06	0.13	18.23	0.55-0.89
165	5	0.63-0.93	0.77±0.05	0.12	15.32	0.63-0.91
180	5	0.74-1.02	0.91±0.06	0.14	14.89	0.74-1.08
210	6	1.00-1.16	1.06±0.02	0.06	6.04	1.01-1.11
240	5	1.00-1.38	1.20±0.07	0.15	12.31	1.01-1.39
270	5	1.00-1.60	1.26±0.10	0.22	17.19	0.98-1.54
300	7	1.25-1.70	1.45±0.05	0.14	9.57	1.33-1.57
330	5	1.46-1.78	1.68±0.06	0.13	7.81	1.51-1.85
360	6	1.56-1.95	1.75±0.06	0.15	8.57	1.60-1.90
390	5	1.47-1.83	1.64±0.07	0.15	9.18	1.45-1.83
420	5	1.78-2.05	1.90±0.05	0.11	5.99	1.76-2.04
450	4	1.92-2.12	2.01±0.04	0.08	4.10	1.88-2.14
480	4	2.00-2.31	2.14±0.07	0.13	6.04	1.92-2.36
510	5	2.00-2.30	2.14±0.05	0.11	5.12	2.00-2.28
540	4	2.20-2.49	2.34±0.06	0.12	5.12	2.15-2.53

Appendix 26. Numerical data for the increase in the neck-root length of M_3 of the Skomer vole:

Age/ days	Sample size	Range/ mm	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35						
42						
49	4	0.06-0.13	0.08±0.02	0.03	41.30	0.02-0.14
60	13	0.06-0.18	0.12±0.01	0.04	36.23	0.10-0.14
72	4	0.14-0.24	0.18±0.03	0.05	25.81	0.08-0.28
80	4	0.16-0.24	0.21±0.02	0.04	18.24	0.15-0.27
90	5	0.21-0.28	0.25±0.01	0.03	10.58	0.22-0.28
100	7	0.21-0.38	0.29±0.03	0.07	22.61	0.22-0.36
120	4	0.27-0.33	0.31±0.02	0.03	8.58	0.25-0.37
135	5	0.24-0.48	0.33±0.04	0.10	29.43	0.22-0.44
150	5	0.32-0.43	0.38±0.02	0.05	12.15	0.32-0.44
165	5	0.22-0.64	0.42±0.08	0.18	41.77	0.20-0.64
180	4	0.46-0.60	0.55±0.04	0.07	12.38	0.42-0.68
210	6	0.41-0.74	0.58±0.05	0.13	22.73	0.45-0.71
240	5	0.50-0.83	0.69±0.05	0.12	17.62	0.55-0.83
270	5	0.50-1.00	0.73±0.08	0.18	24.38	0.51-0.95
300	7	0.60-0.98	0.82±0.05	0.13	16.22	0.70-0.94
330	4	0.87-1.10	1.01±0.05	0.10	10.33	0.85-1.17
360	6	0.88-1.43	1.11±0.09	0.23	20.31	0.88-1.34
390	5	0.70-1.33	1.06±0.11	0.24	23.04	0.75-1.37
420	5	0.96-1.40	1.19±0.08	0.17	14.00	0.97-1.41
450	4	1.10-1.40	1.25±0.09	0.17	13.41	0.96-1.54
480	4	1.15-1.73	1.34±0.13	0.26	19.67	0.93-1.75
510	4	1.25-1.52	1.40±0.06	0.11	8.05	1.21-1.59
540	4	1.17-1.50	1.34±0.07	0.14	10.13	1.12-1.56

Appendix 27. Numerical data for the increase in the neck-root length of $_{M}1$ of the Skomer vole:

Age/ days	Sample size	Range mm	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35						
42	5	0.00-0.12	0.03±0.02	0.05	173.85	0.00-0.09
49	4	0.05-0.15	0.09±0.03	0.05	50.10	0.00-0.19
60	13	0.10-0.32	0.19±0.02	0.07	36.84	0.15-0.23
72	4	0.26-0.27	0.27±0.01	0.01	2.14	0.25-0.29
80	5	0.29-0.48	0.41±0.03	0.07	18.06	0.33-0.49
90	5	0.48-0.58	0.53±0.02	0.04	8.18	0.47-0.59
100	7	0.42-0.69	0.57±0.04	0.10	17.88	0.47-0.67
120	4	0.60-0.83	0.73±0.05	0.10	13.07	0.57-0.89
135	5	0.68-0.89	0.78±0.04	0.09	11.18	0.67-0.89
150	5	0.78-0.87	0.83±0.02	0.04	5.01	0.77-0.89
165	5	0.60-0.99	0.81±0.08	0.17	21.16	0.59-1.03
180	4	0.98-1.25	1.14±0.06	0.12	10.29	0.95-1.33
210	6	0.92-1.41	1.17±0.08	0.19	16.09	0.97-1.37
240	5	1.09-1.50	1.30±0.08	0.18	13.46	1.08-1.52
270	5	1.04-1.84	1.45±0.15	0.33	22.81	1.03-1.87
300	7	1.13-1.90	1.50±0.11	0.28	18.73	1.23-1.77
330	5	1.72-2.10	1.88±0.07	0.16	8.75	1.69-2.07
360	5	1.10-1.95	1.66±0.15	0.33	19.62	1.24-2.08
390	5	1.50-1.91	1.74±0.07	0.16	9.25	1.55-1.93
420	4	1.50-2.40	2.08±0.20	0.40	19.11	1.44-2.72
450	4	1.86-2.46	2.26±0.14	0.27	12.00	1.81-2.71
480	4	2.25-2.80	2.51±0.12	0.23	9.08	2.13-2.89
510	5	2.20-2.76	2.42±0.11	0.24	9.90	2.11-2.73
540	4	2.42-2.64	2.51±0.05	0.09	3.70	2.35-2.67

Appendix 28. Numerical data for the increase in the neck-root length of $_M2$ of the Skomer vole:

Age/ days	sample size	Range mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35						
42	5	0.00-0.10	0.03±0.02	0.05	153.48	0.00-0.09
49	4	0.07-0.10	0.08±0.01	0.01	17.68	0.06-0.10
60	13	0.10-0.30	0.21±0.02	0.07	34.53	0.17-0.25
72	4	0.21-0.36	0.29±0.04	0.08	27.21	0.16-0.42
80	5	0.20-0.42	0.30±0.04	0.08	27.79	0.19-0.41
90	5	0.33-0.64	0.45±0.07	0.15	33.58	0.26-0.64
100	7	0.33-0.59	0.46±0.05	0.12	26.54	0.34-0.58
120	4	0.48-0.65	0.56±0.04	0.07	12.58	0.43-0.69
135	5	0.56-0.70	0.64±0.02	0.05	8.46	0.58-0.70
150	5	0.60-0.88	0.76±0.05	0.12	16.24	0.62-0.90
165	5	0.70-0.84	0.75±0.03	0.06	7.51	0.67-0.83
180	4	0.82-1.02	0.94±0.05	0.09	9.67	0.78-1.10
210	6	0.88-1.13	1.03±0.04	0.09	8.57	0.93-1.13
240	5	0.90-1.33	1.12±0.08	0.18	16.37	0.90-1.34
270	5	0.82-1.55	1.23±0.13	0.28	23.10	0.87-1.59
300	7	1.05-1.74	1.33±0.09	0.24	18.07	1.11-1.55
330	5	1.47-1.82	1.65±0.06	0.13	8.08	1.48-1.82
360	6	1.20-2.00	1.62±0.11	0.26	15.89	1.34-1.90
390	5	1.30-1.75	1.54±0.07	0.16	10.66	1.35-1.73
420	5	1.41-2.20	1.86±0.14	0.31	16.62	1.47-2.25
450	4	1.77-2.00	1.92±0.05	0.10	5.45	1.76-2.08
480	4	1.83-2.50	2.06±0.15	0.30	14.72	1.58-2.54
510	5	1.94-2.50	2.20±0.11	0.24	10.74	1.89-2.51
540	4	2.06-2.37	2.26±0.07	0.14	6.08	2.04-2.48

Appendix 29. Numerical data for the increase in the neck-root length of $_{M}3$ of the Skomer vole:

Age/ days	Sample size	Range mm.	Mean±S.E.	S.D.	V.	Range/mm , 95% c.l.
5						
7						
10						
14						
17						
21						
24						
30						
35						
42	5	0.00-0.08	0.03±0.02	0.04	123.83	0.00-0.09
49	4	0.04-0.17	0.10±0.03	0.05	54.47	0.00-0.20
60	13	0.08-0.21	0.14±0.01	0.05	32.15	0.12-0.16
72	4	0.14-0.20	0.18±0.02	0.03	15.71	0.12-0.24
80	5	0.20-0.49	0.28±0.05	0.12	42.51	0.14-0.42
90	5	0.25-0.40	0.29±0.03	0.06	21.48	0.21-0.37
100	7	0.21-0.52	0.33±0.04	0.10	30.22	0.23-0.43
120	4	0.30-0.50	0.40±0.04	0.08	20.41	0.27-0.53
135	5	0.36-0.61	0.45±0.04	0.10	22.59	0.34-0.56
150	5	0.40-0.56	0.50±0.03	0.06	11.80	0.42-0.58
165	5	0.40-0.72	0.56±0.06	0.14	25.21	0.39-0.73
180	4	0.60-0.80	0.67±0.05	0.09	13.43	0.49-0.83
210	6	0.65-0.86	0.75±0.03	0.08	10.52	0.67-0.83
240	5	0.67-1.06	0.85±0.07	0.15	17.78	0.66-1.04
270	5	0.70-1.26	0.97±0.09	0.20	20.55	0.72-1.22
300	7	0.87-1.35	1.00±0.06	0.16	15.98	0.85-1.15
330	5	1.08-1.23	1.17±0.03	0.06	5.15	1.09-1.25
360	6	0.80-1.53	1.22±0.13	0.32	26.02	1.03-1.41
390	5	0.90-1.30	1.17±0.07	0.16	13.99	0.95-1.39
420	5	0.97-1.53	1.31±0.11	0.24	17.97	1.00-1.62
450	4	1.30-1.60	1.41±0.07	0.13	9.43	1.19-1.63
480	4	1.40-1.78	1.57±0.08	0.16	10.02	1.32-1.82
510	5	1.38-1.86	1.57±0.09	0.21	13.41	1.32-1.82
540	4	1.51-1.90	1.66±0.09	0.17	10.21	1.37-1.95

Appendix 30. Numerical data for the crown height of M_1 of the mainland bank vole:

Age/ days	Sample size	Range mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	4	1.37-1.77	1.52±0.09	0.18	12.00	1.23-1.81
7	4	1.76-1.95	1.85±0.05	0.09	4.98	1.69-2.01
10	4	2.24-2.63	2.41±0.09	0.17	7.00	2.12-2.70
14	4	2.70-2.87	2.82±0.04	0.08	2.80	2.69-2.95
17	4	3.02-3.29	3.11±0.06	0.12	4.00	2.92-3.30
21	6	3.12-3.30	3.23±0.03	0.07	2.05	3.15-3.31
24	6	3.14-3.43	3.26±0.05	0.12	3.80	3.13-3.39
30	9	3.04-3.59	3.35±0.05	0.16	4.82	3.23-3.47
35	5	3.20-3.56	3.34±0.07	0.15	4.39	3.15-3.53
42	5	3.13-3.50	3.30±0.07	0.16	4.86	3.11-3.49
49	11	3.00-3.39	3.18±0.05	C.15	4.65	3.07-3.29
60	21	2.82-3.29	3.06±0.03	0.15	4.78	3.00-3.12
72	7	2.69-3.08	2.88±0.07	0.18	6.39	2.71-3.05
80	11	2.60-3.15	2.88±0.06	0.20	7.08	2.75-3.01
90	7	2.60-3.00	2.78±0.06	0.16	5.89	2.63-2.93
100	11	2.30-2.88	2.64±0.06	0.19	7.25	2.51-2.77
120	11	2.20-2.78	2.51±0.06	0.20	8.12	2.38-2.64
135	6	2.24-2.51	2.38±0.04	0.10	4.23	2.28-2.48
150	7	2.00-2.48	2.28±0.08	0.21	9.02	2.08-2.48
165	8	2.05-2.57	2.28±0.07	0.19	8.24	2.11-2.45
180	12	1.90-2.59	2.26±0.07	0.24	10.46	2.11-2.41
210	17	1.70-2.49	2.06±0.06	0.24	11.42	1.93-2.19
240	9	1.50-2.18	1.87±0.08	0.24	12.97	1.69-2.05
270	8	0.95-1.97	1.60±0.12	0.34	21.38	1.32-1.88
300	4	1.14-1.34	1.25±0.05	0.09	7.32	1.09-1.41
330	7	0.95-1.37	1.20±0.06	0.15	12.83	1.05-1.35
360	7	0.88-1.55	1.10±0.09	0.23	20.47	0.88-1.32
390	4	0.77-1.18	0.93±0.08	0.18	18.94	0.68-1.18
420	4	0.80-1.29	0.91±0.13	0.26	28.47	0.50-1.32
450	7	0.62-1.23	0.92±0.08	0.21	23.26	0.72-1.12
480	4	0.72-1.16	0.87±0.10	0.20	22.82	0.55-1.19
510	3	0.67-1.19	0.85±0.17	0.29	34.66	0.12-1.58
540	3	0.60-0.95	0.77±0.10	0.18	22.73	0.34-1.20

Appendix 31. Numerical data for the crown height of M_2 of the mainland bank vole:

Age/ days	Sample size	Range mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	4	1.00-1.43	1.15±0.10	0.19	16.76	0.83-1.47
7	4	1.34-1.59	1.47±0.07	0.14	9.43	1.25-1.69
10	4	2.00-2.40	2.16±0.09	0.18	8.52	1.87-2.45
14	4	2.36-2.58	2.47±0.05	0.09	3.65	2.31-2.63
17	4	2.68-2.95	2.77±0.09	0.13	4.51	2.48-3.06
21	6	2.90-3.07	2.96±0.03	0.07	2.21	2.88-3.04
24	6	2.82-3.16	2.99±0.06	0.14	4.78	2.84-3.14
30	8	2.80-3.25	3.04±0.05	0.13	4.41	2.92-3.16
35	6	2.86-3.23	2.99±0.06	0.14	4.71	2.84-3.14
42	6	2.72-3.14	2.98±0.06	0.14	4.74	2.83-3.13
49	8	2.70-3.20	2.91±0.06	0.17	6.01	2.77-3.05
60	17	2.64-3.11	2.84±0.04	0.16	5.54	2.76-2.92
72	7	2.50-2.85	2.69±0.05	0.13	4.89	2.57-2.81
80	10	2.50-2.88	2.70±0.04	0.13	4.77	2.61-2.79
90	6	2.46-2.66	2.54±0.03	0.08	2.97	2.46-2.62
100	11	2.23-2.63	2.40±0.04	0.14	5.99	2.31-2.49
120	8	2.17-2.52	2.36±0.04	0.12	5.25	2.27-2.45
135	6	1.85-2.35	2.20±0.07	0.18	8.12	2.02-2.38
150	5	1.95-2.22	2.08±0.05	0.11	5.05	1.94-2.22
165	6	2.03-2.28	2.14±0.04	0.09	4.28	2.04-2.24
180	12	1.87-2.36	2.14±0.04	0.15	7.17	2.05-2.23
210	17	1.67-2.32	1.97±0.04	0.17	8.78	1.89-2.05
240	9	1.40-2.07	1.79±0.08	0.24	13.37	1.61-1.97
270	10	1.00-2.18	1.73±0.11	0.35	20.10	1.48-1.98
300	4	1.06-1.53	1.34±0.10	0.20	14.86	1.02-1.66
330	7	1.00-1.42	1.28±0.06	0.15	11.97	1.13-1.43
360	7	0.80-1.46	1.11±0.09	0.25	22.70	0.89-1.33
390	4	0.81-1.20	1.03±0.08	0.16	15.74	0.78-1.28
420	4	0.78-1.25	0.96±0.11	0.22	22.45	0.61-1.31
450	7	0.72-1.27	0.95±0.08	0.20	20.66	0.75-1.15
480	4	0.71-1.23	0.94±0.11	0.22	23.84	0.59-1.29
510	3	0.68-1.09	0.84±0.13	0.22	26.11	0.28-1.40
540	3	0.62-1.11	0.83±0.14	0.25	30.58	0.23-1.43

Appendix 32. Numerical data for the crown height of M_3 of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7						
10	4	1.01-1.39	1.16±0.09	0.17	14.54	0.87-1.45
14	4	1.57-1.69	1.63±0.03	0.06	3.48	1.53-1.73
17	4	1.94-2.35	2.13±0.09	0.17	8.09	1.84-2.42
21	6	2.12-2.55	2.39±0.06	0.15	6.11	2.24-2.54
24	6	2.33-2.58	2.48±0.04	0.09	3.52	2.38-2.58
30	8	2.40-2.82	2.59±0.06	0.18	6.85	2.45-2.73
35	5	2.60-2.95	2.70±0.06	0.14	5.33	2.53-2.87
42	6	2.48-2.72	2.61±0.03	0.08	3.05	2.53-2.69
49	10	2.16-2.95	2.55±0.09	0.29	11.34	2.35-2.75
60	17	2.24-2.80	2.49±0.04	0.15	5.85	2.41-2.57
72	7	1.92-2.41	2.27±0.07	0.18	7.77	2.10-2.44
80	11	2.00-2.50	2.25±0.05	0.16	6.92	2.14-2.36
90	5	1.90-2.32	2.13±0.08	0.18	8.23	1.91-2.35
100	11	1.88-2.29	2.12±0.04	0.14	6.73	2.03-2.21
120	9	2.00-2.20	2.11±0.02	0.06	2.82	2.06-2.16
135	6	1.60-2.00	1.85±0.06	0.15	8.14	1.70-2.00
150	5	1.74-2.08	1.83±0.06	0.14	7.86	1.66-2.00
165	6	1.68-2.05	1.82±0.06	0.14	7.51	1.67-1.97
180	12	1.62-2.09	1.83±0.05	0.16	8.74	1.72-1.94
210	17	1.30-2.07	1.73±0.05	0.22	12.99	1.62-1.84
240	9	1.25-1.85	1.57±0.07	0.22	14.09	1.41-1.73
270	11	0.80-1.89	1.58±0.10	0.32	20.23	1.36-1.80
300	4	1.17-1.53	1.34±0.09	0.17	12.71	1.05-1.63
330	7	0.94-1.15	1.03±0.03	0.08	7.98	0.96-1.10
360	7	0.82-1.23	1.06±0.06	0.16	14.77	0.91-1.21
390	4	0.71-1.17	0.95±0.10	0.19	19.85	0.63-1.27
420	4	0.81-1.14	0.96±0.07	0.14	14.24	0.74-1.18
450	7	0.77-1.03	0.86±0.03	0.09	10.02	0.79-0.93
480	4	0.73-1.25	0.92±0.13	0.25	26.82	0.51-1.33
510	3	0.70-0.84	0.78±0.04	0.07	9.10	0.61-0.95
540	3	0.76-1.00	0.89±0.07	0.12	13.55	0.59-1.19

Appendix 33. Numerical data for the crown height of M^1 of the mainland bank vole:

Age/ days	Sample size	Range/ mm	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	4	1.31-1.65	1.48±0.08	0.15	9.86	1.23-1.73
7	4	1.70-1.99	1.88±0.07	0.14	7.19	1.66-2.10
10	4	2.27-2.79	2.60±0.12	0.23	8.95	2.22-2.98
14	4	2.90-3.15	3.03±0.07	0.13	4.16	2.81-3.25
17	4	3.20-3.65	3.39±0.10	0.19	5.62	3.07-3.71
21	6	3.47-3.76	3.62±0.04	0.11	3.17	3.52-3.72
24	6	3.25-3.75	3.55±0.07	0.18	5.13	3.37-3.73
30	9	3.56-3.99	3.81±0.05	0.16	4.24	3.69-3.93
35	5	3.70-4.23	3.90±0.09	0.21	5.30	3.65-4.15
42	6	3.60-4.24	3.92±0.09	0.23	5.74	3.69-4.15
49	11	3.50-4.02	3.76±0.05	0.17	4.51	3.65-3.87
60	21	3.42-4.18	3.74±0.05	0.21	5.58	3.64-3.84
72	7	3.21-3.68	3.48±0.07	0.19	5.41	3.31-3.65
80	11	3.30-3.77	3.49±0.05	0.17	4.97	3.38-3.60
90	7	3.10-3.67	3.38±0.08	0.20	6.02	3.18-3.58
100	11	2.80-3.35	3.11±0.06	0.19	5.98	2.98-3.24
120	11	2.75-3.34	3.02±0.05	0.16	5.45	2.91-3.13
135	6	2.41-3.13	2.81±0.12	0.29	10.41	2.50-3.12
150	7	2.45-3.23	2.85±0.11	0.30	10.36	2.58-3.12
165	8	2.70-3.02	2.90±0.04	0.11	3.95	2.81-2.99
180	11	2.31-2.98	2.72±0.08	0.25	9.19	2.54-2.90
210	17	2.04-2.97	2.42±0.07	0.29	12.03	2.27-2.57
240	9	1.82-2.83	2.35±0.11	0.32	13.51	2.10-2.60
270	11	1.60-2.70	2.34±0.12	0.41	17.38	2.07-2.61
300	4	1.61-2.14	1.87±0.11	0.22	11.71	1.52-2.22
330	7	1.12-2.30	1.59±0.16	0.42	26.59	1.20-1.98
360	7	1.05-2.07	1.46±0.16	0.42	28.77	1.07-1.85
390	4	1.04-1.69	1.36±0.14	0.27	19.52	0.91-1.81
420	4	0.97-1.83	1.24±0.20	0.40	32.43	0.60-1.88
450	7	0.94-1.80	1.25±0.11	0.30	24.11	0.98-1.52
480	4	0.93-1.54	1.10±0.15	0.30	26.83	0.62-1.58
510	3	0.83-1.50	1.08±0.21	0.37	34.10	0.18-1.98
540	3	0.95-1.69	1.21±0.24	0.41	34.18	0.18-2.24

Appendix 34. Numerical data for the crown length of M^2 of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	4	0.90-1.17	1.05±0.06	0.11	10.80	0.86-1.24
7	4	1.30-1.50	1.43±0.05	0.09	6.59	1.27-1.59
10	4	1.80-1.99	1.89±0.05	0.09	4.75	1.73-2.05
14	4	2.25-2.50	2.36±0.06	0.11	4.49	2.17-2.55
17	4	2.60-2.99	2.74±0.09	0.17	6.25	2.45-3.03
21	6	2.86-3.15	3.01±0.04	0.10	3.16	2.91-3.11
24	6	2.83-3.36	3.02±0.07	0.18	5.97	2.84-3.20
30	8	3.00-3.34	3.20±0.05	0.13	4.01	3.08-3.32
35	5	3.11-3.35	3.23±0.04	0.10	3.20	3.12-3.34
42	6	2.97-3.37	3.21±0.06	0.14	4.24	3.06-3.36
49	10	2.93-3.33	3.12±0.04	0.13	4.27	3.03-3.21
60	17	2.80-3.43	3.09±0.04	0.18	5.79	3.01-3.17
72	7	2.66-3.05	2.83±0.05	0.14	4.97	2.71-2.95
80	10	2.63-3.00	2.83±0.03	0.11	4.02	2.76-2.90
90	6	2.68-2.93	2.77±0.04	0.10	3.68	2.67-2.87
100	11	2.20-2.76	2.59±0.05	0.15	5.95	2.48-2.70
120	9	2.40-2.70	2.53±0.04	0.12	4.60	2.44-2.62
135	6	1.97-2.69	2.39±0.11	0.27	11.19	2.11-2.67
150	5	2.13-2.83	2.39±0.12	0.27	11.38	2.03-2.72
165	6	2.18-2.55	2.38±0.06	0.15	6.18	2.23-2.53
180	12	1.92-2.57	2.35±0.05	0.17	7.10	2.24-2.46
210	16	1.66-2.43	2.12±0.05	0.21	9.90	2.01-2.23
240	9	1.41-2.27	1.96±0.09	0.27	13.53	1.75-2.17
270	11	1.08-2.38	1.96±0.12	0.40	20.42	1.69-2.23
300	4	1.28-1.73	1.55±0.10	0.19	12.27	1.23-1.87
330	7	1.05-1.94	1.47±0.12	0.32	22.01	1.18-1.76
360	7	0.96-1.82	1.33±0.12	0.31	23.58	1.04-1.62
390	4	0.91-1.46	1.19±0.11	0.22	18.88	0.84-1.54
420	4	0.83-1.40	1.08±0.12	0.24	21.94	0.70-1.46
450	7	0.85-1.45	1.11±0.09	0.23	20.87	0.88-1.33
480	4	0.85-1.30	1.05±0.10	0.20	19.38	0.73-1.37
510	3	0.71-1.39	0.96±0.22	0.38	39.22	0.01-1.91
540	3	0.71-1.45	1.07±0.21	0.37	34.60	0.17-1.97

Appendix 35. Numerical data for the crown height of M^3 of the mainland bank vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7						
10	4	0.91-1.27	1.03±0.08	0.16	15.79	0.78-1.28
14	4	1.33-1.59	1.46±0.06	0.11	7.61	1.27-1.65
17	7	1.43-1.97	1.63±0.08	0.20	11.97	1.43-1.82
21	6	1.97-2.28	2.12±0.04	0.10	4.67	2.02-2.22
24	6	2.00-2.35	2.15±0.05	0.13	6.19	2.02-2.28
30	8	2.25-2.58	2.36±0.04	0.12	5.10	2.27-2.45
35	5	2.23-2.55	2.38±0.06	0.14	5.70	2.21-2.55
42	5	2.30-2.50	2.38±0.04	0.09	3.58	2.27-2.49
49	9	2.10-2.47	2.28±0.05	0.14	6.05	2.16-2.40
60	17	1.91-2.47	2.22±0.04	0.17	7.46	2.14-2.30
72	7	1.73-2.29	2.04±0.08	0.21	10.21	1.84-2.24
80	10	1.88-2.28	2.11±0.04	0.13	6.02	2.02-2.20
90	6	1.86-2.13	2.04±0.04	0.09	4.58	1.94-2.14
100	11	1.61-2.15	1.89±0.05	0.16	8.54	1.78-2.00
120	9	1.72-2.05	1.86±0.04	0.11	5.68	1.77-1.95
135	6	1.54-1.92	1.73±0.07	0.17	9.77	1.55-1.91
150	5	1.43-2.09	1.72±0.11	0.24	13.88	1.41-2.03
165	6	1.63-1.88	1.77±0.04	0.10	5.91	1.67-1.87
180	12	1.32-1.98	1.71±0.05	0.18	10.45	1.60-1.82
210	18	1.37-1.85	1.58±0.04	0.15	9.46	1.50-1.66
240	9	1.26-1.62	1.46±0.04	0.13	8.92	1.37-1.55
270	11	0.93-1.84	1.46±0.08	0.27	18.16	1.28-1.64
300	4	1.07-1.38	1.23±0.08	0.16	12.81	0.98-1.48
330	7	0.85-1.48	1.16±0.11	0.28	24.01	0.89-1.43
360	7	0.76-1.42	1.02±0.08	0.22	21.47	0.78-1.22
390	4	0.84-1.12	1.02±0.07	0.13	12.77	0.80-1.24
420	4	0.78-1.31	1.00±0.12	0.23	22.69	0.62-1.38
450	7	0.65-1.08	0.88±0.06	0.17	18.88	0.73-1.03
480	4	0.63-1.34	0.96±0.15	0.30	31.07	0.48-1.44
510	3	0.60-0.90	0.71±0.10	0.17	23.62	0.28-1.14
540	3	0.66-1.18	0.94±0.15	0.26	27.99	0.29-1.59

Appendix 36. Numerical data for the crown height of M_1 of the Skomer vole:

Age/ days	Sample size	Range mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	2	1.58-1.59	1.59±0.01	0.01	0.44	1.55-1.68
7	4	1.84-1.99	1.93±0.03	0.06	3.24	1.83-2.03
10	3	2.32-2.43	2.38±0.03	0.06	2.39	2.25-2.51
14	4	2.85-2.95	2.91±0.02	0.04	1.48	2.85-2.97
17	4	3.10-3.18	3.14±0.02	0.04	1.23	3.08-3.20
21	4	3.30-3.47	3.38±0.04	0.07	2.11	3.25-3.51
24	4	3.42-3.53	3.49±0.03	0.05	1.43	3.39-3.59
30	10	3.50-3.77	3.61±0.03	0.09	2.40	3.54-3.68
35	8	3.52-3.90	3.68±0.05	0.15	3.95	3.56-3.80
42	4	3.58-3.97	3.74±0.09	0.17	4.41	3.45-4.03
49	4	3.53-3.67	3.61±0.03	0.06	1.61	3.51-3.71
60	13	3.13-3.75	3.46±0.04	0.15	4.40	3.37-3.55
72	4	3.21-3.43	3.30±0.05	0.10	2.90	3.14-3.46
80	5	3.20-3.35	3.27±0.03	0.06	1.92	3.19-3.35
90	5	3.11-3.37	3.25±0.04	0.09	2.87	3.14-3.36
100	7	2.90-3.35	3.15±0.08	1.21	6.68	2.95-3.35
120	4	2.77-3.06	2.94±0.07	0.14	4.77	2.72-3.16
135	5	2.52-3.03	2.81±0.09	0.20	6.96	2.56-3.06
150	5	2.30-2.98	2.73±0.12	0.27	10.02	2.40-3.06
165	4	2.55-2.92	2.68±0.09	0.17	6.42	2.39-2.97
180	5	2.33-2.76	2.54±0.08	0.18	7.07	2.32-2.76
210	6	2.23-2.71	2.47±0.08	0.19	7.69	2.26-2.68
240	5	1.77-2.48	2.11±0.14	0.31	14.70	1.72-2.50
270	4	1.51-2.27	1.90±0.16	0.31	16.36	1.39-2.41
300	6	1.44-2.15	1.85±0.11	0.28	15.21	1.57-2.13
330	5	1.47-2.02	1.71±0.09	0.20	11.82	1.46-1.96
360	5	1.50-1.88	1.67±0.06	0.14	8.40	1.50-1.84
390	5	1.45-1.93	1.64±0.08	0.18	11.02	1.42-1.86
420	4	1.03-1.45	1.29±0.09	0.18	13.90	1.00-1.58
450	4	1.00-1.36	1.18±0.08	0.16	13.14	0.93-1.43
480	4	1.05-1.52	1.23±0.11	0.21	16.83	0.88-1.58
510	5	1.11-1.42	1.19±0.06	0.13	11.19	1.02-1.36
540	4	0.82-1.58	1.12±0.17	0.33	29.83	0.58-1.66

Appendix 37. Numerical data for the crown height of M_2 of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	2	1.20-1.28	1.24±0.04	0.06	4.56	0.73-1.75
7	4	1.60-1.68	1.63±0.02	0.04	2.32	1.57-1.69
10	3	1.92-2.09	2.01±0.05	0.09	4.23	1.79-2.23
14	4	2.56-2.68	2.62±0.03	0.05	1.93	2.52-2.72
17	4	2.80-2.87	2.84±0.02	0.03	1.05	2.78-2.90
21	4	3.07-3.17	3.12±0.02	0.04	1.35	3.06-3.18
24	4	3.20-3.36	3.26±0.04	0.07	2.19	3.13-3.39
30	10	3.20-3.43	3.31±0.03	0.08	2.52	3.24-3.38
35	7	3.30-3.54	3.38±0.03	0.08	2.45	3.31-3.45
42	4	3.23-3.58	3.34±0.08	0.16	4.83	3.09-3.59
49	4	3.24-3.36	3.30±0.03	0.06	1.86	3.20-3.40
60	13	3.04-3.39	3.20±0.03	0.12	3.62	3.13-3.27
72	4	3.00-3.16	3.07±0.04	0.08	2.46	2.94-3.20
80	4	2.90-3.17	3.04±0.07	0.13	4.28	2.82-3.26
90	3	3.00-3.10	3.03±0.03	0.06	1.91	2.90-3.16
100	5	2.73-3.19	2.91±0.09	0.19	6.54	2.66-3.16
120	3	2.63-2.85	2.77±0.07	0.12	4.39	2.47-3.07
135	5	2.46-2.75	2.62±0.06	0.13	5.04	2.45-2.79
150	5	2.30-2.80	2.57±0.10	0.23	8.87	2.29-2.85
165	5	2.38-2.98	2.59±0.12	0.26	9.85	2.26-2.92
180	5	2.30-2.68	2.44±0.08	0.18	7.49	2.22-2.66
210	6	2.00-2.45	2.25±0.07	0.16	7.16	2.07-2.43
240	5	1.90-2.33	2.12±0.07	0.16	7.63	1.93-2.31
270	5	1.50-2.64	2.01±0.19	0.43	21.53	1.48-2.53
300	7	1.43-2.45	1.89±0.12	0.31	16.51	1.60-2.18
330	5	1.38-1.83	1.62±0.08	0.18	11.26	1.40-1.84
360	5	1.30-1.90	1.60±0.10	0.22	13.83	1.32-1.88
390	5	1.45-1.89	1.67±0.08	0.18	10.48	1.45-1.89
420	4	1.00-1.57	1.31±0.12	0.24	18.45	0.93-1.69
450	4	1.04-1.17	1.13±0.03	0.06	5.28	1.03-1.23
480	4	0.90-1.29	1.09±0.08	0.16	14.65	0.84-1.34
510	5	0.81-1.28	1.03±0.08	0.18	17.48	0.81-1.25
540	4	0.65-1.29	0.98±0.14	0.28	28.66	0.53-1.43

Appendix 38. Numerical data for the crown height of M_3 of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7	1	0.56- -	0.56± -			
10	3	1.00-1.19	1.10±0.06	0.10	8.64	0.84-1.36
14	4	1.70-1.85	1.76±0.03	0.06	3.62	1.66-1.86
17	4	2.00-2.19	2.10±0.05	0.10	4.83	1.94-2.26
21	4	2.30-2.69	2.53±0.08	0.16	6.47	2.28-2.78
24	4	2.72-2.85	2.76±0.03	0.06	2.16	2.66-2.86
30	10	2.72-3.05	2.87±0.04	0.12	4.09	2.78-2.96
35	8	2.80-3.04	2.92±0.04	0.10	3.39	2.83-3.01
42	4	2.83-3.05	2.92±0.05	0.10	3.35	2.76-3.08
49	4	2.72-2.93	2.79±0.05	0.09	3.37	2.63-2.95
60	13	2.60-2.91	2.76±0.03	0.10	3.79	2.69-2.83
72	4	2.60-2.76	2.69±0.04	0.08	2.84	2.56-2.82
80	5	2.50-2.85	2.66±0.08	0.18	6.59	2.44-2.88
90	5	2.43-2.74	2.58±0.06	0.14	5.40	2.41-2.75
100	7	2.44-2.68	2.57±0.03	0.08	3.29	2.50-2.64
120	4	2.30-2.51	2.37±0.05	0.10	4.18	2.21-2.53
135	5	2.12-2.50	2.29±0.08	0.17	7.37	2.07-2.51
150	5	2.10-2.47	2.29±0.06	0.14	5.92	2.12-2.46
165	5	2.00-2.55	2.25±0.11	0.25	11.03	1.94-2.56
180	5	2.00-2.24	2.10±0.04	0.09	4.16	1.99-2.21
210	6	1.70-2.13	1.85±0.07	0.17	9.37	1.67-2.03
240	5	1.62-2.14	1.79±0.09	0.21	11.64	1.54-2.04
270	5	1.20-2.04	1.66±0.15	0.33	19.73	1.24-2.08
300	7	1.25-2.20	1.74±0.11	0.29	16.56	1.47-2.01
330	4	1.32-1.65	1.53±0.08	0.15	9.49	1.28-1.78
360	5	1.17-1.89	1.51±0.13	0.28	18.43	1.15-1.87
390	5	1.13-1.82	1.51±0.14	0.31	20.36	1.12-1.90
420	4	1.18-1.68	1.39±0.11	0.21	15.01	1.04-1.74
450	4	1.14-1.27	1.18±0.03	0.06	5.29	1.08-1.28
480	4	0.82-1.24	1.04±0.11	0.21	20.51	0.69-1.39
510	4	0.75-1.17	0.99±0.09	0.18	17.75	0.70-1.28
540	4	0.78-1.12	1.00±0.08	0.15	15.20	0.75-1.25

Appendix 39. Numerical data for the crown height of M^1 of of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	2	1.75-1.83	1.79±0.04	0.06	3.16	*
7	4	2.00-2.06	2.03±0.02	0.03	1.48	1.97-2.09
10	3	2.47-2.58	2.52±0.03	0.06	2.21	2.39-2.65
14	4	3.02-3.15	3.10±0.03	0.06	2.06	3.00-3.20
17	4	3.33-3.36	3.34±0.01	0.01	0.38	3.32-3.36
21	4	3.40-3.68	3.59±0.07	0.13	3.56	3.37-3.81
24	4	3.62-3.86	3.74±0.07	0.13	3.34	3.52-3.96
30	10	3.75-3.99	3.89±0.03	0.09	2.22	3.82-3.96
35	8	4.00-4.26	4.08±0.04	0.10	2.33	3.99-4.17
42	4	4.11-4.28	4.21±0.04	0.07	1.73	4.08-4.34
49	4	4.11-4.30	4.23±0.04	0.08	1.92	4.10-4.36
60	13	3.90-4.37	4.07±0.04	0.14	3.42	3.98-4.16
72	4	3.90-4.00	3.94±0.02	0.04	1.10	3.88-4.00
80	5	3.80-4.09	3.93±0.06	0.13	3.42	3.76-4.10
90	5	3.62-3.90	3.78±0.05	0.12	3.06	3.64-3.92
100	7	3.40-3.80	3.59±0.05	0.14	3.93	3.47-3.71
120	4	3.40-3.51	3.45±0.03	0.06	1.76	3.35-3.55
135	5	3.22-3.66	3.43±0.09	0.21	6.02	3.18-3.68
150	5	3.20-3.30	3.26±0.02	0.04	1.23	3.20-3.32
165	5	3.02-3.75	3.26±0.13	0.29	8.93	2.90-3.62
180	5	2.70-3.49	3.05±0.13	0.29	9.36	2.69-3.41
210	6	2.40-3.04	2.81±0.09	0.22	7.97	2.58-3.04
240	5	2.16-3.00	2.67±0.14	0.32	12.03	2.28-3.06
270	5	1.95-3.21	2.54±0.22	0.50	19.77	1.93-3.15
300	7	1.80-3.23	2.54±0.19	0.50	19.57	2.07-3.01
330	5	1.75-2.45	2.19±0.12	0.27	12.19	1.86-2.52
360	4	2.06-2.30	2.18±0.05	0.10	4.50	2.02-2.34
390	5	1.92-2.62	2.28±0.13	0.28	12.21	1.92-2.64
420	4	1.40-2.60	1.88±0.26	0.51	27.08	1.05-2.71
450	4	1.13-1.99	1.59±0.18	0.36	22.42	1.02-2.16
480	4	1.36-1.67	1.49±0.07	0.13	8.91	1.27-1.71
510	5	1.32-1.89	1.52±0.11	0.24	16.05	1.21-1.83
540	4	1.05-1.78	1.42±0.15	0.30	21.32	0.94-1.90

* The 95% confidence limits were not attached to the mean because the sample size was very small.

Appendix 40. Numerical data for the crown height of M^2 of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5	2	1.20-1.28	1.24±0.04	0.06	4.56	0.73-1.75
7	4	1.42-1.56	1.49±0.03	0.06	3.93	1.39-1.59
10	3	1.92-2.08	1.99±0.05	0.08	4.18	1.77-2.21
14	4	2.47-2.66	2.54±0.04	0.08	3.28	2.41-2.67
17	4	2.70-2.87	2.81±0.04	0.08	2.79	2.68-2.94
21	4	3.03-3.18	3.10±0.03	0.06	1.99	3.00-3.20
24	4	3.20-3.28	3.24±0.02	0.04	1.19	3.18-3.30
30	10	3.31-3.49	3.39±0.02	0.06	1.67	3.34-3.44
35	8	3.40-3.70	3.53±0.04	0.10	2.87	3.44-3.62
42	4	3.52-3.70	3.59±0.04	0.08	2.20	3.46-3.72
49	4	3.40-3.75	3.60±0.08	0.15	4.05	3.35-3.85
60	13	3.30-3.63	3.43±0.04	0.13	3.72	3.34-3.52
72	4	3.26-3.44	3.35±0.05	0.09	2.57	3.19-3.51
80	5	3.28-3.37	3.32±0.02	0.04	1.29	3.26-3.38
90	5	3.12-3.32	3.23±0.03	0.07	2.30	3.15-3.31
100	7	2.91-3.34	3.12±0.07	0.18	5.92	2.95-3.29
120	4	2.90-3.10	3.03±0.05	0.09	2.87	2.87-3.19
135	5	2.72-3.07	2.97±0.06	0.14	4.84	2.80-3.14
150	5	2.72-2.96	2.83±0.04	0.09	3.29	2.72-2.94
165	5	2.55-3.09	2.83±0.10	0.22	7.76	2.55-3.11
180	5	2.50-2.94	2.69±0.10	0.22	8.32	2.41-2.97
210	6	2.47-2.87	2.59±0.06	0.15	5.71	2.44-2.74
240	5	1.90-2.68	2.38±0.13	0.29	12.25	2.02-2.74
270	5	1.70-2.87	2.28±0.21	0.46	19.98	1.70-2.86
300	7	1.64-2.48	2.14±0.10	0.26	12.06	1.89-2.39
330	5	1.70-2.39	2.00±0.12	0.27	13.35	1.67-2.33
360	5	1.86-2.49	2.06±0.12	0.26	12.51	1.73-2.39
390	5	1.66-2.15	1.97±0.08	0.18	9.29	1.75-2.19
420	4	1.40-2.09	1.68±0.15	0.29	17.35	1.20-2.16
450	4	1.33-1.69	1.50±0.09	0.18	11.83	1.21-1.79
480	4	1.17-1.65	1.38±0.10	0.20	14.55	1.06-1.70
510	5	1.00-1.58	1.24±0.11	0.24	19.24	0.93-1.55
540	4	0.88-1.48	1.16±0.13	0.26	22.22	0.75-1.57

Appendix 41. Numerical data for the crown height of M^3 of the Skomer vole:

Age/ days	Sample size	Range/ mm.	Mean±S.E.	S.D.	V.	Range/mm, 95% c.l.
5						
7	1	0.47- -	0.47± -	-	-	*
10	3	1.03-1.10	1.07±0.02	0.04	3.54	0.98-1.16
14	4	1.35-1.68	1.53±0.09	0.17	11.07	1.24-1.82
17	4	1.75-1.89	1.81±0.03	0.06	3.35	1.71-1.91
21	4	2.23-2.39	2.31±0.04	0.08	3.65	2.18-2.44
24	4	2.40-2.54	2.46±0.03	0.06	2.62	2.36-2.56
30	10	2.42-2.79	2.62±0.04	0.12	4.44	2.53-2.71
35	8	2.71-2.88	2.77±0.02	0.05	1.86	2.72-2.82
42	4	2.70-2.84	2.79±0.03	0.06	2.29	2.69-2.89
49	4	2.77-2.88	2.80±0.03	0.05	1.91	2.70-2.90
60	13	2.60-2.83	2.71±0.02	0.07	2.75	2.67-2.75
72	4	2.52-2.76	2.64±0.05	0.10	3.87	2.48-2.80
80	5	2.20-2.75	2.59±0.10	0.23	3.78	2.31-2.87
90	5	2.50-2.67	2.57±0.04	0.08	3.20	2.46-2.68
100	7	2.33-2.64	2.45±0.05	0.12	4.79	2.33-2.57
120	4	2.30-2.47	2.40±0.04	0.07	3.05	2.23-2.57
135	5	2.18-2.45	2.37±0.05	0.11	4.76	2.23-2.51
150	5	2.15-2.45	2.33±0.05	0.12	5.15	2.19-2.47
165	5	2.07-2.48	2.30±0.09	0.20	8.67	2.05-2.55
180	5	2.05-2.38	2.17±0.06	0.13	6.14	2.00-2.34
210	6	2.02-2.15	2.07±0.02	0.06	2.68	2.02-2.12
240	5	1.81-2.18	2.00±0.07	0.15	7.37	1.81-2.19
270	5	1.30-2.29	1.81±0.16	0.36	19.89	1.37-2.25
300	7	1.20-2.28	1.87±0.13	0.35	18.79	1.55-2.19
330	5	1.58-1.97	1.73±0.07	0.15	8.51	1.54-1.92
360	5	1.47-1.99	1.70±0.11	0.25	14.49	1.39-2.01
390	5	1.50-1.88	1.65±0.07	0.16	9.62	1.46-1.84
420	4	1.30-1.89	1.52±0.13	0.26	17.33	1.11-1.93
450	3	1.25-1.47	1.37±0.06	0.11	8.20	1.11-1.63
480	4	1.02-1.59	1.30±0.13	0.26	20.23	0.89-1.71
510	5	1.08-1.65	1.25±0.10	0.23	18.67	0.97-1.53
540	4	1.05-1.25	1.13±0.05	0.09	7.54	0.97-1.29

* The 95% confidence limits were not attached to the mean because the sample composed of one animal only.

Appendix 42. Numerical data for the increase in the dry weight of the eye lens of the mainland bank vole:
The values represent the dry weight of a single eye lens

Age/ days	Sample size	Range/ mg.	Mean±S.E.	S.D.	V.	Range/mg, 95% c.l.
5	4	0.300-0.345	0.325±0.0088	0.0196	0.0602	0.2939-0.3561
7	5	0.420-0.450	0.430±0.0063	0.0141	0.0329	0.4101-0.4499
10	6	0.550-0.740	0.625±0.0309	0.0758	0.1212	0.5524-0.6976
14	4	0.815-0.885	0.839±0.0138	0.0320	0.0381	0.7947-0.8829
17	7	0.915-1.110	0.993±0.0265	0.0702	0.0160	0.9279-1.0577
21	9	1.085-1.190	1.156±0.0107	0.0321	0.0277	1.1313-1.1799
24	6	1.165-1.335	1.273±0.0246	0.0603	0.0474	1.2156-1.3310
30	13	1.200-1.575	1.429±0.0329	0.1186	0.0830	1.3596-1.4974
35	5	1.535-1.680	1.620±0.0274	0.0613	0.0379	1.5519-1.6881
42	10	1.700-1.880	1.826±0.0210	0.0663	0.0363	1.7785-1.8685
49	11	1.880-2.200	2.034±0.0343	0.1139	0.0560	1.9611-2.1071
60	21	1.825-2.325	2.109±0.0320	0.1464	0.0694	2.0438-2.1738
72	7	2.150-2.495	2.331±0.0390	0.1033	0.0443	2.2412-2.4202
80	8	2.340-2.590	2.461±0.0325	0.0921	0.0374	2.3681-2.5545
90	7	2.315-2.595	2.501±0.0368	0.0974	0.0389	2.4180-2.5843
100	7	2.370-2.805	2.613±0.0679	0.1799	0.0688	2.4589-2.7669
120	9	2.455-2.905	2.623±0.0546	0.1639	0.0625	2.5045-2.7421
135	6	2.505-2.950	2.702±0.0669	0.1640	0.0597	2.5470-2.8564
150	7	2.510-2.910	2.736±0.0541	0.1433	0.0524	2.6130-2.8584
165	10	2.650-3.140	2.868±0.0501	0.1582	0.0551	2.7606-2.9754
180	7	2.810-3.260	3.041±0.0540	0.1431	0.0471	2.8943-3.1871
210	12	2.900-3.275	3.082±0.0334	0.1156	0.0375	3.0114-3.1520
240	7	3.000-3.300	3.138±0.0359	0.0951	0.0303	3.0564-3.2194
270	11	2.955-3.495	3.165±0.0475	0.1577	0.0498	3.0635-3.2655
300	4	3.140-3.550	3.320±0.1002	0.2003	0.0603	3.0440-3.5960
330	7	3.045-3.730	3.459±0.0890	0.2358	0.0682	3.2566-3.6606
360	6	3.070-3.940	3.488±0.1160	0.2842	0.0815	3.2159-3.7607
390	4	3.235-3.710	3.505±0.0990	0.1980	0.0565	3.2321-3.7779
420	3	3.410-3.725	3.577±0.0915	0.1583	0.0443	3.2557-3.8977
450	4	3.610-3.660	3.631±0.0116	0.0232	0.0064	3.5993-3.6633
480	5	3.200-3.910	3.622±0.1263	0.2829	0.0781	3.3074-3.9366
510	3	3.700-3.920	3.793±0.0657	0.1137	0.0300	3.5629-4.0237
540	3	3.275-4.040	3.633±0.2224	0.3848	0.1059	2.8534-4.4132

Appendix 43. Numerical data for the increase in the dry weight of the eye lens of the Skomer vole: The values represent the dry weight of a single eye lens.

Age/ days	Sample size	Range/ mg.	Mean±S.E.	S.D.	V.	Range/mg, 95% c.l.
5	2	0.360 days	0.360± -	-	-	*
7	4	0.400-0.480	0.438±0.0165	0.0330	0.0755	0.3850-0.4900
10	5	0.560-0.670	0.596±0.0209	0.0468	0.0786	0.5379-0.6541
14	4	0.790-0.895	0.839±0.0224	0.0448	0.0534	0.7676-0.9100
17	4	0.905-0.995	0.948±0.0186	0.0371	0.0391	0.8834-1.0066
21	4	1.090-1.175	1.121±0.0190	0.0379	0.0338	1.0609-1.1817
24	4	1.200-1.220	1.211±0.0043	0.0085	0.0070	1.1976-1.2250
30	10	1.350-1.470	1.412±0.0126	0.0398	0.0282	1.3830-1.4400
35	8	1.580-1.695	1.641±0.0132	0.0373	0.0227	1.6093-1.6719
42	4	1.740-1.890	1.824±0.0324	0.0647	0.0355	1.7208-1.9268
49	4	1.880-2.120	1.979±0.0514	0.1027	0.0519	1.8153-2.1423
60	13	2.070-2.285	2.155±0.0190	0.0686	0.0318	2.1140-2.1968
72	4	2.240-2.430	2.339±0.0418	0.0835	0.0357	2.2059-2.4717
80	5	2.280-2.440	2.380±0.0276	0.0619	0.0260	2.2033-2.5567
90	5	2.425-2.730	2.564±0.0527	0.1180	0.0460	2.4175-2.7105
100	7	2.440-2.740	2.571±0.0370	0.0981	0.0381	2.4807-2.6621
120	4	2.635-2.735	2.679±0.0227	0.0453	0.0169	2.6066-2.7510
135	5	2.610-2.830	2.748±0.0373	0.0835	0.0304	2.6443-2.8517
150	5	2.660-2.935	2.817±0.0540	0.1209	0.0429	2.6669-2.9671
165	5	2.605-3.080	2.896±0.0857	0.1919	0.0663	2.6578-3.1342
180	5	2.765-3.055	2.953±0.0564	0.1263	0.0428	2.7962-3.1098
210	6	2.910-3.320	3.159±0.0598	0.1466	0.0464	3.0055-3.3129
240	5	3.115-3.290	3.209±0.0305	0.0684	0.0213	3.1242-3.2938
270	5	3.180-3.545	3.321±0.0621	0.1392	0.0419	3.1484-3.4936
300	7	3.255-3.475	3.372±0.0276	0.0732	0.0217	3.3045-3.4397
330	5	3.370-3.650	3.486±0.0522	0.1170	0.0336	3.3409-3.6311
360	5	3.300-3.700	3.501±0.0669	0.1498	0.0428	3.3150-3.6870
390	5	3.475-3.650	3.569±0.0339	0.0759	0.0213	3.4748-3.6632
420	4	3.430-3.640	3.545±0.0530	0.1060	0.0299	3.3765-3.7135
450	4	3.415-3.800	3.650±0.0830	0.1650	0.0452	3.3861-3.9139
480	4	3.530-3.815	3.680±0.0718	0.1436	0.0390	3.4517-3.9083
510	5	3.675-3.760	3.722±0.0171	0.0382	0.0103	3.6745-3.7695
540	4	3.550-3.890	3.675±0.0746	0.1491	0.0406	3.4378-3.9122

*

* The 95% confidence limits were not attached to the mean because the only two values were similar.

Appendix 44. Growth attained, expressed as a percentage of of maximum growth of the different measurable age characters in the mainland bank vole:

Age/ days	HB	T	E	HF	SK	ZB	LJ
5	44.41	23.73	23.81	46.62	56.86	58.45	60.50
7	49.10	30.68	25.17	58.16	62.31	62.90	66.93
10	56.70	38.90	39.30	68.71	73.38	75.70	75.42
14	60.94	47.95	57.07	80.48	75.64	75.63	79.15
17	67.35	59.71	68.56	86.07	78.87	80.59	83.25
21	72.70	69.65	80.12	92.77	83.73	83.03	85.81
24	73.82	77.07	79.37	95.10	83.48	83.90	84.49
30	75.99	77.14	82.39	94.34	84.86	86.05	86.54
35	80.13	81.47	81.18	95.69	87.25	87.63	86.39
42	81.42	84.22	83.67	96.45	89.69	88.43	88.66
49	86.65	93.31	87.83	99.83	92.08	91.16	88.66
60	85.98	87.79	85.93	96.39	91.78	91.73	90.49
72	86.42	90.93	86.62	96.21	94.05	92.24	91.00
80	89.61	89.85	86.62	94.58	94.88	92.60	92.98
90	88.99	88.76	91.46	95.75	94.47	92.02	91.37
100	89.12	93.92	88.51	97.20	95.26	93.75	91.51
120	91.91	98.05	92.13	97.49	96.35	95.97	94.88
135	90.00	93.09	95.24	97.09	95.93	95.03	93.86
150	91.98	93.09	91.61	96.04	97.03	98.13	97.66
165	93.75	95.04	92.06	98.48	96.10	96.33	95.25
180	91.78	93.63	95.69	97.90	95.64	95.69	96.85
210	94.57	95.11	93.20	97.73	97.23	96.48	95.76
240	93.88	100.00	96.98	100.00	97.49	96.55	97.22
270	96.54	94.93	93.80	97.09	97.36	97.05	97.51
300	96.96	94.18	96.37	96.91	98.62	97.84	95.39
330	97.14	98.25	98.03	98.95	100.00	99.23	99.27
360	95.73	97.42	96.15	96.45	98.24	97.41	97.66
390	96.71	95.69	98.49	97.03	98.83	98.49	97.95
420	98.29	95.97	99.77	97.32	100.00	99.35	100.00
450	97.95	94.72	99.24	96.74	99.57	100.00	97.95
480	97.11	99.05	98.26	97.67	98.07	98.92	98.98
510	100.00	93.81	100.00	98.66	99.71	99.23	99.63
540	96.39	92.01	96.98	93.65	97.74	96.19	95.46

HB: head-body length
T : tail length
E : ear pinna length
HF: hind foot length
SK: skull length
ZB: zygomatic breadth
LJ: lower jaw length

Appendix 44. Continued

Age/ days	BW	ELW	RM_1	RM_2	RM^1	CM_1	CM_2
5	13.06	8.57	-	-	-	45.37	37.83
7	15.96	11.34	-	-	-	55.22	48.36
10	20.82	16.48	-	-	-	71.94	71.05
14	24.66	22.11	-	-	-	84.18	81.25
17	32.64	26.17	-	-	-	92.84	91.12
21	38.74	30.46	-	-	-	96.42	97.37
24	40.77	33.57	-	-	-	97.31	98.36
30	50.42	37.66	-	-	-	100.00	100.00
35	56.95	42.71	0.40	0.50	-	99.70	98.36
42	59.70	48.07	2.82	3.43	2.41	98.51	98.04
49	59.85	53.62	6.05	6.86	6.43	94.93	95.72
60	62.39	55.59	10.48	9.80	8.43	91.34	93.42
72	73.63	61.44	16.13	15.20	12.85	85.97	88.49
80	64.31	64.89	18.15	19.12	17.27	85.97	88.82
90	65.80	65.94	20.97	20.59	22.49	82.99	83.55
100	73.12	68.88	23.79	25.00	22.89	78.81	78.95
120	74.36	69.16	28.63	30.88	27.31	74.93	77.63
135	68.88	71.22	31.85	34.31	34.54	71.04	72.37
150	70.95	72.12	37.50	42.16	36.14	68.06	68.42
165	77.98	75.61	37.10	41.18	35.74	68.06	70.39
180	68.19	80.16	40.73	39.71	39.36	67.46	70.39
210	89.95	81.24	47.98	49.51	46.18	61.49	64.80
240	74.36	82.72	60.08	58.33	57.03	55.82	58.88
270	88.50	83.42	62.25	60.29	55.42	47.76	56.91
300	90.61	87.52	73.79	73.53	71.08	37.31	44.08
330	95.76	91.18	82.26	77.94	77.11	35.82	42.11
360	93.36	91.96	87.50	82.35	83.13	32.84	36.51
390	92.46	92.40	88.31	88.24	84.34	27.76	33.88
420	89.66	94.29	91.94	90.20	89.56	27.16	31.58
450	100.00	95.73	93.15	89.22	90.36	27.46	31.25
480	82.44	95.48	95.56	90.20	90.36	25.97	30.92
510	94.41	100.00	100.00	100.00	100.00	25.37	27.63
540	79.72	95.78	97.58	97.06	95.58	22.99	27.30

BW: body weight

ELW: eye lens weight

RM_1: root length of M_1

CM_1: crown height of M_1

Appendix 45. Some additional notes on statistical techniques employed:

Another method was considered to analyse the measurable data of some of the characters used (the body weight, head-body length, skull length, and the eye lens weight). This method employed the logarithmic transformation as an alternative to the arithmetic scheme. Measurements were converted to logarithms and plotted against age.

The resulting line was found to be two nearly rectilinears (Fig. 56). The first goes up steeply indicating fast growth, and the second was nearly horizontal because of the slow growth during this stage of life. This effect can be seen just as easily from the arithmetic plots , (Fig. 4, page 31).

The data did not give a linear logarithmic relationship, because the curve of growth is concave downward whereas the logarithmic function assumes an ever increasing rate of growth (Simpson _et al_, 1960). Therefore the logarithmic transformations were not used any more, and data were presented using the arithmetic scheme, though the mathematics of curvilinear functions are too complex to permit as precise and detailed an analysis as one might wish.

Simpson, G. G., Roe, A. & Lewontin, R. C. (1960). Quantitative Zoology. Harcourt, Brace and World, New York.

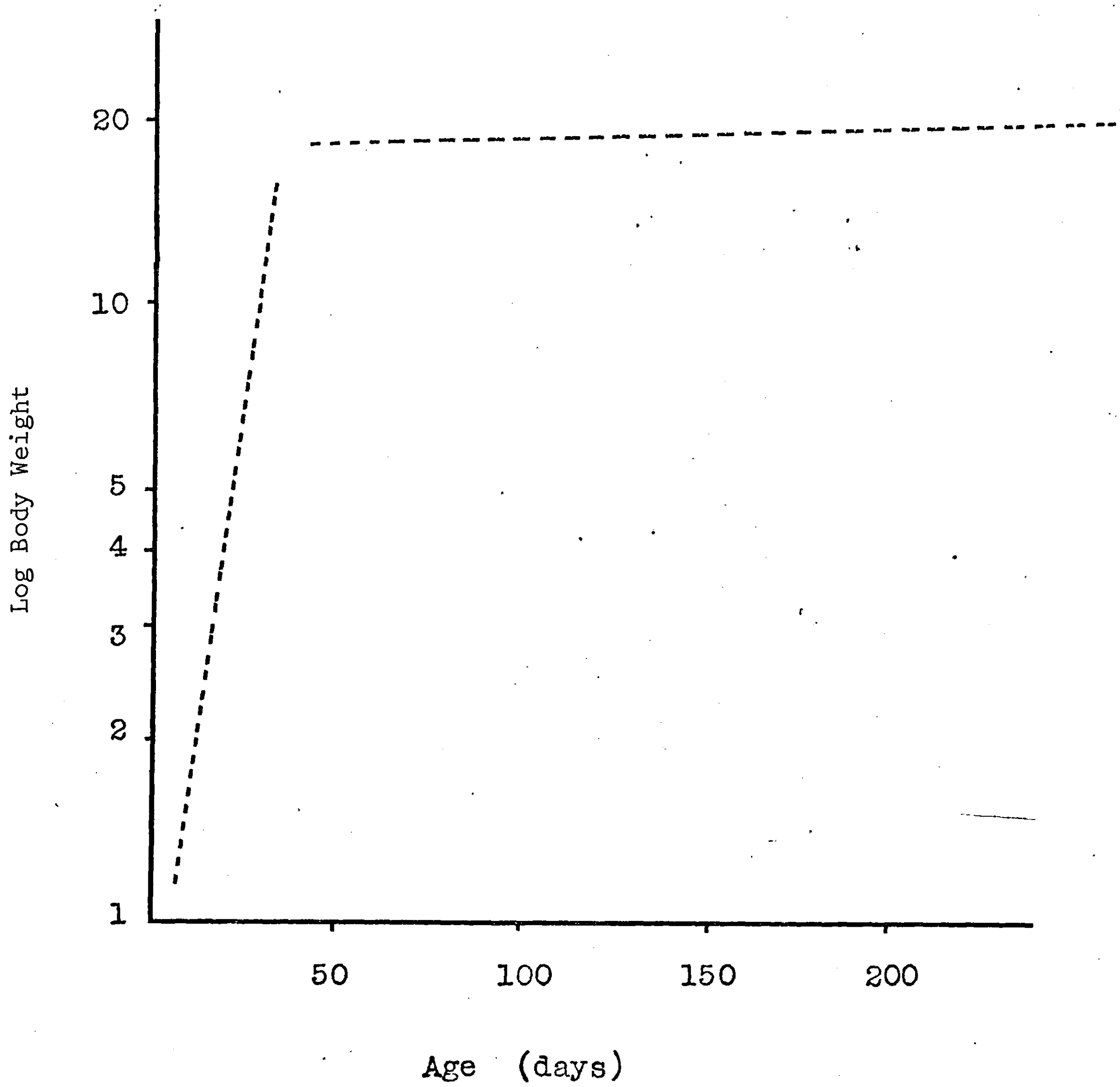

Fig. 56. A diagram showing the relation between age and logarithm of body weight of the mainland bank vole.

A scatter diagram which is the convenient way of displaying results does not give a reliable way of deciding whether there is a significant correlation between two variables. This is better explained statistically using the correlation coefficient. The equation for r expresses the relationship between the two variables in terms of the variances within each of them, and is a measure of how nearly the observed measurements approximate to a straight-line relationship. Time (age in the present study) can be used as one variable, as in this case there is no particular reason why it should not (Bishop, 1974).

The correlation coefficient between age and every measurable character was given in the text.

Since the growth curves for most of the measurements (body weight, body measurements, skull measurements, and eye lens weight) show two components - an early phase of rapid growth followed by a later phase of slow or no growth-, the correlation coefficient for each of these variables was calculated up to the point at which the change in phase occurs in order to show the rapid growth in early ages. The correlation coefficient then was calculated for the whole sample (from the age of 5 days to 18 months). This simple r has not been used in the present study for subsequent analyses, such as the multiple regression analysis which was used for instance, by Lidicker & MacLean (1969) for setting ageing equations for _Microtus californicus_. It was used in the present study only to provide a rough indication of the degree of correlation between each character and age.

The simple r value alone was not an acceptable index of correlation with age because it assumes a straight-line relationship between parameters, yet all the measurements obtained followed a curvilinear relationship with time, (though Lidicker & MacLean appear to have used a simple correlation coefficient, in a similar way as in the present study). Moreover it does not adequatdy reflect how variable each character is with age, thus the variability of each of them was calculated and represented by the value of the coefficient of variation (v). Again using v value alone to compare the degree of correlation is also not enough because it does not give any idea about the correlation of each character with age. It shows only how variable each character is. Hence when making comparisons between different methods of age determination, both factors were taken into account.