

## Morphological variability of a root vole population in high mountain habitats, Hardangervidda, South Norway

Janusz MARKOWSKI and Eivind ØSTBYE

Markowski J. and Østbye E. 1992. Morphological variability of a root vole population in high mountain habitats, Hardangervidda, South Norway. Acta theriol. 37: 117 - 139.

The variability of body and skull dimensions was examined in a population of the root vole, *Microtus oeconomus* (Pallas, 1776) from high mountain habitats, Hardangervidda, southern Norway. Morphometric analysis was made on 530 of 915 specimens obtained over an 8 year trapping period (1970 - 1978), taking into account sex, age class, season and population cycle. Sexual dimorphism was distinct in the oldest age group, in which males were significantly larger than females. The specimens from the peak phase were larger in body and skull dimensions (Chitty Effect). The influence of age structure on fluctuations in body size during the microtine cycles is discussed.

Department of Ecology and Vertebrate Zoology, University of Łódź, 90-237 Łódź, Banacha str. 12/16, Poland (JM); Department of Biology, Division of Zoology, University of Oslo, PO Box 1050, Blindern - Oslo 3, N-0316 Norway (EØ)

*Key words:* *Microtus oeconomus*, population cycle, Chitty Effect, body size, Norway

### Introduction

The study of morphological variation in mammals is widely used in investigations on the structure and function of a species and analysis of its evolutionary transformations (Mayr 1963, Yablokov 1966, Schwarz 1969). Mammalogists are particularly interested in different morphological characteristics as related to cyclic fluctuating populations of microtines (Chitty 1952, Zimmermann 1955, Krebs 1964, Krebs and Myers 1974, Boonstra and Boag 1987).

Microtine species with cyclic populations have showed a relatively repeatable pattern of changes in body size, growth, age structure, age of sexual maturity and length of breeding season (see Krebs and Myers 1974, Krebs 1978, Boonstra and Krebs 1979, and others). The characteristic feature of multiannual cycles is the occurrence of the largest specimens, particularly males, during the peak density - the Chitty Effect (Chitty 1952, Chitty and Chitty 1962, Krebs 1964, Krebs and Myers 1974, Boonstra and Krebs 1979, and others).

Chitty (1958, 1967) proposed a genetic-behavioral hypothesis for explaining this phenomenon. It assumes a genetic basis in spacing behaviour traits and alternating selection for different genotypes as populations increase and decline,



and has received close attention (Krebs 1964, 1966, 1978; Krebs *et al.* 1969, 1976; Taitt and Krebs 1985, see Krebs and Myers 1974 and Gaines 1985 for review). The necessary genetic heritabilities for body weight, growth rate, age and weight at sexual maturity which are indispensable for determining the Chitty hypothesis, have not, however, been reported (Boonstra and Boag 1987). Although the Chitty Effect remains an interesting phenomenon its relevance to density fluctuations is questionable (Lidicker 1988).

The purpose of this paper is analysis of variations in body and skull size in relation to sex, age, dynamics of seasonal generations and population density in a free-living population of root voles in mountain habitats.

### Study area

The study area is situated at Finse (60°36' N, 7°30' E) in the northwestern part of the Hardangervidda mountain plateau in South central Norway (Fig. 1). Elevation of the trapping area is 1200 – 1400 m a. s. l. and includes the low and mid-alpine zone. The climate is mountain influenced, with cool summers and mild winters, with high precipitation the year round (Østbye *et al.* 1975). The vegetation mosaic has many phytosociological associations (Østbye *et al.* 1975). Most of the area (83%) is covered by oligotrophic types of vegetation (Østbye *et al.* 1975).

Eight grids for trapping of small mammals were distributed in the gradient across the valley at Finse (Fig. 1). They were placed in four typical, relatively homogenous vegetation types: marshy

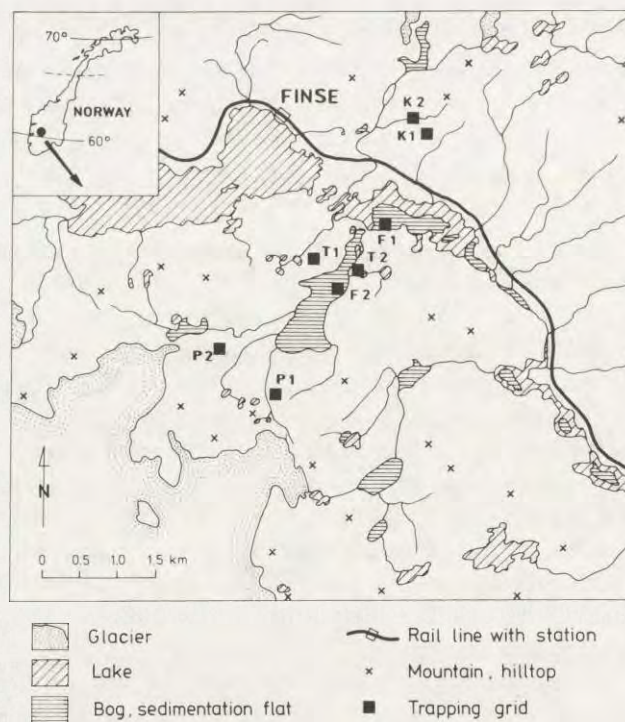


Fig. 1. Map of the study area at Finse.

ground on sediment flats in the valley bottom (2 grids: F1, F2), southern exposed eutrophic meadows (2 grids: K1, K2), northern exposed oligotrophic heath communities (2 grids: T1, T2) and pioneer communities (2 grids: P1, P2).

Each grid consists of 10 x 10 trap stations placed every 10 m. During the removal period, two snap traps were placed at each station and baited with wick or wool thread soaked in cooking oil. The trappings were carried out twice a year, just after snow melt in late June (so called "Spring sample"), and before regular snow fall in late August or early September ("Autumn sample"). The grids were worked for six days. In years with low density of rodents the trapping lasted only four days. Only three grids (K1, P1, T1) were used from 1970 through 1980. In years 1970 – 1972 five additional grids were established. In 1974 grid K2 was trapped instead of K1 due to other trapping experiments.

## Materials and methods

### Material

Specimens were obtained during the period 1970 – 1978. A total of 915 specimens (Table 1) of the root vole were collected (E. Østbye, unpubl.). The animals were sexed, measured and weighed. The eye lenses were removed and fixed in 10% formaldehyde and used to determine age (Hagen *et al.* 1980). For further biometric investigations the heads of all specimens were taken and the skulls were cleaned using papain enzyme. Only 530 skulls were used for statistical analysis (Table 1) due to the high number of broken skulls as a result of using snap traps.

Following Markowski (1980), the available material was divided into 5 age classes according to morphological descriptive characters, development of crests, obliteration of suture and eye lens

Table 1. Total number of trapped root vole and number of specimens biometrically analysed in sex and age groups.

Year and season	Total number caught	Age groups										Total analysed
		I		II		III		IV		V		
		M	F	M	F	M	F	M	F	M	F	
1970 S	401	2	5	2	1	3		2		11	10	216
1970 A		17	27	8	2	39	31	14	14	11	18	
1971 S	3											
1971 A												
1972 S	3						1					3
1972 A						2						
1973 S	126	2	2	2	1	3		1	1	6	3	86
1973 A		5	7	7		24	8	6	5	3		
1974 S	367	2	6	6	3	5	1	2	1	18	7	212
1974 A		23	30	10	11	22	21	1	5	21	17	
1977 S	10											
1977 A						3	1	2	2			8
1978 S	5					1			2	2		5
1978 A												
Total	915	51	77	35	18	102	63	28	30	71	55	530



weight: I – juveniles (up to one month), II – subadults (4 – 6 weeks), III – adults I (6 weeks to 3 months), IV – adults II (4 to 7 months), V – senex (> 7 months). The last age group consists of individuals caught in the second calendar year of their life.

#### Measurements and indices

The following four basic measurements were made: total length, head and body length (H & BL), hind foot length (HFL) and body weight  $\pm 0.5$  g (E. Østbye, unpubl.). The total length was omitted from statistical calculations as it is rarely used in biomorphological studies, whereas the tail length (TL), which was calculated as a difference between total and head and body length, was used for each specimen.

Ten linear measurements were made on the skulls Markowski (1980): 1. Condylbasal length (CbL), 2. Brain-case length (BcL), 3. Diastema length (DL), 4. Maxillary tooth row length (MxTRL), 5. Mandibular length (MdL), 6. Brain-case breadth (BcB), 7. Zygomatic breadth (ZyB), 8. Interorbital constriction (IC), 9. Rostrum breadth (RB), 10. Brain-case height between bullae (BcH). These abbreviations are used throughout in the text.

Basic statistical parameters: mean ( $\bar{x}$ ), standard deviation (SD), coefficient of variation (CV) were calculated for samples according to sex age classes and trapping periods. The differences between sexes were checked using the *t*-test. Variability within age groups and years was compared by computing the variance component for each skull measurement in one-way analysis of variance (Sokal and Rohlf 1981). All the calculations were made at the Computer Center of Łódź University using "Odra 1305" computer.

## Results

### Fluctuating density pattern

Cyclic variation in the density of the root vole is very distinct in the Hardan-gervidda area (Fig. 2). The population increased in 1969 and peaked in 1970. There was a rapid decline in the spring 1971, however, as only a few specimens were caught. Through 1972 the population density remained low, whereas in 1973 there was an increase. In spring 1974, the density was moderate and then reached a very high value in the autumn. During the winter of 1974/1975 a rapid decline

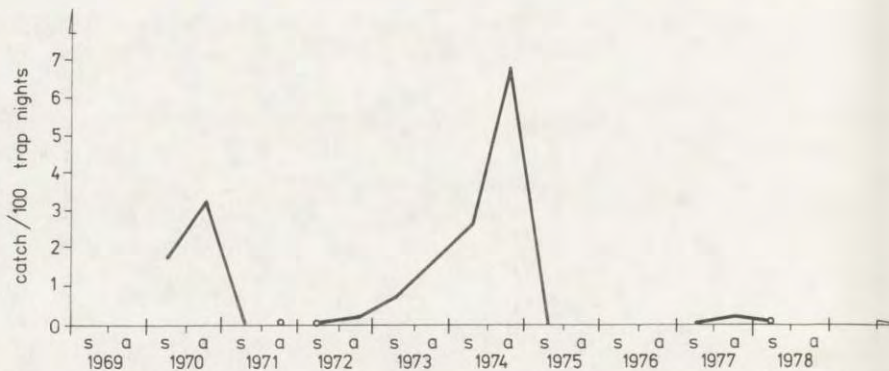


Fig. 2. Total captures of the root vole per 100 trap-nights for all trapping grids in spring and autumn. Open circle – single specimens.

was observed, and no root voles were caught in 1975 – 1976. In 1977, there was a slight increase in density to a pre-peak level in the autumn period. The population again declined during the winter of 1977/1978, and a few specimens were caught in the spring of 1978 (Fig. 2).

#### Sexual dimorphism

Sexual dimorphism is most clearly displayed in the oldest age group (senex), where the differences between mean values in most cases are highly statistically significant ( $p < 0.01$ ) (Table 2). These differences were smaller in younger classes, with only one measurement in class III. Males are statistically larger than females, except ZyB in class III. In our material no statistical differences were recorded between males and females or between age groups in the values of the coefficient of variation (two-way analysis of variance:  $F_{(\text{sex})} = 0.587$  ns,  $F_{(\text{age})} = 0.343$  ns,  $F_{(\text{interaction})} = 0.191$  ns, for body dimensions;  $F_{(\text{sex})} = 0.912$  ns,  $F_{(\text{age})} = 470$  ns,  $F_{(\text{interaction})} = 0.480$  ns, for skull dimensions. For females in age classes III and IV and males in age classes IV and V, almost all skulls and body dimensions are distinguished by their higher growth rates (Table 3).

#### Age differentiation

The results of one-way analysis of variance and Duncan multiple range test between all subsets of all age groups means in body and skull dimensions have shown statistically significant differences in most cases. There were some body measurements, such as tail, hind foot lengths and skull measurements (BcH, IC)

Table 2. Comparisons of differences between males and females in different age groups. \*, \*\* – differences significant at  $p = 0.05$  and  $p = 0.01$ , + mean values higher for females.

Measurements	Age groups				
	I	II	III	IV	V
Head and body length	**	**			**
Tail length					
Hind foot length	*			**	**
Body weight	**			**	**
Cbl		**			
Bcl		*			
DL	*	**			
MxTRL					
Mdl	*	*		**	**
BcB		*		**	
ZyB		*	+		**
IC				**	
RB					**
BcH					**



Table 3. Increase in body and skull dimensions in different age groups for males and females (%). The mean values for age group I were taken as 100%. M – males, F – females.

Measurements	Age groups							
	II		III		IV		V	
	M	F	M	F	M	F	M	F
H & BL	4.13	-0.56	9.60	29.95	28.16	34.07	35.36	38.43
TL	5.21	3.33	7.33	13.86	28.09	31.62	28.58	31.28
HFL	-2.11	2.76	0.65	3.32	5.85	3.30	3.87	2.99
Body weight	14.52	14.22	37.34	58.61	143.09	128.81	190.28	166.67
CbL	5.65	4.01	9.15	12.25	20.38	20.52	26.85	23.93
BcL	3.42	3.15	6.16	9.88	16.69	17.93	22.36	20.01
DL	4.12	2.42	7.72	10.35	19.37	19.55	27.43	23.02
MxTRL	2.51	1.39	4.89	4.49	10.69	8.62	12.63	11.41
MdL	3.34	2.26	6.06	8.86	15.91	16.14	21.60	20.17
BcB	2.63	1.03	4.75	6.37	13.64	12.19	18.52	16.84
ZyB	2.85	0.72	5.12	9.22	20.85	20.39	28.22	27.68
IC	2.40	2.08	1.92	2.35	5.61	2.17	3.76	3.15
RB	2.81	1.73	5.70	6.92	18.74	16.81	23.31	17.07
BcH	1.33	-0.40	1.64	2.95	7.46	6.15	8.42	6.90

Table 4. Results of analysis of variance in body and skull dimensions between five age groups (I – V) of males and females. Non-significant subsets of averages underlined.

	Males					Females				
	I	II	III	IV	V	I	II	III	IV	V
Body measurements										
H & BL	—	—				—	—			—
TL	—	—		—		—	—		—	—
HFL	—	—	—	—		—	—	—	—	—
Body weight	—	—				—	—			
Skull measurements										
Cbl										
BcL									—	
DL										
MxTRL	—			—		—				
MdL										
BcB	—	—				—				
ZyB	—	—				—				—
IC		—	—	—	—		—	—	—	—
RB						—			—	—
BcH	—	—	—	—		—	—		—	—

Table 5. Comparisons of significance of differences in mean values of body and skull dimensions in the spring and autumn generations in age groups using *t*-test at  $p = 0.05$ . Mean values higher in the spring generation are underlined. s – significant, ns – not significant.

Measurements	Age groups					
	Males			Females		
	I	II	III	I	II	III
H & BL		ns	ns	ns		
TL	s	ns	ns	ns		
HFL	s	ns	ns	s		
Body weight	ns	ns	ns	ns		
CbL			ns			
BcL			ns			
DL	ns	ns	ns	ns	ns	
MxTRL	ns	ns	ns	ns	ns	
MdL	ns	ns	ns	ns	ns	
BcB						
ZyB		ns	ns	ns		
IC	ns	ns	ns	ns	ns	
RB	ns	ns	ns	ns	ns	
BcH		ns	ns			

Table 6. Sex differences within each of the seasonal generations in adequate age groups (I – III) using *t*-test at  $p = 0.05$ . Mean values higher for males are underlined.

Measurements	Spring generation			Autumn generation		
	I	II	III	I	II	III
H & BL	ns		ns	s		ns
TL	s			ns		ns
HFL	ns			ns		ns
Body weight	ns			ns	s	ns
CbL				ns	s	ns
BcL				ns	ns	ns
DL		ns	ns	ns	ns	ns
MxTRL		ns	ns	ns	ns	ns
MdL		ns	ns	s	s	ns
BcB				ns	ns	ns
ZyB				ns	s	s
IC		ns	ns	ns	ns	ns
RB		ns	ns	ns	ns	
BcH				ns	s	ns



Table 7. Distribution of *Microtus oeconomus* individuals according to eye lens weight.

Year and season	Sex	Eye lens weight (mg)											
		> 1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	6.5
1969													
Spring	M		1		1				1				
	F		1	1					1	1			
Autumn	M	1	2	4	3	9	5		2				
	F	4	1	6	8	6	2	2	2				
1970													
Spring	M		7	6	4	1			3	7	14	5	4
	F	3	11	10	2		1	2	1	11	14	2	1
Autumn	M	2	20	41	47	50	28	12	4	5	13	5	9
	F	2	22	59	48	42	38	7	7	13	16	9	2
1973													
Spring	M	1	3	11	7			1	1	3	7		
	F	1	3	4					5		1	1	
Autumn	M		9	18	46	17	11	1			1		
	F		8	21	11	20	5	1		2			
1974													
Spring	M		7	16	11	3	1		1	10	17	3	
	F		6	18	10	1			6	14	6		
Autumn	M		5	31	27	22			1	3	10	12	
	F	1	13	36	22	13	7	1	3	10	10	3	1

Table 8. Percentage frequencies of males and females in the youngest and overwintering class of the root vole. \*, \*\* – differences significant at  $p = 0.05$  and  $p = 0.01$  between sexes within groups.

Eye lens weight	Years			
	1969 n = 64	1970 n = 610	1973 n = 228	1974 n = 370
up to 2.5 mg				
Male	26.7*	26.5**	30.7**	31.7**
Female	38.2	33.1	47.0	38.1
Male + Female	32.8	30.0	34.7	34.9
over 4.5 mg				
Male	10.0	24.0	8.6	30.3
Female	11.8	22.6	10.2	29.4
Male + Female	10.9	23.3	9.2	29.9



where the number of differences among means was lower. Also, the number of differences in means between the sexes was similar (Table 4).

#### Variability of seasonal generations

The *t*-test was used to check differences in means of the body and skull dimensions in the spring and autumn generations. Because the material from spring trapping periods was scarce the comparisons were limited. Both sexes were treated separately according to the differences in the growth rate of this species as documented by Kratochvíl and Rosický (1955), Karaseeva *et al.* (1957), Snigirevskaja (1961) and Markowski (1980). Statistically significant differences were shown in only three measurements. However, most means values of body and skull dimensions were higher for the spring specimens (Table 5).

The differences in mean values of body and skull dimensions between sexes within each of the generations were tested using the *t*-test at the  $p = 0.05$  level of significance. Limited possibilities to test the spring generation (too scarce material) precluded the occurrence of statistical differences. In the autumn generation most statistically significant differences were in the second age group, where males had higher mean values than females. In the other age classes most differences were not statistically significant; mean body and skull dimensions were, however, higher for females (Table 6).

#### Between - year differences

One way analysis of variance and Duncan test of equality of means were used to compare the mean values of body and skull measurements in subsequent years. Males and females were treated separately. Body dimensions, such as: body, tail and hind foot lengths were not recorded in 1974, so they were not used in the analysis of variance. Neither does the present analysis include the scarce material from 1977 and 1978.

The results obtained suggest few differences between the compared years. Hence, of 15 pairwise comparisons of body weight, only two were statistically significant for males and only two for females. Also, in the skull dimensions and quotient indices most comparisons were not statistically significant.

#### Weight of eye lenses

The distributions of the weight of eye lenses were bimodal for both sexes; however, they differed in their peak values. The first peak occurs at 2.5 mg, the second at 5.5 mg for females, and 3.0 and 6.0 mg for males (Fig. 3). The clear bimodality in the distribution of eye lens weights reflects the two major cohorts in the samples; overwintered and young of the year (see Table 7).

No intersexual differences in the distribution of eye lens weights were apparent (Kolmogorov-Smirnov test). However, restricting the sample to eye lens weight  $> 4.5$  mg, significant differences between the sexes were found in autumn 1973, spring 1974 ( $p < 0.05$ ) and for the whole year of 1974 ( $p < 0.01$ ). Interseasonal

differences in distributions of eye lens weights for each sexes were statistically significant ( $p < 0.05$ ) between years 1970 – 1974 and 1973 – 1974 in both sexes of young animals.

Percentage frequencies of overwintering specimens were more variable than the frequencies of quite young ones (up to 2.5 mg of eye lens weight). Particularly high frequencies of overwintering specimens were noted for the peaks in 1970 and 1974 (Table 8). The differences in frequencies between males and females of overwintering animals did not exceed 2%, while for the young ones females, lens weights were higher, and statistically significantly so ( $p < 0.05$ ), in the years of increased densities, when the domination of females was observed (see Table 8).

#### Body weight

The bimodality of the body weight frequency distribution in both sexes reflects the distinction between overwintering and current years' individuals. The first peak occurs at 20 g for both sexes, the second peak occurs at 40 g for females and at 55 g for males (Fig. 4a).

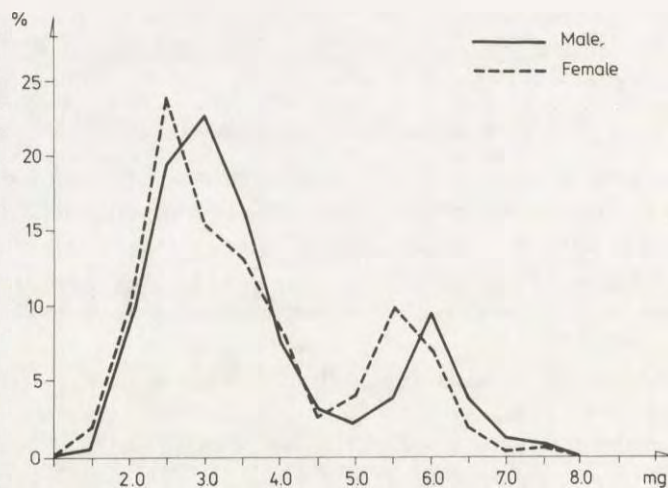


Fig. 3. Frequency distribution of dry eye lens weight in males and females.

Table 9. Statistical description of body weight in overwintering females in spring trapping.

Year	N	Min. – max.	$\bar{x}$	SD	CV
1969	16	28.0 – 63.0	42.53	9.86	23.18
1970	41	25.0 – 63.0	44.59	7.35	16.48
1973	10	37.0 – 57.0	43.78	5.78	13.21
1974	25	34.0 – 67.0	49.24	7.11	14.44



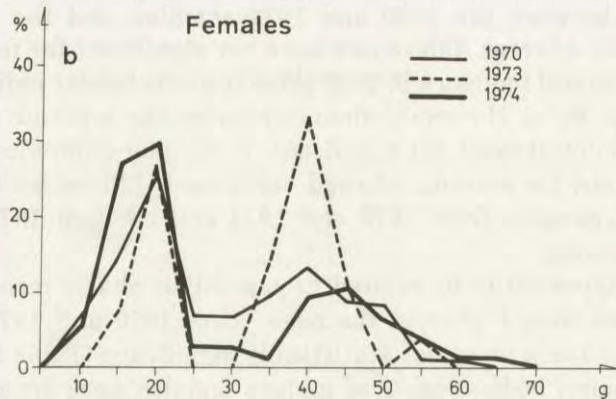
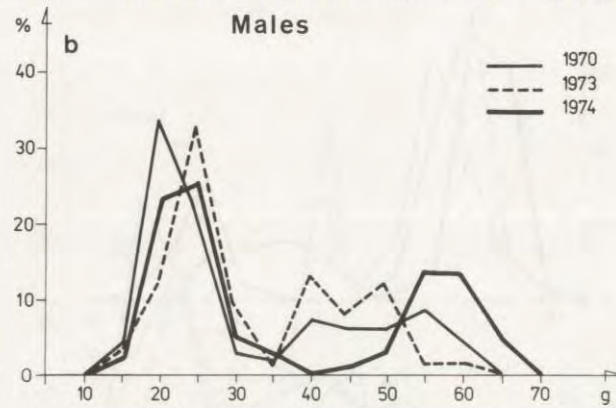
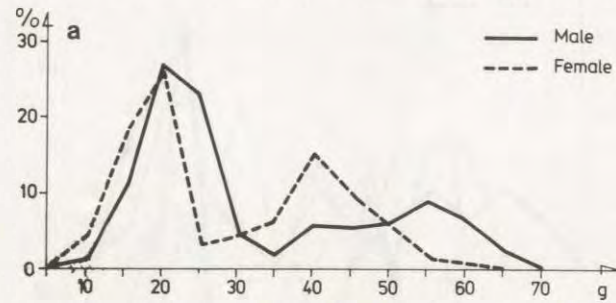


Fig. 4. Frequency distribution of body weight for males and females (a), in successive study years for males and females (b), in trapping seasons of successive years for males (c), and females (d). This Figure is continued on next pages.

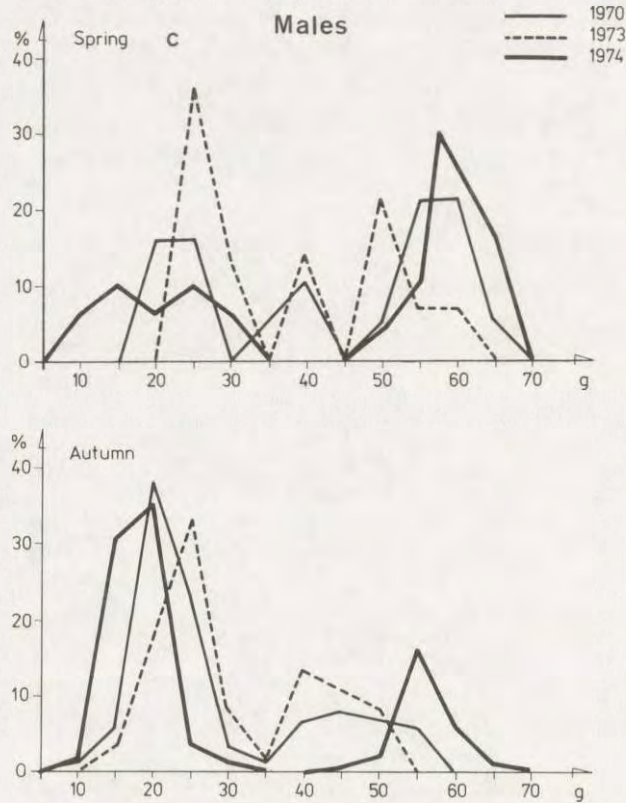


Fig. 4c, continued.

Body weight distributions differed significantly in the Kolmogorov-Smirnov tests ( $p < 0.05$ ) between the 1973 and 1974 samples, and the 1970 and 1974 samples for males, whereas differences were not significant for females.

There was a general tendency in both sexes towards lighter individuals in 1973 than in 1974 (Fig. 4b, c). However, when comparing the separate age classes, the differences were in most cases not significant. Testing for differences between body weight distributions by seasons, showed significant differences ( $p < 0.05$ ) only between autumn samples from 1970 and 1974 and between 1973 and 1974 for males and for females.

Body weight appeared to be related to population phase; mean body weights of mature females were higher in the peak years 1970 and 1974, however the differences among them were not statistically significant (Table 9). In the same peak years minimum body weights of mature females were lowest. The highest body weights were found during the maximum peak density (1974). Monthly trappings from December 1973 to May 1974 (E. Østbye, unpubl.) showed loss of body weight during autumn and winter periods (Fig. 5).



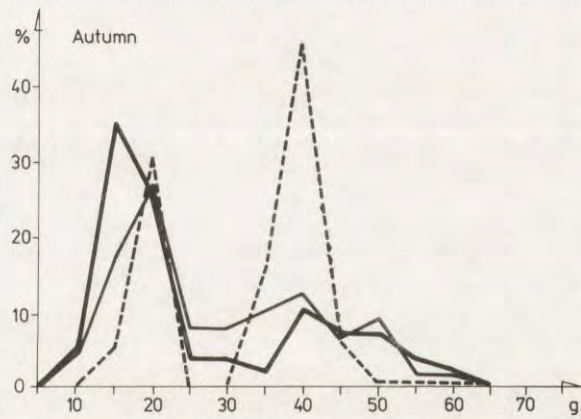
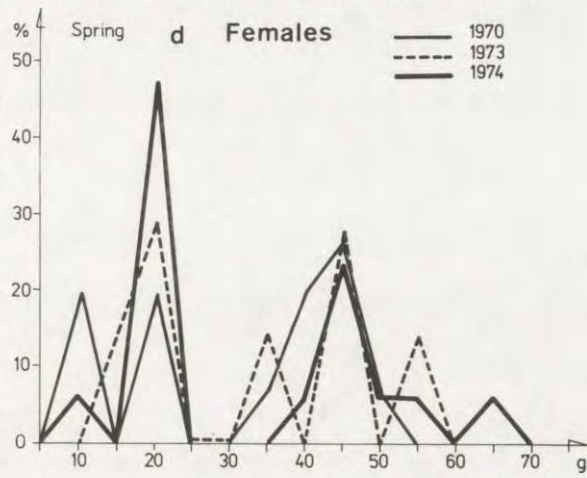


Fig. 4d, concluded.

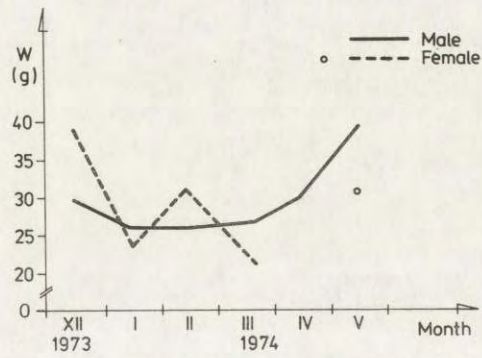


Fig. 5. Changes in mean body weight during the winter season for males and females.

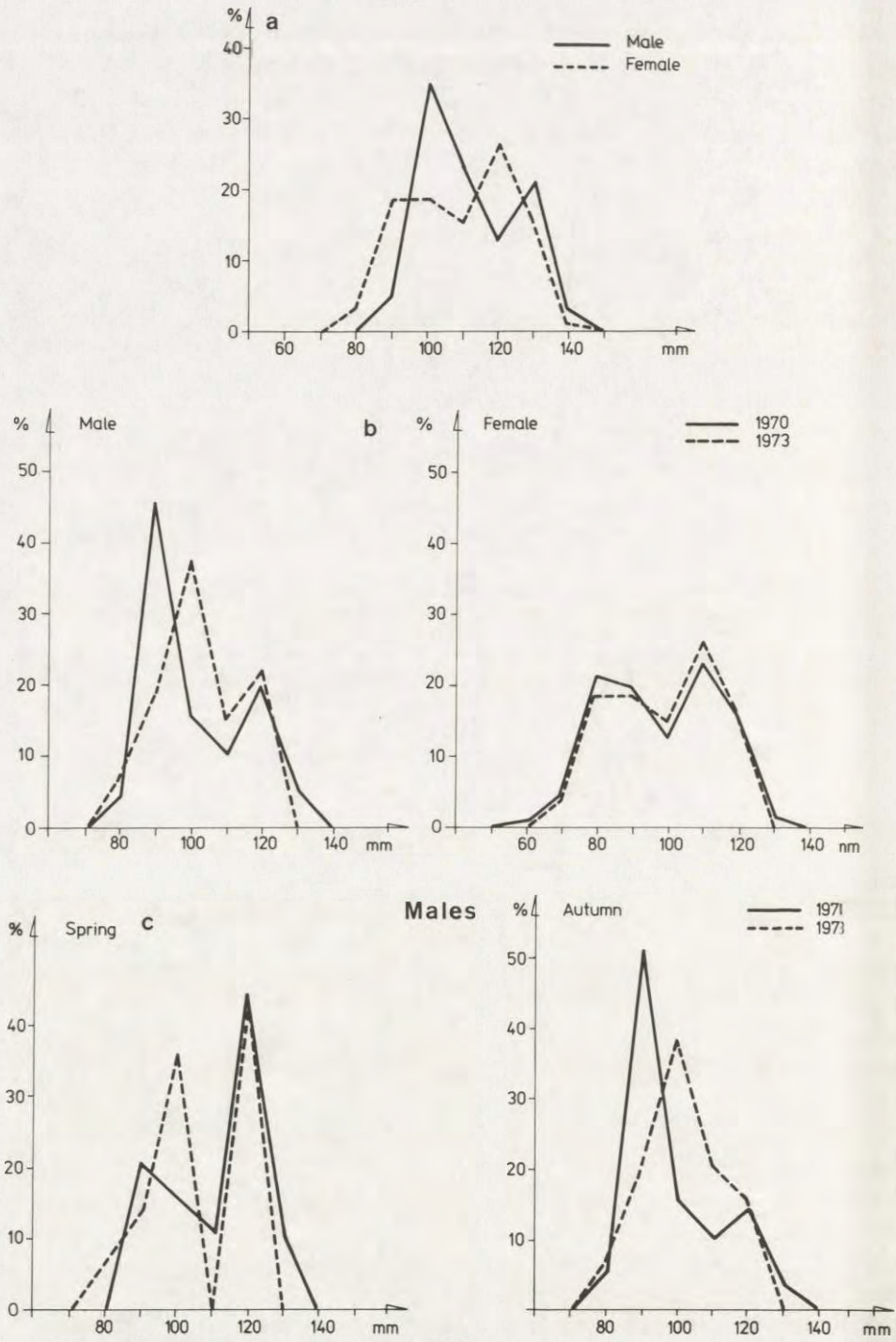


Fig. 6.



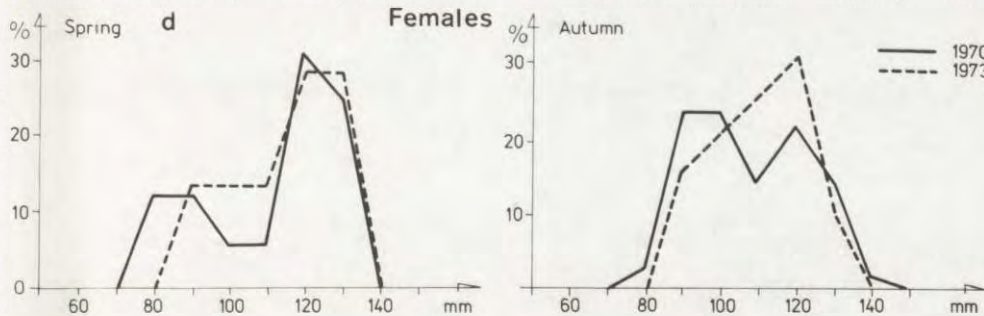


Fig. 6. Frequency distribution of body length for males and females (a), in successive study years for males and females (b), in trapping seasons of successive years for males (c), and females (d).

#### Body length

The distributions of the body length frequencies were bimodal for both sexes: the first peak at 90 mm and 100 mm, the second peak at 120 mm and 130 mm for females and males, respectively (Fig. 6a). As body measurements were not taken in 1974 *inter* a years comparisons were restricted to 1970 and 1973. The distributions of body length frequencies for both years were similar for females, while in males, the first modal peak in 1973 was higher than in 1970 (Fig. 6b).

In the spring sample the bimodal distribution in body length was distinct for males, but less so for females. The autumn samples from 1970 and 1973 differed; body length distribution was bimodal in 1970, but uni-modal in 1973 for both sexes (Fig. 6c, d).

Differences between distributions of body length tested by the Kolmogorov-Smirnov test showed no significant differences between years and seasons of years for each of the sexes.

#### Condylbasal length

The distributions of the condylbasal length frequencies showed the same bimodal distribution as did the two previously analysed parameters, though the first peak was not as distinct as for body weight and body length distribution. The second peak for condylbasal length was at 26 mm for females and 28 mm for males (Fig. 7a).

CbL distributions differed significantly in the Kolmogorov-Smirnov tests ( $p < 0.05$ ) between the 1970 and 1974 samples, and autumn samples the 1970 and 1974 for females, whereas no statistical differences were found for males. Cb length distributions were significantly different ( $p < 0.05$ ) between sexes in spring, whereas no significant differences were found in the autumn seasons.

The distributions of this measurement in successive years differed for both sexes, not only by the value of peaks but also by the character of distribution (Fig. 7b). This is due to a large number of autumn specimens (Fig. 7c, d for comparisons).

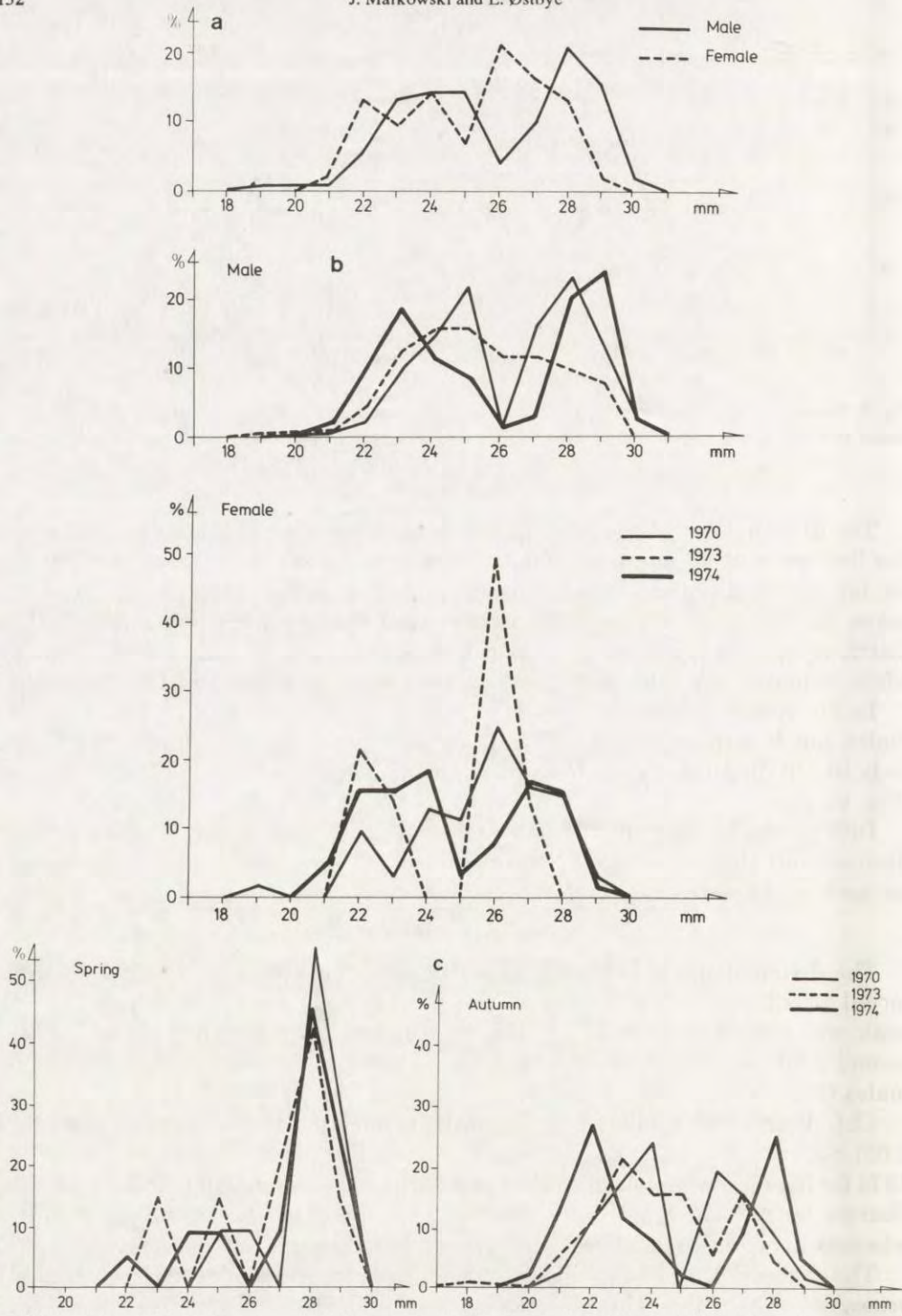


Fig. 7.



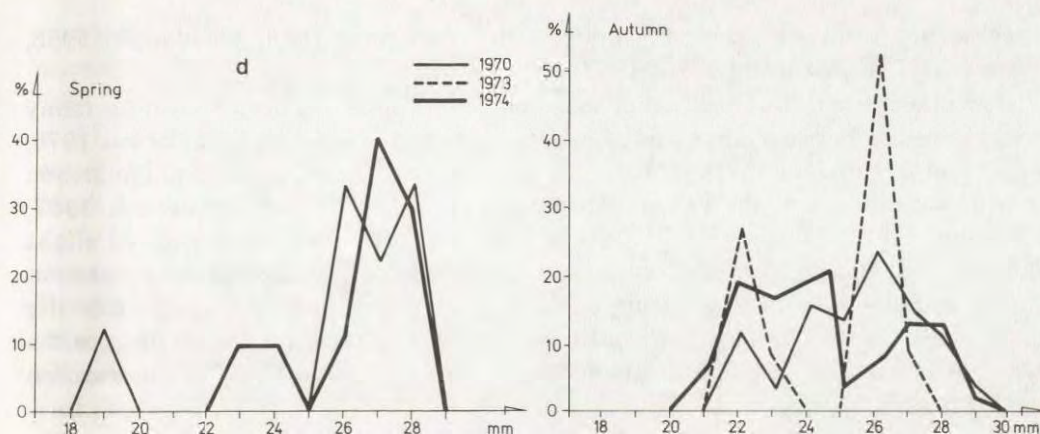


Fig. 7. Frequency distribution of condylobasal length for males and females (a), in successive study years for males and females (b), in trapping seasons of successive years for males (c), and females (d).

### Discussion

Although the data on sex dimorphism in the root vole are divergent, most authors have shown larger body and skull dimensions for males (Dehnel 1946, Ehik 1953, Bauer 1953, Kratochvíl and Rosický 1955, Saint-Girons and Mazák 1971, Bashenina 1977, Markowski 1980); see however Wasilewski 1956 and Kanep 1967.

Kratochvíl and Rosický (1955) have suggested that larger males were a result of better survival allowing them to reach larger body size. The different survival of both sexes of the root vole due to season and phases of populational cycles is indicated by Markowski (1980). Analysis of age structure of the study population, based on eye lens weight only, though limited to increase and peak phases, has shown that the overwintering males are older than females (see Table 7). This supports Kratochvíl and Rosický's thesis. This phenomenon is well known for other microtine species with fluctuating populations (Chitty and Phipps 1966, Krebs and Myers 1974), though males do not survive better than females in all cases (Krebs and Myers 1974, Beacham 1979).

Body size of the root vole is affected by other factors such as time of birth, which is closely associated with sexual maturity (Karaseeva *et al.* 1957, Bojkova and Bojkov 1971 after Panteleyev and Terechina 1976, Wasilewski 1956, Schwarz *et al.* 1964, Markowski 1980). Recently, Bondrup-Nielsen and Ims (1990) presented a reversed sexual size dimorphism hypothesis in microtines. They suggest that the relationship between home range size and body weight dimorphism reflects different selection pressures on males and females in competition for resources.

Thus sex dimorphism could be viewed relative to the conditions in which a given population occurs. It would then appear that ignoring the above mentioned facts may lead to discrepancies in the data on the sex dimorphism of some vole

species (see Ruprecht 1974, Pantaleyev and Teerchina 1976, Wasilewski 1956, Kanep 1967, Gębczyńska 1964, 1967).

Morphological differentiation of seasonal generations has been shown for many rodent species to occur at regular intervals (Schwarz *et al.* 1964, Anderson 1970, and others). Previous investigations on the root vole supported this phenomenon in different parts of its range (Karaseeva *et al.* 1957, Schwarz *et al.* 1967, Pjastolova 1971, Markowski 1980), whereas the study population showed slight differentiation. This results from a poor representation of the spring generation in the samples because the spring samples were predominated by overwintering specimens. The individuals born in the spring were usually immature despite the fact that their body and skull dimensions were larger than those of the autumn generation.

Table 10. Cumulative percentage increase in selected body and skull dimensions in the root vole in different age classes (both sexes) in relation to the trapping year. The mean values for age class I were taken as 100%.

Measurements	Sex	Age classes			
		II	III	IV	V
1970					
Body weight	M	13.8	23.5	132.7	168.9
	F	19.1	54.7	124.4	167.7
Head & Body length	M	2.2	5.3	28.7	34.7
	F		20.1	34.3	41.5
CbL	M	9.5	7.7	19.9	25.0
	F		14.5	22.9	26.4
MdL	M	3.2	5.0	15.5	20.9
	F		7.7	13.6	18.8
1973					
Body weight	M	9.1	37.4	88.4	127.6
	F	14.9	92.7	102.6	123.4
Head & Body length	M	6.4	16.0	26.2	36.7
	F	2.7	22.6	23.6	28.9
CbL	M	4.0	10.4	19.0	23.4
	F	3.6	15.7	16.2	17.5
MdL	M	4.9	7.8	13.3	22.3
	F		9.5	12.3	16.0
1974					
Body weight	M	11.9	32.4	243.3	238.2
	F	13.6	38.8	147.8	182.5
CbL	M	5.7	8.6	18.8	28.2
	F	3.4	9.5	21.5	24.0
MdL	M	3.0	5.9	17.3	22.4
	F	4.7	9.3	20.0	22.6



The root vole at Finse was found to lose body weight during the autumn and winter (Fig. 5). This is well known for other microtine species (Karaseeva *et al.* 1957, Schwarz *et al.* 1964, Brown 1973, Iverson and Turner 1974, and others), and has been called the Dehnel phenomenon occurring as an adaptation to winter conditions, in which a smaller body size may be favourable (Schwarz 1962, Mezhzherin 1964). Tast (1972) attributed the loss of body weight from autumn to early winter in a root vole population in north Finland to higher mortality in sexually mature individuals from the previous summer. On the other hand Beacham (1980) found that body weight increased during a pre-peak winter in *Microtus townsendii*. Thus, winter weight loss in voles is not a general feature of all microtine species during populational cycles. Also, winter breeding, although rather rarely noted in root vole populations (Tast 1976, Hagen *et al.* 1975), could cause increased body weight.

Chitty (1952) was the first to describe peak populations of voles, typically containing 20 – 30% of adults, especially males, which are larger than adults during low or declining populations. This phenomenon, known as The Chitty Effect, has been regarded as a characteristic feature of multiannual cycles in microtines (Chitty and Chitty 1962, Krebs 1964, Krebs and Myers 1974, Boonstra and Krebs 1979, Taitt and Krebs 1985). The larger specimens are not only older or fatter individuals, but show skeletal change (Zimmermann 1955, Krebs 1964).

Chitty (1967) suggested that this phenomenon could be based on genetic polymorphism for body size and that large individuals were selected during population increases and peaks. Gaines (1985) concluded, however, that such changes seemed to be an effect, not a cause of density changes. Also Boonstra and Boag (1987) showed that the heritabilities of morphological traits are too low for natural selection to produce the body size-change syndrome characteristic of microtine cycles.

Krebs and Myers (1974) presented three possible ways of relating changes in body size to population density: 1) during the increase and peak phases voles live longer and attain maximum body size; 2) voles grow more rapidly during increase and peak phases than during decrease phases (this assumes that animals of the same age are larger in increase and peak phases); 3) the growth rate of young specimens may be identical in each year of the population cycle, but their maximum weight may differ with cycle phases.

The first hypothesis associated with changes in age structure is based on differential survival of male and female cohorts. Our data indirectly support (analysis of given classes of eye lens weight, percentages) greater survival, especially of males at the peak phase of density (Table 7). Despite many controversial opinions about survival, numerous data support better survival in the increase and especially peak phase (see Krebs and Myers 1974, Beacham 1979, and others). Vole body size increased from increase phase to the peak density (Chitty Effect) and the higher the peak, the larger the body size and higher the percentage frequencies of overwintering individuals (Table 8). A similar effect was



recorded by Markowski (1990) in the fluctuating population of the root vole in a drained sphagnum bog (Augustów Forest, northeastern Poland) before its numbers decreased nearly to extinction.

In our case the second and third hypotheses are difficult to verify due to the way the material was collected. The recorded higher increases in many body and skull dimensions in the years of peak density (Table 10) might be attributed to variability of growth rates of overwintering and current years' individuals. The specimens of class II and III have lower growth rates in peak years. However, the possibility of influence of season (birth time) has to be considered and time of sexual maturity and data on instantaneous growth rates would be indispensable in solving this problem. Some of the observed variabilities in body size and other biological characters in the peak density, such as: growth rates of young specimens, mean body weight of sexually mature overwintering females (Table 9) are partially adjusted to the  $\alpha$ -selected types hypothesis (Stenseth 1978).

Karaseeva *et al.* (1957) in their study on the root vole population, and also other studies on microtine species (Krebs 1969, Krebs *et al.* 1973, Krebs and Myers 1974), attributed the highest growth rates to increase and peak phases. Modelling of small rodents' populational cycles at Finse in previous years Hagen *et al.* (1975) determined for young voles that the maximum growth rates were lower and growth was much reduced in winter. For adults the growth rate is much lower and seems to be stable during the summer and autumn. Beacham (1980) in turn demonstrated that individuals of *Microtus townsendii* under 40 g had the same growth rates in 3 populational phases. As a result of this body size is an effect of various asymptotic body weights.

#### Conclusions

The Finse root vole population showed distinct 3 – 4 year density cycles where the magnitude of peaks differed greatly (Fig. 2). Peaks are usually reached in the autumn, and the population crashed during the winter. The increase phase may last for a year with its density peak reached in next calendar year.

Sexual dimorphism manifested itself distinctly in mature individuals. Males showed greater body and skull dimensions as a result of their better survival.

Vole body size increased from the increase phase to peak density (Chitty Effect) and the higher the peak, the larger is the body size and higher percentage frequencies of overwintering individuals (Table 8).

Acknowledgements: Nils C. Stenseth and Rolf A. Ims are thanked for commenting on an earlier draft of this manuscript. We are also indebted to Tom Warren for correcting English.

#### References

- Anderson P. K. 1970. Ecological structure and gene flow in small mammals. Symp. zool. Soc. Lond. 26: 299 – 325.  
Bauer K. 1953. Zur Kenntnis von *Microtus oeconomus* mehelyi Ehik. Zool. Jb. 82, 1/2: 70 – 94.



- Bashenina N. V. 1977. Puti adaptacii myshevidnykh gryzunov. Nauka. Moskva: 1 – 352.
- Beacham T. D. 1979. Survival in fluctuating populations of the vole, *Microtus townsendii*. Can. J. Zool. 57: 2375 – 2384.
- Beacham T. D. 1980. Demography of declining populations of the vole, *Microtus townsendii*. J. Anim. Ecol. 49: 453 – 464.
- Boonstra R. and Boag P. T. 1987. A test of the Chitty hypothesis: inheritance of life-history traits in meadow voles *Microtus pennsylvanicus*. Evol. 41: 929 – 947.
- Bondrup-Nielsen S. and Ims R. A. 1990. Reversed sexual dimorphism in microtines: are females larger than males or are males smaller than females? Evol. Biol. 4: 261 – 272.
- Brown E. B. III. 1973. Changes in patterns of seasonal growth of *Microtus pennsylvanicus*. Ecology 54: 1103 – 1110.
- Chitty D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936 – 39. Phil. Trans. R. Soc., ser. B. 236: 505 – 552.
- Chitty D. 1958. Self regulation of numbers through changes in variability. Cold Spring Harb. Symp. Quant. Biol. 22: 277 – 280.
- Chitty D. 1967. The natural selection of self-regulatory behaviour in animal populations. Proc. of the Ecol. Society of Australia 2: 51 – 78.
- Chitty H. and Chitty D. 1962. Body weight in relation to population phase in *Microtus agrestis*. Symp. Theriologicum, Brno, 1960: 77 – 86.
- Dehnel A. 1946. Przyczynek do znajomości przedstawicieli *Microtus* Schrank z Polesia i Wileńszczyzny. Fragm. Faun. Muz. Zool. Pol. 5: 1 – 24.
- Ehik G. 1953. The occurrence of the root vole (*Microtus oeconomus* (Pall.)) at the Kisbalaton. Ann. Hist.-Natur. Mus. Nat. s. nova, 3: 521 – 526.
- Gaines M. S. 1985. Genetics. [In: Biology of New World Microtus. R. H. Tamarin, ed.]. Amer. Soc. Mammal., Stillwater. OK.
- Gębczyńska Z. 1964. Morphological changes occurring in laboratory *Microtus agrestis* with age. Acta theriol. 9: 67 – 79.
- Gębczyńska Z. 1967. Morphological variability of *Lagurus lagurus* (Pallas, 1773) in laboratory conditions. Acta theriol. 12: 535 – 543.
- Gourley R. S. and Jannett F. J. 1975. Pine and montane vole age estimates from eye lens weight. J. Wildl. Manage. 39: 550 – 556.
- Hagen A., Kjølvik S., Liestøl K., Østbye E., Skar H.-J. and Swartzman G. 1975. Reports from the High Mountain Ecology Research Station, Finse, Norway. A simple ecosystem-model with emphasis on small rodents. University of Oslo: 1 – 104.
- Hagen A., Stenseth N. C., Østbye E. and Skar H.-J. 1980. The eye lens as an age indicator in the root vole. Acta theriol. 25: 39 – 50.
- Iverson S. L. and Turner B. N. 1974. Winter weight dynamics in *Microtus pennsylvanicus*. Ecology 55: 1030 – 1041.
- Kanep S. V. 1967. Opyt biometricheskogo issledovanya priznakov cherepa nekotorykh blizkikh vidov serykh polevok fauny SSSR. Acta theriol. 12: 111 – 134.
- Karaseeva E. V. Narskaja E. V. and Bernstein A. D. 1957. Polevka-ekonomka, obitayushchaya v okrestnostakh ozera Nero Jaroslavskoy oblasti. Biull. MOIP, 62: 5 – 18.
- Kratochvíl J. and Rosický B. 1955. Hraboš severní (*Microtus oeconomus*), relikv z doby lodové v CSR. Prace Brněnské Zaklady ČAV. 27: 33 – 72.
- Krebs C. J. 1964. Cyclic variation in skull-body regression of lemmings. Can. J. Zool. 42: 631 – 643.
- Krebs C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. 36: 273 – 273.
- Krebs C. J. 1978. A review of the Chitty hypothesis of population regulation. Can. J. Zool. 56: 2463 – 2480.
- Krebs C. J. and Myers J. H. 1974. Population cycles in small mammals. Adv. Ecol. Res. 8: 267 – 399.



- Krebs C. J., Keller B. L. and Tamarin R. H. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology* 50: 587 – 607.
- Krebs C. J., Gaines M. S., Keller B. L., Myers J. H. and Tamarin R. H. 1973. Population cycles in small rodents. *Science* 179: 35 – 41.
- Krebs C. J., Wingate J., Ledne J., Redfield J. A., Taitt M. and Hillborn R. 1976. *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. *Can. J. Zool.* 54: 79 – 95.
- Lidicker W. Z., Jr. 1988. Solving the enigma of microtine cycles. *J. Mammal.* 69: 225 – 235.
- Markowski J. 1980. Morphometric variability in a population of the root vole. *Acta theriol.* 25: 155 – 200.
- Mayr E. 1963. Populations, species and evolution. The Belknap Press, Harvard Univ. Press, Cambridge: 1 – 779.
- Mezherin V. A. 1964. Javlenie Denela i jego vozmozhnoye obiasnienie. *Acta Theriol.* 8: 95 – 114.
- Morris P. 1972. A review of mammalian age determination methods. *Mamm. Rev.* 2: 69 – 104.
- Ognev S. I. 1950. Zveri SSSR i prilzhajschikh stron. vol. 7. Gryzuny Izd. Akad. Nauk SSSR, Moskva-Leningrad: 1 – 706.
- Østbye E., Berg A., Blehr O., Espeland M., Gaare E., Hagen A., Hesjedal O., Hagvar S., Kjelvik S., Lien L., Mysterud I., Sandhaug A., Skar H.-J., Skartveit A., Skre O., Skogland T., Sollhoy T., Stenseth N. C. and Wielogolaski F. E. 1975. Hardan-gervidda, Norway. [In: Structure and function of tundra ecosystems. T. Rosswall and W. O. Heal, eds]. *Ecol. Bull. Stockholm*, 20: 225 – 264.
- Pantaleyev P. A. and Terechina A. N. 1976. Issledovanya vnutripopulyacyonnoy izmenchivosti na primere vodyanoy polevki. *Fauna i ekologija gryzunov.* 13: 99 – 163.
- Pjastolova O. A. 1971. Polevka-ekonomka. *AN Nauk SSSR, Ural. Fil. Trud. Inst. Ekol.* 80: 127 – 149.
- Pucek Z. 1963. Seasonal changes in brain-case of some representatives of the genus *Sorex* from the Palearctic. *J. Mammal.* 44: 523 – 536.
- Ruprecht A. L. 1974. Craniometric variations in central European populations of *Ondatra zibethica* (Linnaeus, 1776). *Acta theriol.* 19: 436 – 507.
- Saint-Girons M.-C. and Mazák V. 1971. Donneés morphologique sur queleques micromammiferes en Laponie. *Z. Säugetierk.* 36: 179 – 190.
- Schwarz S. S. 1962. Morfologicheskiye i ekologicheskiye osobiennosti zemloroyek na kraynem severnom predele ich rasprastraniyena. *Tr. In-ta Biol. Ural. Fil. AN SSSR.* 29: 45 – 51.
- Schwarz S. S. 1969. Evoluonnaya ekologiya zhivotnykh. *AN SSSR Ural. Fil. Sverdlovsk:* 1 – 198.
- Schwarz S. S., Pokrovskij A. N., Istchenko V. G., Oljenev V. G., Ovtschinnikova N. A. and Pjastolova O. A. 1964. Biological peculiarities of seasonal generations of rodents with special references to the problem of senescence in mammals. *Acta theriol.* 8: 11 – 41.
- Schwarz S. S., Bolshakov V. N., Olenjev V. G., Ovtschinnikova N. A. and Pjastolova O. A. 1969/70. Population dynamics of rodents from northern and mountain geographical zones. [In: Small mammals populations. K. Petruszewicz and L. Ryszkowski, eds]. PWN, Warszawa: 187 – 201.
- Snigirevskaja E.M. 1961. Nabludenja nad polevkoj-ekonomkoj na ostrovach sredniej Volgi. *Tr. Zool. In-ta. AN SSSR.* 29: 137 – 155.
- Sokal R. R. and Rohlf J. F. 1984. *Biometry.* W. H. Freeman and Company, San Francisco: 1 – 859.
- Stenseth N. C. 1978. Demographic strategies in fluctuating populations of small rodents. *Oecologia* 33: 149 – 172.
- Taitt M. J. and Krebs C. J. 1985. Population dynamics and cycles. [In: *Biology of New World Microtus.* R. H. Tamarin ed.]. *Spec. Publ. Amer. Soc. Mamm.* 8: 567 – 620.
- Tast J. 1972. Annual variations in the weight of root voles, *Microtus oeconomus*, in Finish Lapland. *Aquilo (ser. zool.)* 15: 25 – 32.
- Tast J. 1976. Winter breeding of the root vole, *Microtus oeconomus*, in 1972/73 at Kilpisjärvi, Finish Lapland. *Ann. Zool. Fenn.* 13: 174 – 178.



- Tast J. 1982. *Microtus oeconomus* (Pallas, 1776) – Nordische Wühlmaus, Sumpdmaus. [In: Handbuch der Säugetiere Europas. J. Niethammer and F. Krapp, eds]. Bd 2/1. Rodentia: 374 – 396.
- Wasilewski W. 1956. Untersuchungen über die Veränderlichkeit des *Microtus oeconomus* Pall. in Białowieża – Nationalpark. Anns. Univ. M. Curie-Skłodowska C. 9: 355 – 386.
- Zimmermann K. 1942. Zur Kenntnis von *Microtus oeconomus* (Pallas). Arch. f. Naturgesch. Leipzig. 11: 174 – 197.
- Zimmermann K. 1955. Körpergröße und Bestandsichte bei Feldmaus (*Microtus arvalis*). Z. Säugetierk. 20: 114 – 118.
- Yablokov A. V. 1966 (Orig. in Russian) 1974. Variability of Mammals (Izmenchivost' Mlekopitayushchikh). Revised ed. Amerind Publ. Co. Pvt. Ltd., New Delhi: XV + 1 – 350.

Received 26 February 1992, accepted 29 June 1992.