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Morphological variation and population structure of Finnish muskrats, Ondatra zibethica (L.)

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The morphological variation and population structure of muskrats were studied using muskrat carcasses (n=637) collected in spring from trappers in four areas in Finland. In the cohort born during the previous summer ("young"), males were larger than females (body and carcass weight, skull length); in animals that were one year older ("old"), sexual dimorphism was less prominent in weight but significant in skull length. Tooth wear was greater in males (young), resulting in lower molar index values. Muskrats showed greater body dimensions during the first half of the trapping season (April) than during the second half (May), probably because of intraspecific competition (social dominance).

The animals differed in size and molar wear between the localities and also between several habitats within a local population. Large size correlated with low molar wear, both characteristics depending on the availability and quality of food in the habitat. In order to describe habitat suitability, growth index values were calculated by dividing the carass weight by the amount of the tooth wear.

The relative densities of muskrat populations were highest and the animals were largest and had the highest growth indices in habitats with a good supply of high quality food. In southern Finland *Scirpus lacustris* is a valuable food for muskrats. Besides macrophyte species composition, the animal condition depend on mussel supply and on water level fluctuations (especially combined with a shallow waterside profile). Muskrats of largest size and high growth index were trapped in rivers with high diversity and abundance of preferential food plant species, relativelity good mussel supply and moderate water level fluctuations.

Most (91 %) individuals in the spring populations were young; 9 % were one year older. Only one individual seemed to have overwintered three times. Males predominate over females in catch numbers in both cohorts. The sex ratio remained constant during the spring trapping period.

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1. Introduction

The muskrat (*Ondatra zibethica* (L.)) was introduced into Finland as a valuable fur-bearing animal in the 1920s and 1930s, whereafter it rapidly inhabited a wide spectrum of waters throughout the whole country, excluding only the poorest lakes and rivers in northernmost Lapland (Artimo 1960). Because of Artimo's (1949, 1952, 1960) extensive study the process of acclimatization and the general ecology of the muskrat in Finland are reasonably well known. His data were mainly based on inquiries and field observations (investigation of muskrat nests and feeding platforms), while the analysis of trapped animals was less important. The same is also true of the extensive ecological muskrat studies by Danell (1977a, b, 1978a, b, 1979) in northern Sweden. However, analysis of the variation in body dimensions and other morphological characteristics of muskrats is important for assessing the effect of environmental factors on muskrat populations.

Population turnover rate, proportion of females and the number of offspring produced per female are central variables in estimating the productivity of mammalian populations. The two former aspects will be discussed in this study; the third one forms a topic for a later paper. Rather abundant literature is available concerning the ecology of muskrats in North America and Central Europe, but this knowledge is perhaps not directly applicable in Finland. For example the qualities of the most productive muskrat habitats may vary geographically. An insight into the suitability of different habitats for muskrats, as well as a knowledge of the above-mentioned aspects of population ecology are of paramount importance in making correct decisions concerning this game animal species.

The annual muskrat catch in Finland usually varies between 200 000 and 300 000 individuals, e.g. 244 000 and 339 000 ind. were trapped in 1981 and 1982 respectively (Source: Finnish Game and Fisheries Research Institute). In Finland, muskrats are trapped only in spring, the most efficient trapping concentrating around the short time when the ice breaks up on lakes and rivers. Therefore it is relatively easy to get material for studies of the morphological variation and population structure of muskrats by organizing the collection of muskrat carcasses from trappers. The present study is based on this kind of material from April and May only. In this study I will describe individual and population characteristics of Finnish muskrats as well as investigate differences between localities and habitats.

2. Material and methods

The material was collected by local muskrat trappers in 1978-80 at four localities (Fig. 1): (1) *southern Finland* (1978-80): Lohja, Lake Lohjanjärvi (60°15′ N, 24°00′ E), *eastern Finland,* North Karelia (1979-80): (2) Kitee, Lake Kiteenjärvi (62°10′ N, 30°10′ E) and (3) Ilomantsi, rivers Koitajoki and Ilomantsinjoki (62°45′ N, 30°45′ E) and (4) *northern Finland* (1979-80): Kemijärvi (66°30′ N, 24°45′ E), Lake Kemijärvi, River Kemijoki and nine smaller lakes. The trappers weighed and skinned the animals and deep-froze the carcasess. Most of the animals were trapped between April 15 and May 15, or in Kemijärvi during the second half of May (Table 1).

In the laboratory the skinned carcasses were weighed and sexed and the head of the animal was removed, boiled for 1-1.5 h and cleaned. The age groups of the muskrats were defined according to Pankakoski (1980): molar index value >40 % = "young" (less than 1 year), <40 % = "old" (more than 1 year) (but see p. 215). The age in months was determined using the formula presented by Pankakoski (1980) (but see again p. 215). The skull length (condylobasal length; see, e.g., Boyce 1978) was measured with a sliding caliper to an accuracy of 0.1 mm.

The muskrats were weighed to an accuracy of 5-25 g by the trappers, but due to several sources of error the total body weight measurements also include unreliable values. The skinned carcasses were weighed by me in the laboratory (the Kemijärvi sample by the trapper) to an accuracy of 1-5 g, and only these weights were used in most calculations. The skinned carcass weight has commonly been used as a measure of animal size in comparisons of muskrat populations. In this material the relationship between the carcass and body weight proved to be the same as that reported by McCann (1944) and Smith & Jordan (1976).

Table 1. Numbers of muskrats trapped in four localities during April and May trappings in 1978-80. The material is grouped into 10-day classes.

	Lohja	Ilom.	Kitee	Kemij.	Total
April 1-10	3	0	0	0	3
April 11-20	44	38	8	0	90
April 21-30	198	116	20	1	335
May 1-10	100	16	8	4	128
May 11-20	29	5	0	15	49
May 21-31	13	0	0	19	32
Total	387	175	36	39	637

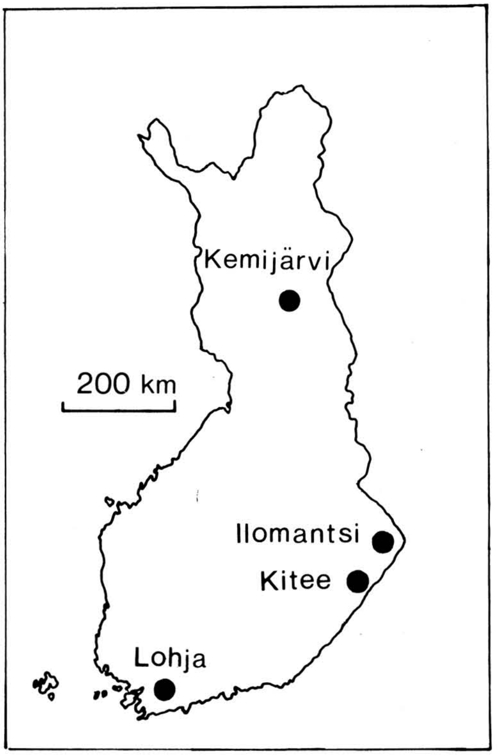

Fig. 1. Trapping localities of the muskrats.

3. Study area

3.1. General description of the trapping localities

Lohja. Lake Lohjanjärvi, one of the largest lakes (max. length c. 20 km) in southernmost Finland, is irregularly broken by islands and headlands (Fig. 2) and is somewhat polluted by the pulp industry and agriculture. The species composition of aquatic macrophytes varies according to the shore topography and exposure of the sites to wave action, but usually the watersides are rather steep and the vegetation belts reasonably narrow (mostly < 30 m). In the trapping sites (1-5 in Fig. 2 and 3), *Phragmites australis* is the most abundant plant species. Depending on the habitat, *Phragmites* is intermingled with *Carex* species (mainly *C. acuta,* commonly also *C. rostrata*), *Typha angustifolia* (occasionally *T. latifolia*), *Scirpus lacustris,* and floating leaved or eloeid plant species (*Nuphur lutea, Potamogeton perfoliatus, P. natans* and *Polygonium amphibium*). *Equisetum fluviatile* occurs sparsely in this area. Habitat analyses of the trapping sites of Lake Lohjanjärvi are presented in Table 2.

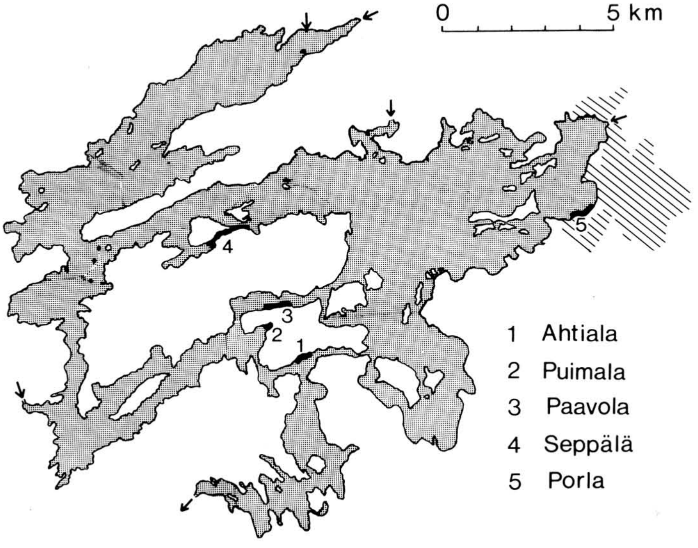

Fig. 2. Trapping sites of local muskrat populations in Lake Lohjanjärvi. The arrows indicate direction of water flow. The area of the town of Lohja is hatched.

Kitee. Päätyenlahti bay in Lake Kiteenjärvi, from which the muskrats were trapped, is a shallow (mainly <1 m deep), mesotrophic sheltered bay, 4 km in length, 0.6 km in width. According to the unpublished data of Dr. J. Suominen the vegetation in Päätyenlahti bay is dense and plant production high. The bay is apparently gradually becoming over-grown with helophytes. The dominant plant species in the area is *Equisetum fluviatile;* in some places *Sagittaria sagittifolia, Eleocharis palustris, Sparganium friesii, Potamogeton natans* and *P. perfoliatus* are also abundant. Aquatic mosses are very abundant, almost totally covering the bottom. There are small stands of *Scirpus lacustris,* sparsely also *Nuphar lutea, N. pumila* and *Typha latifolia. Phragmites australis* is absent, as is, e.g., *Nymphaea* and *Polygonum amphibium.*

Ilomantsi. River Koitajoki is about 75-200 m, occasionally even 800 m, in width in the area where trappings were performed. The meandering river, which has many small isles and inlets, has vast shore meadows (up to 200-300 m wide), dominated by *Carex* species (*C. aquatilis, C. rostrata* and *C. acuta*) and mixed on the land side with *Salix* bushes and different herbids and graminids; on the water side of the shore meadow *Equisetum* is a dominant species, mostly in dense and continuous stands. Floating leaved and submerged plants (*Nuphar lutea, Potamogeton* spp. and *Polygonum* spp.) are found in many places. Stands of *Scirpus lacustris* and *Phragmites australis* are uncommon and usually small in size. Some muskrats were trapped from River Ilomantsinjoki, which flows into the watercourse of River Koitajoki and has similar vegetation.

Kemijärvi. The largest sample of muskrats (n=16) in this area was trapped from Lake Kemijärvi, which is a c. 30 km long lake with clear water; three animals were caught from River Kemijoki, which flows through Lake Kemijärvi. The other muskrats (n=21) were from nine small lakes (max. length 0.3-4 km) of different types, varying from densely vegetated lakes with brown (humic) water and muddy bottoms to oligotrophic clear water lakes with mineral bottoms and sparse vegetation cover. The dominant aquatic macrophyts on the shore in the Kemijärvi area are *Carex* species (*C. aquatilis* and *C. rostrata*), combined in many places on the water side with *Equisetum fluviatile* (cf. also Rintanen 1976). The amount of *Equisetum* is clearly smaller in this area than in the trapping areas of Kitee and Ilomantsi, however. *Scirpis lacustris* and *Typha* species are absent, and sparse *Phragmites* stands are found only in a few places.

Table 2. Habitat analysis of trapping sites of Lake Lohjanjärvi. The relative scale of species abundance in vegetation is:
- = absent or very sparse ++ = species forms homogeneous stands or is rather abundant in mixed stands with other species
+ = reasonably sparse +++ = very abundant or dominant species or in dense stands

	1 Ahtiala	2 Puimala	3 Paavola	4 Seppälä	5 Porla
Vegetation *Equisetum fluviatile*	-	-	+	-	-
Scirpus lacustris	+	-	++	++	-
Phragmites australis	++	+++	++	++	++
Typha spp.	-	+	+	-	-
Carex spp.	+	+++	+	++	+
Nymphaeids	++	+	++	++	-
Herbids	+	++	++	+++	+
Vegetation density (scale: -, +, ++, +++)	+	++	++	+++	+
Waterside profile	steep	shallow	rather steep	shallow/ intermed.	steep
Mussel feeding (scale: -, +, ++)	++	-	+	+	+

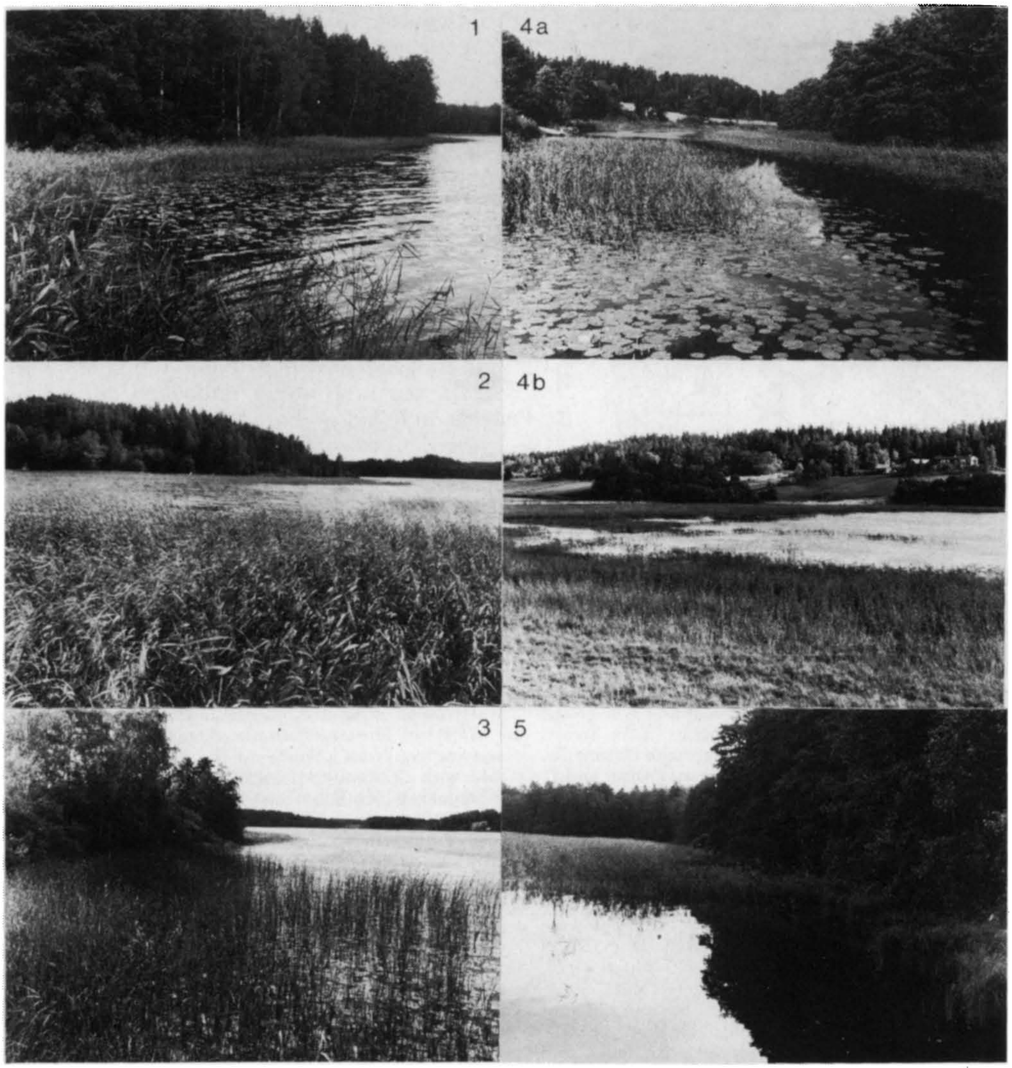

Fig. 3. Muskrat trapping habitats in Lake Lohjanjärvi. 1 = Ahtiala (3.VIII.1981), 2 = Puimala (3.VIII.1981), 3 = Paavola (3.VIII.1981), 4a = Seppälä sound (3.VIII.1981), 4b = Seppälä bay (9.IX.1982), 5 = Porla (16.VIII.1981).

3.2. Mussel supply

Empty shells of freshwater mussels (Unionidae) eaten by the muskrats are often found in heaps on the shores, especially after the winter. The numbers of mussel shells found gives a rough indication of the amount of mussel feeding in the area concerned, although the shore profile and type of vegetation affect the chances of finding the shells. Empty shells were systematically searched for in the trapping sites of Lake Lohjanjärvi during the period of open water, mainly in spring (Table 2). The following mussel species were found to be eaten by muskrats: *Anodonta cygnea, A. piscinalis, Unio tumidus, U. pictorum* and *U. crassus.*

Mussel shells were not searched for systematically in the other localities; the following features are based mainly on the observations by local muskrat trappers and also on my occasional findings of shells. Mussels are almost totally absent from Päätyenlahti bay, Kitee, possibly due to the extremely dense bottom moss vegetation. Heaps of empty mussel shells are frequently found in the rivers Koitajoki and Ilomantsinjoki in springtime (observations of *Pseudanodonta complanata* only). In Kemijärvi, mussel shells are found less frequently: they have been observed occasionally in River Kemijoki and also in one smaller lake (only *A. piscinalis*).

3.3. Water level fluctuations

Because of water level regulation for hydro-electric purposes the water level fluctuates in most of the lakes and rivers in the present study. The variation in the monthly means of the water level in Lohja and North Karelia (Kitee and Ilomantsi) is about 50–70 cm. In the Kemijärvi area the water level fluctuations area very much more prominent, however: during the study period they averaged 300 cm. In the small lakes in the Kemijärvi area which are not connected with the regulated watercourse of River Kemijoki, the water level fluctuations are small (c. 20 cm).

The water levels attain their peak after the thaw in late spring or early summer. In Lohja and North Karelia there are two minima, one in March-April and the other in September-October. On the other hand there is no autumn minimum in Kemijärvi; instead the water level is gradually lowered first during the winter and early spring.

4. Results

4.1. Morphological variation

Variation between sexes

In spring, the sexes of muskrats born during the previous summer (later: "young") differ statistically highly significantly in all the characteristics studied (Table 3). Males have a 13 % greater body and carcass weight and a 2 % longer skull than females. On the other hand, the molar index is lower and consequently the estimated "age" (which is calculated from the molar index) is 0.8 months greater in males (lower molar index = older animal; note, however, that the variation in "age", besides reflecting differences in true age is also sensitive to different amount of molar wear (see later)). Due to this sexual dimorphism, the sexes must be treated separately when comparing these characteristics, e.g. between different populations. The range of body weight is 700–1750 g in males, 635–1545 g (1600 g when pregnant) in females. The skinning of the muskrat causes an average reduction of 18 % in the body weight of the animal.

One year later, when the muskrats are nearly two years old (later: "old"), males are still a little larger than females, but the difference is significant only in skull length (nearly so (P=0.065) in carcass weight, too; Table 3). The differences in molar index and "age" between sexes are neglible.

Relationship between "age" and size

The correlation coefficients between the individual "age" and size values are significantly positive in the whole material (Table 4), implying naturally that body dimensions increase with age (see also Table 3). However, when the material is divided into different sexes and year classes, the correlations between "age" and carcass weight in young muskrats indicate negative values (although coefficients of determination (r^2) are fairly low). In old males the correlation is not significant; in old females it is close to zero, perhaps obscured by the observed early pregnancies in this category. However, my sample size for old muskrats is too small for definitive conclusions.

Body size mesurements, carcass weight and skull length, are significantly positively correlated in all age and sex classes (Table 4).

Variation between localities

Differences in the molar index, weight and skull length of young muskrats between the four trapping localities were investigated by using two-way analysis of variance between sexes and localities. The populations differ significantly in each characteristic (Table 5). The paired comparisons of localities (Fig. 4) are more often significant in males than in females, probably because of the smaller sample size in females.

The molar index is lowest in muskrats from Lohja and highest in Kitee. These extremes differ significantly from other populations in males. In

Table 3. Comparison of age and body dimensions between sexes. Arcsin-transformation was used for molar index values here as well as in later comparisons. Statistical significance: * = 0.05>P>0.01, ** = 0.01>P>0.001, *** = P<0.001.

	Males		Females		Difference
	Mean ±*SE*	*n*	Mean ±*SE*	n	*t*
Young					
Molar index %	60.3±0.43	313	63.1±0.49	229	4.34***
Age in months	10.4±0.14	313	9.6±0.15	229	4.08***
Body weight g	1167±10.9	306	1035±12.2	216	8.01***
Carcass weight g	962±8.6	309	849±9.2	227	8.88***
Skull length mm	63.62±0.118	281	62.47±0.1344	207	6.43***
Old					
Molar index %	33.0±1.20	24	32.9±1.06	24	0.05 ns
Age in months	21.8±0.78	24	21.8±0.65	24	0.04 ns
Body weight g	1317±32.3	24	1257±36.0	23	1.23 ns
Carcass weight g	1101±25.9	23	1026±30.0	24	1.89 ns
Skull length mm	66.46±0.360	21	65.07±0.371	19	2.68*

Table 4. Correlation coefficients (r) between age and body dimensions of muskrats. As "age" a molar index value of (100 % — molar index) was used. For the relationship between calculated and true age, see p. 215.

	"Age"	Carcass weight	n
Young males			
Carcass weight	-0.148**		313
Skull length	-0.062 ns	+0.736***	
Young females			
Carcass weight	-0.178**		229
Skull weight	-0.062 ns	+0.669***	
Old males			
Carcass weight	-0.269 ns		24
Skull length	+0.158 ns	+0.596***	
Old females			
Carcass weight	+0.040 ns		21
Skull length	+0.078 ns	+0.595**	
Total sample			
Carcass weight	+0.119***		587
Skull length	+0.231***	+0.752***	

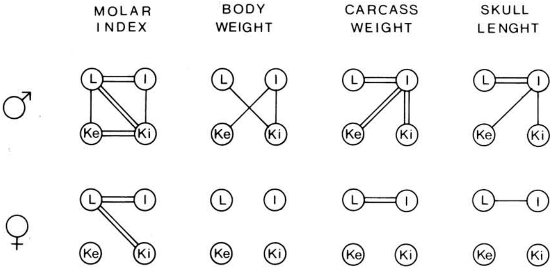

Fig. 4. Paired comparisons between localities in muskrat characteristics (Student-Newman-Keuls method after the analysis of variance in Table 5). The statistical differences are expressed by lines: no connecting line = P>0.05, single line = 0.05>P>0.01, double line = P<0.01. L = Lohja, I = Ilomantsi, Ki = Kitee, Ke = Kemijärvi.

females, fewer differences are significant, although the differences between the means are of the same order in both sexes (Table 5). Body and carcass weight and skull length are greatest in Ilomantsi in both sexes. In males, these differ significantly from the muskrats of other localities. The smallest males are in Kemijärvi, the smallest females in Kitee. There is great variation in the size values of the small Kemijärvi sample, especially in females, which show relatively great mean values.

In the small sample of old muskrats, there are no significant differences in the above-mentioned characteristics between the localities. However, the direction is about the same as in young animals: the muskrats in Ilomantsi are largest and have the highest molar index values.

In the localities where muskrats have a high molar index their size is usually also large, as was already revealed by the negative correlation coefficients in Table 4 (in which "age" was based on 100 % — molar index values). To get a single value, which takes into account both the molar index and weight of the animal, a *growth index* was calculated for each young muskrat:

$$\text{Growth index} = \frac{\text{Carcass weight (g)}}{(100\ \% - \text{Molar index}\ \%)}$$

The growth index thus describes the weight gain per one worn molar index percentage unit. The mean of this growth is 24.7 g/% in the total sample of young muskrats ($SD = \pm 6.55$, $n = 536$). (Because molar index values do not change linearly according to age of the animal (Pankakoski 1980), it would be more appropriate to use actual age in months as as divisor in the formula. In the present

Table 5. Comparison between localities in values of molar index, weight and skull length of young muskrats. F-values of two-way classification of analysis of variance between sexes and between localities also contain variation caused by interaction (sex × locality). Interaction was small in each case, however.

	Molar index (%)		Body weight (g)		Carcass weight (g)		Skull length (mm)	
Locality	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n
Males								
A Lohja	57.5±0.50	172	1174±16.2	167	945±11.7	171	63.38±0.194	155
B Ilomantsi	63.4±0.68	93	1196±17.8	92	1024±14.9	93	64.31±0.196	89
C Kitee	67.0±1.78	24	1092±25.5	24	924±24.0	24	62.95±0.178	20
D Kemijärvi	60.7±1.65	24	1082±27.1	23	885±27.1	22	62.85±0.164	15
Females								
A Lohja	61.0±0.60	135	1025±17.6	126	820±12.0	135	62.23±0.197	120
B Ilomantsi	66.0±0.85	72	1064±16.7	69	907±14.2	72	63.03±0.179	69
C Kitee	68.1±2.44	10	930±42.2	10	802±36.8	10	61.82±0.133	9
D Kemijärvi	64.0±1.86	12	1060±61.2	11	865±46.0	10	62.37±0.240	9
F Sex	6.99***		18.26***		23.46***		11.20***	
Localities	17.27***		2.60*		8.05***		4.40***	
Interactions	0.34 ns		1.05 ns		1.34 ns		0.17 ns	

material the deviation from linearity in young muskrats was not important, however).

A *condition factor,* which indicates the "fatness" of the muskrat, was calculated from the following formula:

$$\text{Condition factor} = \frac{\text{Carcass weight (g)} \times 1000.}{(\text{Skull length (mm)})^3}$$

The mean of the condition factor is 3.63 in the total sample of young muskrats ($SD = \pm 0.407$, n = 484). Values of growth index and condition factor are strongly correlated on the individual level (young males: r =+0.600*** (n = 311), young females: r = +0.594*** (n = 230)).

The sexes do not differ significantly from each other in growth index, although, as a rule, males seem to have somewhat higher values than females (Fig. 5). On the other hand, there are highly significant differences between the four localities: the growth index is high in Ilomantsi and Kitee and low in Lohja and Kemijärvi. In females, the mean of the growth index of the small Kemijärvi sample is closer to the values of North Karelia than to those of Lohja.

The condition factor is significantly greater in males than in females, i.e. the former are stouter (Fig. 5). The condition factor of males has the highest average value in Ilomantsi and the lowest in Kemijärvi. In females, the highest average value is found in Kemijärvi and the lowest in Kitee, but this result is presumably due to the small samples from these two localities. In females the only significant difference is between Ilomantsi (high) and Lohja (low; Fig. 5).

Variation within localities

The characteristics of the muskrats in the Lohja sample (young individuals) were further investigated between five separate local populations in Lake Lohjanjärvi (Table 6 and Fig.6). The differences between populations are significant with regard to carcass weight, growth index and condition factor. In addition, skull length differs significantly between the populations, but significant interaction between sexes and populations makes it difficult to draw any conclusions (Table 6). In molar index, the difference between populations is not significant, but high molar wear seems to correlate with small animal size in the five trapping sites.

Puimala (population 2) is clearly distinguished from the others by lower values in carcass weight, growth index and condition factor (Table 6 and Fig. 6). In carcass weight the differences between Puimala and all other populations are statistically significant with the exception of population 5 in females. In Paavola and Seppälä (populations 3 and 4) the muskrats are biggest and grow most rapidly and have the highest average condition factor. The animals in Porla (population 5) are rather small and their growth index and condition factor are low.

The effect of population density on the observed differences between local muskrat populations in Lake Lohjanjärvi was studied by comparing the muskrat characteristics with the catch indices in trappings (Table 7). The catch index was lowest in the populations with the lowest values of weight, skull length, growth index and condition factor, and with greatest "age".

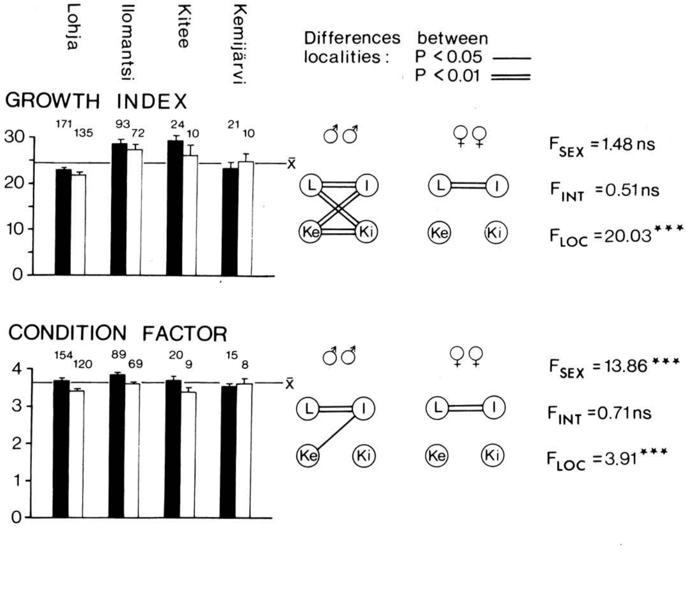

Fig. 5. Comparison of growth and condition factors of young muskrats between trapping localities. Black columns = males, white columns = females. The figures above the columns indicate sample size. The mean of the total sample is indicated as a horizontal line. For further explanations, see also Table 5 and Fig. 4.

Table 6. Comparison between populations of Lake Lohjanjärvi in values of molar index, carcass weight and skull length of young muskrats. *F*-values of two-way classification of analysis of variance between sexes and between populations (trapping areas) also contain variation caused by interaction (sex × population). Interaction was significant in skull length only, however.

Population	Molar index (%) Mean ± *SE*	*n*	Carcass weight (g) Mean ± *SE*	*n*	Skull length (mm) Mean ± *SE*	*n*
Males						
1 Ahtiala	57.4±0.92	29	969±27.5	29	63.90±0.268	28
2 Puimala	55.0±1.22	28	844±32.4	27	62.92±0.474	23
3 Paavola	57.7±1.26	31	996±30.5	31	64.17±0.365	30
4 Seppälä	59.0±0.83	67	956±14.0	67	62.98±0.229	60
5 Porla	56.7±1.50	16	946±40.1	16	63.16±0.620	14
Females						
1 Ahtiala	59.6±1.20	24	819±26.8	24	62.15±0.458	21
2 Puimala	59.7±1.26	32	730±24.9	32	61.73±0.278	21
3 Paavola	62.7±1.04	17	851±34.3	17	62.26±0.490	16
4 Seppälä	62.7±1.19	44	884±15.9	44	62.86±0.245	41
5 Porla	59.9±1.60	18	793±32.2	18	61.53±0.716	17
F Sex	5.25***		11.08***		6.15***	
Populations	1.80 ns		5.62***		2.47*	
Interaction	0.34 ns		1.15 ns		2.55*	

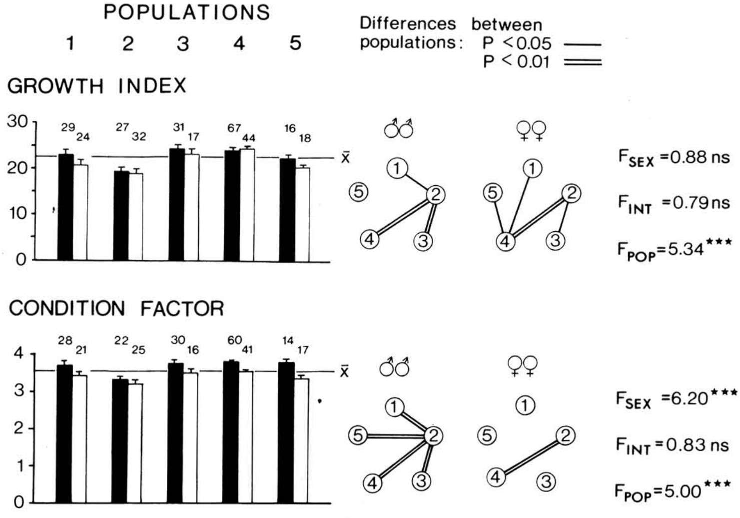

Fig. 6. Comparison of growth and condition factor of young muskrats between the populations of Lake Lohjanjärvi. Populations: 1 = Ahtiala, 2 = Puimala, 3 = Paavola, 4 = Seppälä, 5 = Porla. For further explanations, see also Table 6 and Fig. 4.

Table 7. Relative abundance of muskrats in five trapping areas of lake Lohjanjärvi. The catch indices (muskrats/100 trap-nights) are based on trappings (steel leg-hold traps) performed in spring 1979.

Trapping area	Trapped muskrats	Trap-nights	Catch index	Difference between trapping areas
1 Ahtiala	27	352	7.7	
2 Puimala	11	180	6.1	
3 Paavola	28	231	12.1	χ^2 = 27.43***
4 Seppälä	85	509	16.7	*df* = 4
5 Porla	11[1]	192	5.7	

[1] Good catch in wire-net traps.

Due to the low number of degrees of freedom (*df* = 3) the correlations were statistically significant only with respect to "age" (negative), however.

Changes during the trapping period

In order to study possible changes in muskrat characteristics during the spring trapping period, only the Lohja sample, with the deviating Puimala animals excluded, was used (Table 8). The animals were larger in April than in May, the differences being significant in carcass weight, but not in skull length. The condition factor of muskrats was also higher during the first half of the trapping period than the second half, though the difference was significant only in males (Table 8). The molar index values and consequently the growth index values naturally also differed between the months (not tabulated). There were no significant interannual differences in muskrat characteristics in the Lohja sample between 1978 and 1979.

Table 8. Comparison of size and condition of muskrats between the early and late half of the spring trapping period (Lohja, with the deviating Puimala sample excluded).

	April		May		t
	Mean ± *SE*	*n*	Mean ± *SE*	*n*	
Males					
Carcass weight (g)	994±15.4	81	930±17.0	62	2.80**
Skull length (mm)	63.7±0.21	70	63.2±0.25	62	1.26 ns
Condition factor	3.85±0.042	70	3.66±0.044	62	3.17**
Females					
Carcass weight (g)	872±14.2	58	817±21.4	45	2.20*
Skull length (mm)	62.7±0.27	51	62.0±0.34	44	1.51 ns
Condition factor	3.53±0.043	51	3.42±0.054	44	1.64 ns

4.2. Population structure

Age structure

In spring the molar index shows a bimodal frequency distribution in each locality (North Karelia = Ilomantsi and Kitee samples combined): a high peak corresponding to the individuals born during the previous summer and a much lower one reflecting the number of individuals nearly two years old (Fig. 7). The separation of year classes in Fig. 7 is not complete, mainly because of the great variation in the molar index values, but also due to the pooling of the data over two months and both sexes. The molar index values were earlier shown to differ between the trapping localities (p. 211), which is also seen in the frequency distributions. Therefore, the age class separation points are also different. A molar index value of 40 % was used as the critical value in the Lohja sample (Pankakoski 1980); for other localities a value of 45 % was used for separating the age classes. This change in the critical point only affects the classification of eight individuals in the North Karelian and one in the Kemijärvi samples. It is difficult to distinguish individuals nearly three years old from younger age classes (Pankakoski 1980) but on the basis of figure 5 in Pankakoski (1980) a molar index value of 15 % was chosen as the critical value for separation. By applying these principles the muskrats were classified in the three year classes shown in Table 9. There is no difference in the age structure between localities ($\chi^2 = 0.07$ ns, $df = 2$), and would not be even if no change had been made in the critical point between the one and two year age classes.

The formula presented in Pankakoski (1980) for estimating real age in months from molar index values was based on the Lohja sample only. As a result of the higher means of the molar index, the average age is lower and consequently the average time of birth later in North Karelia and

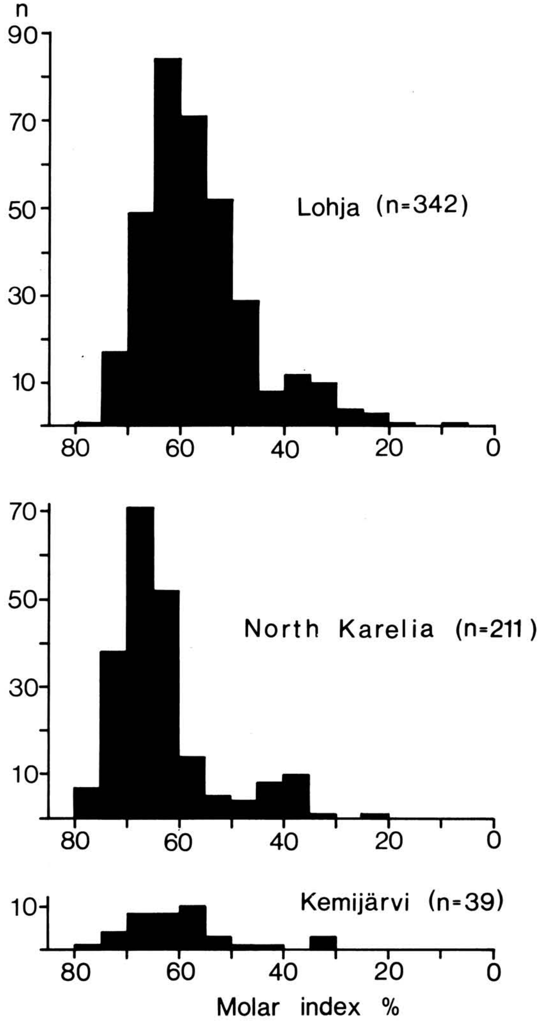

Fig. 7. The distribution of molar index values of muskrats in spring. The age of the animals increases to the right on the horizontal axis.

Table 9. Age structure of muskrat populations in spring. For details see text. Age: 1 year = animals born during the previous summer, 2 years = animals born one year earlier, etc.

	Age in years						Total
	1		2		3		
	n	%	*n*	%	*n*	%	*n*
Lohja							
Males	173	(91.5)	16	(8.5)	0	(0.0)	189
Females	138	(90.2)	14	(9.2)	1	(0.7)	153
Total	311	(90.9)	30	(8.8)	1	(0.3)	342
North Karelia							
Males	111	(90.2)	12	(9.8)	0	(0.0)	123
Females	80	(90.9)	8	(9.1)	0	(0.0)	88
Total	191	(90.5)	20	(9.5)	0	(0.0)	211
Kemijärvi							
Males	23	(88.5)	3	(11.5)	0	(0.0)	26
Females	12	(92.3)	1	(7.7)	0	(0.0)	13
Total	35	(89.7)	4	(10.3)	0	(0.0)	39
Total							
Males	307	(90.8)	31	(9.2)	0	(0.0)	338
Females	230	(90.6)	23	(9.1)	1	(0.4)	254
Total	537	(90.7)	54	(9.1)	1	(0.2)	592

Kemijärvi than in Lohja, when calculated according to the formula (Table 10).

Sex ratio

Males predominate over females in the spring catch numbers (Table 11). The deviation from an even sex ratio is significant in the total material, as well as in the samples from each trapping locality. There is no significant difference in the sex ratio between the trapping localities ($\chi^2 = 2.07$ ns, $df = 2$), neither does the sex ratio alter during the trapping season (divided here into 10-day intervals). The male dominance in the sex ratio remains the same in both the young and old cohorts (57.2 % and 57.4 %, respectively, see Table 9).

5. Discussion

5.1. Morphological variation

Geographical aspects of muskrat size

The mean size of muskrats is generally somewhat smaller in countries into which this species has been introduced than in its original range in North America (Ruprecht 1974, Le Boulengé & Le Boulengé-Nguyen 1981). Thus, the mean size of Finnish muskrats is about the same as the values presented in the European literature (e.g., Hoffman 1958, Marcström 1964, Teodoreanu 1975, Doude van Troostwijk 1976, Le Boulengé & Le Boulengé-Nguyen 1981), but does not reach the highest mean sizes of North American muskrats (Dozier 1950, Schacher & Pelton 1976, Smith & Jordan 1976). Clinal variation in muskrat size over large geographical areas has been observed in several studies, especially in craniometric measurements (Gould & Kreeger 1948, Petrov & Krasnikova 1970, Pietsch 1970, Ruprecht 1974, Boyce 1978). Habitat differences often confuse the study of geographical differences, however (Ruprecht 1974). Variation in muskrat size is rather high in the present material, but because of habitat differences no examination of clinal changes in Finland is possible, at least not in the values reflecting total size of the animals (see Boyce 1978).

Table 10. Comparison of average age and time of birth of muskrats between trapping localities using an age determination formula developed for muskrats in Lohja (Pankakoski 1980). In the formula, sexes were not separated, and so this cannot be done for comparisons of age estimates, either. Molar index values >40 %.

	Lohja	N. Karelia	Kemijärvi
Average age (months)	10.8	9.0	9.9
n	307	199	36
Deviation from age in Lohja (months)	-	-1.8	-0.9
Average trapping date	25 April	25 April	20 May
Average time of birth	early June	late July	late July

Table 11. Sex ratio of muskrat populations in spring. The figures include also 29 muskrats trapped in 1980 in Lohja by one trapper, who sexed the animals by autopsy. The values are grouped into 10-day classes.

		Lohja ♂	Lohja ♀	N.Karelia ♂	N.Karelia ♀	Kemij. ♂	Kemij. ♀	Total ♂	Total ♀
April 1-10		2	1	0	0	0	0	2	1
11-20		23	21	29	17	0	0	52	38
21-30		110	88	81	55	1	0	192	143
May 1-10		53	47	10	14	2	2	65	63
11-20		19	10	3	2	10	5	32	17
21-31		7	6	0	0	13	6	20	12
Total		214	173	123	88	26	13	363	274
% males		55.3		58.3		66.7		57.0	
Sex ratio (♂♂/♀♀)		1.24		1.40		2.00		1.32	
Deviation from 1 : 1 (df=1)	χ^2	4.34*		5.81*		4.33*		12.43***	
Difference betw. 10-day classes	χ^2	1.04 ns		2.14 ns		0.05 ns		3.85 ns	
	df	3		2		1		4	

Sexual dimorphism

Finnish muskrats show clear sexual dimorphism in size: young males are 13 % heavier than females. Comparisons of individuals of the same age classes, as done in the present study (Tables 5 and 6), give more reliable results for sexual differences (Dorney & Rush 1953). Most muskrat studies state that the size of males exceeds that of females (by 7-13 %, Dozier 1945, 1950, Dozier et al. 1948, Marcström 1964 etc., or less: 3-5 % Parker & Maxwell 1980; for a contradictory result, see Buss 1941). In Finnish muskrats, the difference between sexes is distinct also in the skull length, in which some authors have demonstrated sexual dimorphism to different degrees (Gould & Kreeger 1948, Sather 1956, Ruprecht 1974, Boyce 1978), and some have not (Pietsch 1970).

Different wear on the molars explains the lower molar index values and consequently also greater estimates of age in males than in females. Evidently the greater energy requirements resulting from the greater size of the males leads to more severe wear on their molars (Pankakoski 1980). Different wear might also result if the sexes differed in food selection, but this kind of observation has not been presented in the literature.

The most probable cause of sexual dimorphism in muskrat size is sexual selection (see Ralls 1977, Halliday 1978). The alternative explanation, intraspecific avoidance of competition (Selander 1966), is unlikely, because in muskrats there seems to be no nice separation between sexes in the feeding habits or in the habitat selection such as that observed e.g. in the weasel *Mustela erminea* (Erlinge 1979).

Growth index and condition factor in muskrat population studies

A connection similar to that suggested to cause differences between the sexes in the amount of eaten food and tooth wear is also valid at the population level. This is the reason for the observed negative correlation between the "age" (molar wear) and the weight of the muskrats, as well as the differences in growth index values between localities and habitats (see also Marcström 1964). Where the food situation is good, muskrats are able to select the best, most nourishing, often soft species and parts of plants. These muskrats grow large in size and their teeth are worn only a little. On the other hand, under less favourable conditions, muskrats are forced to use food of lower quality and, moreover, to eat it in greater amounts to obtain the same amount of energy as in more favourable places. Because the growth index value combines these two characteristics, molar wear and animal size, it can be considered a useful measure of the suitability of the habitat for muskrats.

The growth index and condition factor as calculated in the present study do not measure exactly the same characteristics of the muskrat population, although these two properties are highly correlated with each other. The former describes mainly the speed of muskrat growth and the latter the stoutness of the individual. For assessing the suitability of the habitats, the growth index gave better results (higher F-values in comparisons) than the condition factor. However, the calculation of condition factors might replace the use of growth indices in studies in which molar index has not been measured. Moreover, aspects condemed with time (e.g. comparisons of early and late parts of the trapping period, Table 8) cannot be made by using growth index values, in which "time" is incorporated in the form of molar index (or age) values.

Influence of environmental factors

Vegetation

According to Artimo (1960), Finnish muskrats prefer the same species or at least corresponding species of the same plant families as food plants as in their original range in North America. The best plant species in order of preference in Finland are *Typha* spp., *Sparganium erectum*, *Scirpus lacustris*, *Carex* spp. and *Equisetum fluviatile* (Artimo 1960).

In the Lake Lohjanjärvi the trapping sites with dense and varied vegetation (Table 2, p. 209) supported the highest muskrat densities and greatest averages of size, growth index and condition factor. In these areas (Paavola and Seppälä, populations 3 and 4, especially) *Scirpus lacustris* is also an abundant plant species. On the other hand the habitats in Ahtiala, Puimala and Porla (populations 1, 2 and 5, respectively) are either sparsely vegetated or the vegetation is less diversified. The muskrats were smallest and their growth index and condition factor were poorest in Puimala, where the vegetation is dominated by *Phragmites australis.* In Puimala *Scirpus* is totally absent and *Typha angustifolia* is present only in one stand (Table 2). Artimo (1960) emphasizes that *Phragmites,* a very common plant species in Finnish muskrat habitats, is not especially preferred as a food plant by the muskrat. Bellrose (1950) also found that *Phargmites* was not chosen if other food plants were present. In North America, stands of *Typha* and *Scirpus* species can support the highest densities of muskrats and produce the largest animals (Errington 1941, Aldous 1947, Bellrose 1950, Bednarik 1956; see also Akkermann

1975). It is typical of the food searching habits of the muskrat that although the species attempts to select its food objects, it also strives to utilize the nearest growing vegetation (e.g., Takos 1947, Bednarik 1956, Danell 1978b), if it is reasonably suitable as food. Therefore, the small *Typha* stand in Puimala was evidently not sufficient to affect the size and growth of muskrats in that area. Because the muskrat population density was rather low in Puimala (Table 7), overpopulation cannot be a reason for the poor condition of its animals.

In the material of the present study, the rivers Koitajoki and Ilomantsinjoki in Ilomantsi supported muskrat populations in which the mean size and growth index are greatest and the condition of the animals best. River ecosystem have also previously been observed to afford better conditions for muskrats than lake or pond habitats (McCann 1944, Schacher & Pelton 1976). The vast waterside meadows by the rivers Koitajoki and Ilomantsinjoki are very suitable feeding areas for muskrats. Animals trapped from Lake Kiteenjärvi did not reach the size of the Ilomantsi animals, but because their teeth showed rather slight wear, the growth index of these muskrats is high. This is most probably due to the divergent and suitable species composition of the food plants, mainly *Equisetum* and many herbaceous plant species. The relatively small size and poor growth and condition of the muskrats from Kemijärvi (cf. the small size of muskrats in Marcström's (1964) study in Norrbotten, northern Sweden) may be a consequence of the generally short growing period of plants in northern Finland, and of the predominance of *Carex* species which are only occasionally mixed with more favourable species and *Equisetum* among the aquatic macrophytes on the habitats (see also Errington 1963: 483). A drawback in the Kemijärvi sample is, however, that the muskrats have been trapped from several different types of lakes and a river, which adds to the variation in the results. Furthermore, the large sample from Lake Lohjanjärvi shows considerable variation in individual characteristics: the animals have been trapped from both excellent and rather poor habitats. Relatively narrow vegetation belts, dominanted by *Phragmites* in many places, lower the mean size of muskrats in Lake Lohjanjärvi.

The relative density of the muskrat populations of Lake Lohjanjärvi was higher in habitats with an abundant supply of preferred plant species. This relationship was observed earlier by, e.g., Bellrose (1950), Errington (1963), Neal (1968) and Laanetu (1982). According to Neal (1968) muskrats have larger home ranges and consequently lower population densities in poorer habitats. Dozier & Allen (1942) also observed that the size of the muskrats depends on plant production, not on the population density of the area.

The differences in the vegetation of the five trapping sites of Lake Lohjanjärvi are partly caused by the muskrats themselves. They have caused a reduction in the vegetation and changes in the plant species composition at least in Ahtiala and Puimala (cf. also Časčuhin 1975, Rintanen 1976, Smith & Jordan 1976, Danell 1977b, 1979, Ahlgén 1980, Toivonen & Meriläinen 1980, Laanetu 1982). According to the local people, stands of *Equisetum* have considerably decreased in Ahtiala; in Puimala the *Typha* stand was degenerative (H. Toivonen, pers. comm.) and *Scirpus* has most probably been completely eaten out. As a result of the impact of the muskrats, areas of open water among the vegetation (Danell 1979) have also been created in some places.

Mussel supply

Mussels are important food objects for muskrats, especially during the winter (Errington 1941, Brander 1951a, Bednarik 1956, Artimo 1960, Marcström 1964, Akkermann 1975). In contrast to the other trapping sites in Lake Lohjanjärvi, mussel feeding must be insignificant in Puimala, where empty mussel shells were found notably less often than in other sites (Table 2). This doubtless has a significance in the poor growth of the animals in Puimala. On the other hand, a good mussel supply in Ahtiala may have compensated for the reasonably sparse vegetation in the area· (*Scirpus* is present in small stands, however), resulting in much higher size and growth index values of the muskrats in this population. A similar connection between mussel supply and animal size can be demonstrated in North Karelia (Ilomantsi: good supply — large animals; Kitee: poor supply — small animals).

Water level fluctuations and waterside profile

Water level fluctuations have earlier been shown to have a negative effect on both the population density and body size of muskrats (Bellrose & Brown 1941, Bellrose 1950, Brander 1951b, Artimo 1960, Friend et al. 1964, Donohoe 1966, Boyce 1978). Water level fluctuations as such are one kind of stress situation for muskrats, but combined with a shallow waterside profile they can be particularly detrimental. If the water level is lowered during the winter, the ability of muskrats to swim under the ice cover becomes very difficult in shallow waters and the animals are unable to gain access to food supplies (Friend et al. 1964, MacArthur 1978, see also Ahlgrén

1980). In Lohja this might be the case in the shallow Puimala area (Table 2), because the level of Lake Lohjanjärvi is at a minimum in late winter. Also in Kemijärvi the extreme variation in the water level of most trapping places undoubtedly has a detrimental effect on the muskrat populations in that area.

To summarize the effect of environmental factors, there seem to be three main reasons for differences in the size and condition of muskrats: differences in (1) food plant species composition, (2) mussel supply and (3) water level fluctuations (especially combined with shallow waterside profile). Moreover, it is possible that smaller individuals have to accept poorer habitats as a consequence of intraspecific dominance relations (cf. Fretwell 1972, Le Boulengé & Le Boulengé-Nguyen 1981). This may serve as a partial explanation for the observed differences between habitats in this study. The mutual order of importance of these factors is difficult to assess, and the order perhaps differs between habitats.

Temporal variation

Intraspecific competition is most probably the reason for the observation that during the later part of the spring trapping season (May) the muskrats were smaller and in poorer condition than in the beginning of the season (April). In spring, when the home ranges are being established and the dispersal is at its greatest in muskrat populations (Errington 1940, 1963, Le Boulengé & Le Boulengé-Nguyen 1981), the dominant individuals, which in voles are usually larger, enter the traps first (Smith et al. 1975). The smaller subordinate individuals will occupy the vacated home ranges only after the removal of these dominant individuals (Myllymäki 1974, Le Boulengé & Le Boulengé-Nguyen 1981; cf. also Dozier et al. 1948).

5.2. Population structure

Age structure

The most reliable picture of the turnover rate of muskrat populations is offered by live-trapping studies in which the animals are individually marked, preferably as nestlings. Based on this kind of investigation in Wisconsin, USA, Mathiak (1966) states that "for all biologically significant purposes it would seem that the muskrat population had a complete turnover in 2 years"; 87 % of the muskrats died during the first year and 98 % during the first two years. Among the 1579 marked muskrats of his study there was only one female, which had overwintered three times (Mathiak 1966). The turnover rate of the Finnish muskrat populations is of the same order. Similarly, Le Boulengé & Le Boulengé-Nguyen (1981) observed that, in muskrats inhabiting a river in southern Belgium, the annual mortality was 80–90 %.

When determining the age structure of an unmarked muskrat population, the results are affected by the ageing method used (Pucek & Lowe 1975). Methods based on molar wear are generally considered belonging to the best for age determination of muskrats (see Pankakoski 1980 for references). Considering the great variation in the molar index values of the present study, the proportions of different year classes cannot be accurate, however.

The age structure of the present study also corresponds reasonably well with the results of studies in Germany (Becker 1967), Belgium (Moens 1978), the Netherlands (Doude van Troostwijk 1976) and Czechoslovakia (Kratovil 1956), although the proportion of the youngest age group is somewhat less dominant in most of these Central European populations (Table 12). The slower turnover rate of muskrat populations

Table 12. Percentages of different year classes in spring material of some European muskrat studies. Some of the data are calculated from original tables to receive the best temporal correspondence to the present study. Age: 1 year = animals born during the previous summer, 2 years = animals born one year earlier, etc.

Country	Age in years 1	2	3	4	Trapping time	Ageing method	Source
Germany	85	15	0	0	Spring	molar wear	Becker (1967)
Belgium	88.5	10.8	0.7	0	March-April	"	Moens (1978: Table 3)
France	67	24	9	0	April	eye lens weight	Vincent & Quéré (1972: Table 11)
Czechoslovakia	86.8	9.8	2.6	0.8	Spring	body weight	Kratovil (1956)
Finland[1]	58.5		41.5		April	molar wear	Artimo (1960)
Sweden	64		36		May	"	Marcström (1964)
Netherlands	83–95		17–5		April	"	Doude van Troostwijk (1976: Table 2)
Present study	90.7	9.1	0.2	0	April-May	molar wear	

[1]Males only (n = 70).

in France (Vincent & Quere 1972) than in the present and above-mentioned studies may be a consequence of different ageing methods (eye lens weight), or the possibility that the French muskrats lived in areas with a lower trapping intensity. The proportion of older individuals is even greater in Artimo's (1960) and Marcström's (1964) studies, performed in Finland and northern Sweden, respectively. The deviation of these two studies is difficult to interpret other than by invoking methodological differences. Both Artimo (1960) and Marcström (1964) used Cygankov's (1955) molar wear ageing method, which tended to classify at least the muskrats of Lake Lohjanjärvi as too old (Pankakoski 1980). The method of Cygankov (1955) was perhaps developed for muskrats living under better conditions and with lower tendency for molar wear than that prevailing in northern Fennoscandia. Kratovil (1956) states that some muskrats in his material had overwintered four times. However, the animal size used for ageing by Kratovil (1956) cannot be regarded as a reliable ageing method in muskrats (see above; Pucek & Lowe 1975, Pankakoski 1980).

The formula presented in Pankakoski (1980) for estimating the real age in months is based on the Lohja sample only. With this formula, the average time of birth of young muskrats was calculated as early June in Lohja and late July in northern Karelia and Kemijärvi. However, the latter seems to be rather late for the average time of birth (cf. Artimo 1960). This indicates that the formula is not completely applicable outside the area in which it was initially developed if the habitats differ to such an extent that differences in molar wear occur.

Sex ratio

The literature on the sex ratios in muskrat populations is extensive. In most studies there is a clear prepoderance of males in spring (e.g., Marshall 1937, Errington 1940, McCann 1944, Anderson 1947, Lahtinen 1954, Donohoe 1966, Neal 1968, Doude van Troostwijk 1976, Schacher & Pelton 1976; see Le Boulengé & Le Boulengé-Nguyen 1981, however). Male dominance in numbers has been attributed either to different mortality of the sexes (Errington 1940, Buss 1941, McCann 1944, Neal 1968) or the differences in activity resulting in a greater proportion of males being taken in traps (Schacher & Pelton 1976, Moens 1978), or both (Errington 1940, Donohoe 1966). If males are more heavily harvested by effective trapping from year to year, female preponderance in older age groups (observed by Becker 1969) should result. This was not the case in the present study, however.

Both Dozier (1945) and Anderson (1947) state that the muskrat trappers commonly believe that a preponderance of females is taken in traps towards the close of the trapping season. This was the case in the study of Dozier & Allen (1942), but most studies, the present one included, do not show this (Marshall 1937, Dozier 1945, 1950, Anderson 1947, Dozier et al. 1948, Bednarik 1956).

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