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Variation in the tooth wear of the shrews *Sorex araneus* and *S. minutus*

Erkki Pankakoski

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Tooth wear was studied in 1040 *S. araneus* and 201 *S. minutus* in Southern Finland. Total height, as well as the absolute and relative amount of tooth pigment, was measured from the first molar in the lower jaw (M_1). During the whole life span of the shrews, the average tooth wear/month is 39 µm in *S. araneus* and 26 µm in *S. minutus*. However, clear differences in tooth wear exist between year classes: wear is almost twice as fast in sexually mature overwintered adults as in immature current-year juveniles. This difference is even greater in the relative height of tooth pigment (pigment index). Differences between age groups in tooth hardness or in the amount or quality of food eaten are suggested. There is sexual dimorphism in tooth measurements (significant in *S. araneus*): males have lower means in tooth height and in pigment index especially for adults. In juvenile shrews, great differences in tooth height, pigment index and body size exist between years, tending to be higher during rainy summers. This probably is a result of different availability of food between years, resulting in differences in tooth size or tooth wear, or both. Method of measuring tooth height is a better method for differentiating year classes than the method for measuring tooth pigment. The amount of tooth pigment exhibits sexual dimorphism and is more susceptible to measuring errors.

E. Pankakoski, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.

1. Introduction

In contrast to rodents, insectivores have no renewal system for the teeth. Because shrews and moles mainly feed on soil invertebrates, their teeth wear severely because the soil particles grind the occlusal surfaces (Crowcroft 1956). Accordingly, estimation of tooth wear has been widely used for approximate age determination of these mammals (e.g., Pearson 1945, Conaway 1952, Pruitt 1954, Crowcroft 1956, Dapson 1968a,b, Funmilayo 1976, Jeanmaire-Besancon 1986). Usually the separation of year-classes according to the degree of tooth wear has been possible, but the separation of subsequent litters has mostly failed (however, see Pernetta 1977).

The reddish brown cusps of young individuals of *Sorex* gradually wear away with age. Skarén (1979) suggested a method for classification of *S. isodon* samples into age groups, based on assessing the proportion of this pigmented area to the total height of the tooth. Other workers have either taken several measurements of the cusps or only measured the total height of the tooth. One aim of the present study is to compare the method of Skarén (1979) with the most common method of measuring tooth height.

Similar tooth wear in the two sexes, age groups, and years is usually assumed (e.g., Funmilayo 1976), but has not been demonstrated. A similar assumption for the muskrat was, however shown to be premature (Pankakoski 1980, 1983). These aspects, as well as their possible links with the ecology of the shrews, were also studied in southern Finland on two species of shrews: the common shrew, *Sorex araneus* L. and the pygmy shrew, *S. minutus* L.

2. Material and methods

2.1. Trapping and classification of the shrews

Shrews were trapped with pitfall cone traps during 1975–80 on Jalassaari in Lohja, southern Finland (Pankakoski 1979, Pankakoski & Tähkä 1982). Trapping was carried out at intervals of about one month, from April to November. Because

Table 1. Classification of the monthly catches according to the year-class and reproduction condition of the individuals. The shrews born during the previous summer are still called juveniles during the two first months of the year (marked with '*'); from March onwards they become sexually mature and are called adults. Exceptionally matured females during their year of birth are called mature juveniles (for details, see text).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
S. araneus													
Immature juv.	40*	23*	0	0	0	70	184	176	70	53	38	17	671
Mature juv.	0	0	0	0	0	9	8	4	1	3	0	0	25
Mature adults	–	–	16	105	49	87	55	23	4	5	0	0	344
Total	40	23	16	105	49	166	247	203	75	61	38	17	1040
S. minutus													
Immature juv.	0	0	0	0	0	4	16	44	31	22	17	0	134
Mature juv.	0	0	0	0	0	0	4	2	0	2	0	0	8
Mature adults	–	–	2	21	9	9	12	4	1	1	0	0	59
Total	0	0	2	21	9	13	32	50	32	25	17	0	201

pitfall traps are not effective during the winter due to the snow cover, the earlier catch of December to March 1969–71, using live traps (occasionally snap traps) in the same area was included. A sample of 25 *S. araneus*, live trapped in January 1980 on Lohjansaari, a large island nearby, was also included. "Ugglan-special" (in a few cases "Longworth") live traps were used.

Live traps are not especially suitable for morphometric studies of shrews, as the shrews quickly starve to death in live traps leading to lowering of body weight. Moreover, the shrews break their teeth more often in live traps than in cone or snap traps (individuals with a broken M_1, both shrew species combined: live traps: 7/205 ind. = 3.4%; other traps: 5/1036 ind. = 0.5%; $P<0.01$, Fisher's test). Therefore, live trapped individuals were used only in calculating tooth wear during the total life span of shrews. All the other analyses are based on cone trappings in 1975–80.

The small mammals caught were put in plastic bags and deep-frozen. In the laboratory, the length of the animal was measured by a ruler to an accuracy of 1 mm and weighed with a "Pesola" spring-scale (capacities of 10 or 30 g) to an accuracy of 0.1 g. The age grouping of shrews was done according to the general size of the individual, and to the colour and condition of the coat, especially the coat of the hind feet and tail (Crowcroft 1957). The reproductive status was evaluated according to Pankakoski & Tähkä (1982).

Young shrews are called *juveniles* during their year of birth. Most females and all males of the juveniles were sexually immature (Table 1). In January and February the shrews were always immature and were also classified as juveniles. Sexual maturation of male shrews begins in early March in southern Finland; in females this occurs in late March or early April (Pankakoski, unpubl.). From March onwards the shrews born during the previous summer were classified as *adults*. Among the juveniles there were 25 female common shrews and 8 female pygmy shrews that were sexually mature (Table 1).

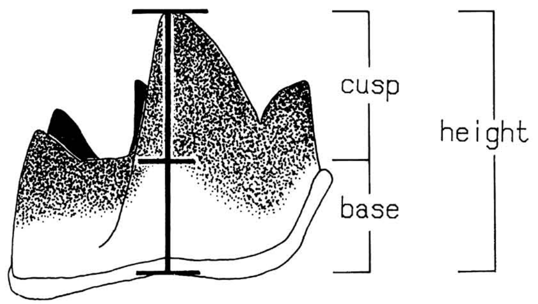

Fig. 1. The tooth measurements taken in the study. The total height of the tooth ("height") and the height of the pigmented area ("cusp") were measured under a dissecting binocular microscope along the largest cusp of the first lower molar (M_1). The height of the unpigmented basal part of the tooth ("base") was calculated by subtraction.

2.2. Measuring of teeth

After dissection, the shrews were preserved for some years in 80% alcohol before the tooth measurements were taken. They were measured without detaching and cleaning the skulls, because in shrews the gum does not cover the teeth. The measurements were taken under a dissecting binocular microscope, by using a micrometer eyepiece (magnification 50×) from the fourth (tallest) tooth in the lower jaw (= first lower molar, M_1, according to Skarén 1979). The total height of the tooth (*height*) and the height of the pigmented cusp (*cusp*) were measured. The height of the unpigmented basal part of the tooth (*base*) was calculated by subtraction (Fig. 1). The mean of the right and left

Table 2. Correlation between the results of the two measurers. N = sample size. *S. araneus*, juveniles, autumn samples 1975–80. The levels of statistical significance in tables and figures: ns = not significant, o = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Individuals N=163	Annual means N=6
Height	+0.710 ***	+0.979 ***
Cusp	+0.682 ***	+0.905 *
Base	+0.655 ***	+0.525 ns
Pigment index	+0.666 ***	+0.786 o

tooth was used, when possible. *Pigment index* was calculated as a percentage of the pigmented cusp over the total height of the tooth (Skarén 1979). Arcsin-transformation (Sokal & Rohlf 1981) was used in statistical tests of the pigment index, but the means given in the tables and figures are based on untransformed values.

2.3. Assessment of measurement error

All the shrews were measured by one person (A). To assess the amount of measurement error, six samples of juvenile *S. araneus* (21–30 individuals from late summer trappings of each year, 1975–80) were measured again by another person (B) who did not know the earlier results. On the individual level the correlations between the two measurings are significant in all traits, but not as high as could be expected (Table 2). This implies that measuring of the teeth is difficult and results in a considerably great measuring error. (Notice that the ranges of the measurements are rather small, because samples of restricted age and time periods were used; i.e. the real total variation in the data is low.) The six annual means (1975–80) of the two measurers correlate significantly in the height and cusp values (Table 2). Both the annual means and individual values of the two measurers have the highest correlations in tooth height, which indicates that it is easier to measure tooth height than to assess the location of the borderline between the pigmented cusp and the unpigmented tooth base. Different interpretation of this pigment borderline increase the measurement error in cusp, base and pigment index values (Table 2). Furthermore, when comparing the means obtained by the two measurers, the difference between the results is smallest in total height of the tooth. The means obtained by measurer B are 1.1% greater in tooth height and 3.8% smaller in cusp, which leads to a remarkably greater values of the tooth base (6.2%, base = height – cusp) and pigment index (4.8%) for measurer B.

Because the annual differences in tooth measurements are great and, moreover, there was an increasing trend in most of the means (see 3.3.), the possibility of systematic measurement error arises. The annual trends in tooth height, cusp and pigment index values were quite similar in both data sets (Fig. 2). The differences between years are smaller in the remeasuring, but the years differ statistically highly significantly in both. In the tooth

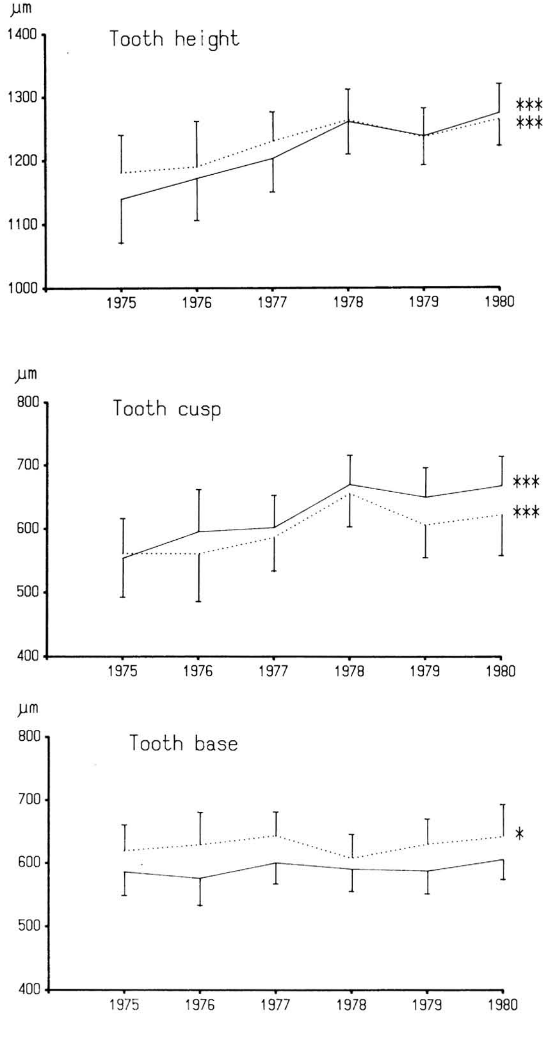

Fig 2. Comparison of the tooth measurements (mean ± *SD*) taken from annual samples of *S. araneus* (*N*=163) by two people. Solid line = measurer A, who measured all the animals of the present study; broken line = measurer B, who measured these samples only. Asterisks indicate statistical significance in the samples between the years.

base there is significant difference between years only in the results of B (Fig. 2).

Because in the first measuring the animals were measured in the order of years, measurer A may have obtained higher values towards the end of the work (perhaps gradually the position of the animals under the microscope was inadvertently changed). However, this possible error cannot explain the great differences between the years (see 3.3).

Table 3. Variability of tooth measurements reflecting tooth wear of the two shrew species. Variability (coefficient of variation in percentages) was calculated according to the formula $CV = 100(s/\bar{x})\,[1+(1/4n)]$ (Sokal & Braumann 1980) during the period April–September (see Table 6). Statistical comparison of *CV*s was tested with *t*-tests, according to formula 12 in Sokal & Braumann (1980). Differences from the lowest value (tooth height) are indicated with asterisks after the value of cusp and pigment index (one-sided tests). The *CV* values of the pigment index were calculated from arcsin -transformed data (not in Table 6). Significance symbols as in Table 2.

	Juveniles		Adults	
	Males	Females	Males	Females
S. araneus				
Height	5.59	5.57	12.75	10.69
Cusp	10.14 ***	10.26 ***	41.20 ***	27.94 ***
Pigment index	6.95 ***	7.06 ***	35.34 ***	21.12 ***
S. minutus				
Height	5.20	7.95	10.27	9.51
Cusp	10.42 ***	13.16 ***	48.70 ***	42.93 **
Pigment index	8.03 ***	10.00 o	41.46 ***	36.56 **

2.4. Variability of the traits

The trait with the lowest variability (among those describing tooth wear) would perhaps be the most reliable indicator of tooth wear. Low variability in a trait may indicate low measurement error, unless strong canalization in the development of the trait reduces its variation (e.g., Pankakoski et al. 1987). The variabilities were compared among the three traits describing tooth wear by calculating coefficients of variation (*CV*, ratio of standard deviation and mean) for each species, age group and sex (Table 3). In all of these groups, the variability of tooth height value is lower (usually significantly) than the variability of cusp or pigment index.

3. Results

3.1. Tooth wear according to age

Two male *S. araneus* in the spring samples had extremely worn teeth (no pigment remaining; dates of trapping 22.4.1970 and 20.3.1971). They may represent individuals that have exceptionally lived through two winters. Because age grouping of these two animals is unreliable, they were excluded from the material. No such individuals were recorded in *S. minutus*.

Among the juveniles there were 25 female *S. araneus* (7.3% of juvenile females) and 8 female *S. minutus* (11.9% of juvenile females) that were sexually mature. Mature juveniles are most frequent in the early part of the reproductive season. This exceptional maturation of year-born females (Pucek 1960) increases the female's body size: body length and weight were significantly greater ($P<0.001$) than those of immature females in both species of shrew. Tooth measurements in the small samples of mature juvenile females did not deviate significantly from those of immature females. Growth and breeding increase energy needs and food intake, and may have affected the tooth wear of these exceptional females, which therefore were excluded from later calculations.

Most of the tooth measurements (height, cusp, pigment index) clearly diminish during the life-span of the two shrew species, but the value of the tooth base remains rather constant (Figs. 3–5). Although these trends are very distinct, the monthly means do not always diminish successively. This is a consequence of differences in the measurements between the years (see below), because the years are differently represented in the monthly means. Shrews have several litters during the reproduction season. During the summer, when litters are born, new very young individuals with unworn teeth continually enter the shrew population. This makes the decrease in tooth wear less rapid during the summer months (cf. Grainger & Fairley 1978). Therefore, the regression analyses that are given below were calculated in juveniles from 15 August onwards.

In the regression analyses, the life-time was calculated in days from the trapping date after 1 June in the summer of birth. Naturally, for most individuals this "age" is not their real age, but the fixation of time

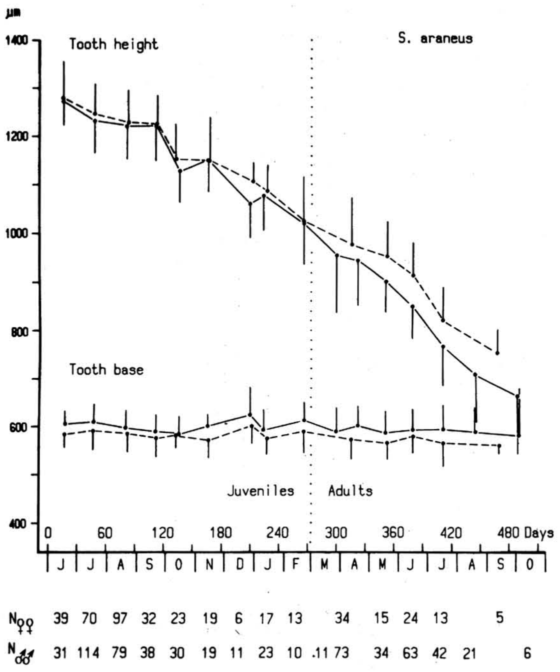

Fig. 3. The change in monthly means (±*SD*) of tooth height and tooth base according to the life span of *S. araneus*. Solid lines = males, broken lines = females. The vertical dotted line indicates the border between juvenile (sexually immmature) and adult (sexually mature) shrews. The means were plotted according to the mean "age" of each sample on the horizontal axes. "Age" was calculated in days from the 1st of June in the year of birth to the trapping date of each individual. Smallest monthly samples of 1–4 individuals were combined with those of the nearest month. For clarity, tooth cusp values are not given, but they closely parallel tooth height values, beginning from means of ca. 700 µm in the first June of the animal.

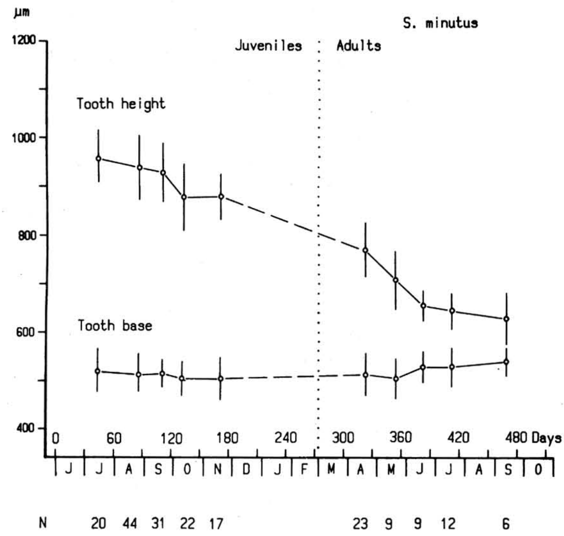

Fig. 4. The change in monthly means (±*SD*) of tooth height and tooth base according to the life span of *S. minutus*. Sexes are pooled, because sample sizes are usually small (samples are totally lacking from December to March). For clarity, tooth cusp values are not given, but they closely parallel the tooth height values, beginning from means of ca. 450 µm in the first June of the animal. For details, see Fig. 3.

is essential for the analysis. The average tooth wear/month (in 30 days) is 39 µm in *S. araneus* and 25 µm in *S. minutus* (Table 4). These figures correspond reasonably well to those given by Crowcroft (1956) for *S. araneus*: approximately 0.05 mm/month and by Jeanmaire-Besancon (1986) for *Crocidura russula*: 32 µm/month. Tooth base seems to increase with age in *S. minutus* (Table 4), but this is most probably explained by differences in this value between the years (see below). The mean of the pigment index in juveniles is lower in *S. minutus* (45.2, $SD = 3.74$) than in *S. araneus* (51.9, $SD = 3.37$; $t = 17.18^{***}$, $df = 552$; see also Fig. 5).

The tooth wear of adults (mature individuals) is significantly more rapid than that of the juveniles (immature individuals) in both species of shrews (Table 5). In tooth height, adults have rates of wear that are nearly twice as great as in juveniles; in the pigment index the differences between age classes are even greater. Samples of *S. minutus* are lacking for winter months (Fig. 4), which may affect the regression coefficients of this species. The tooth base does not change with age within species or within age classes, because tooth wear cannot affect this measurement.

3.2. Differences between sexes in tooth and body dimensions

According to Figs 3 and 5 there seems to be differences between sexes in tooth wear in *S. araneus*. Statistical comparison of sexual dimorphism in tooth measurements, as well as that in body size, was performed with *t*-tests (or Kruskal-Wallis -tests if sample variances differed significantly; Table 6). Moreover,

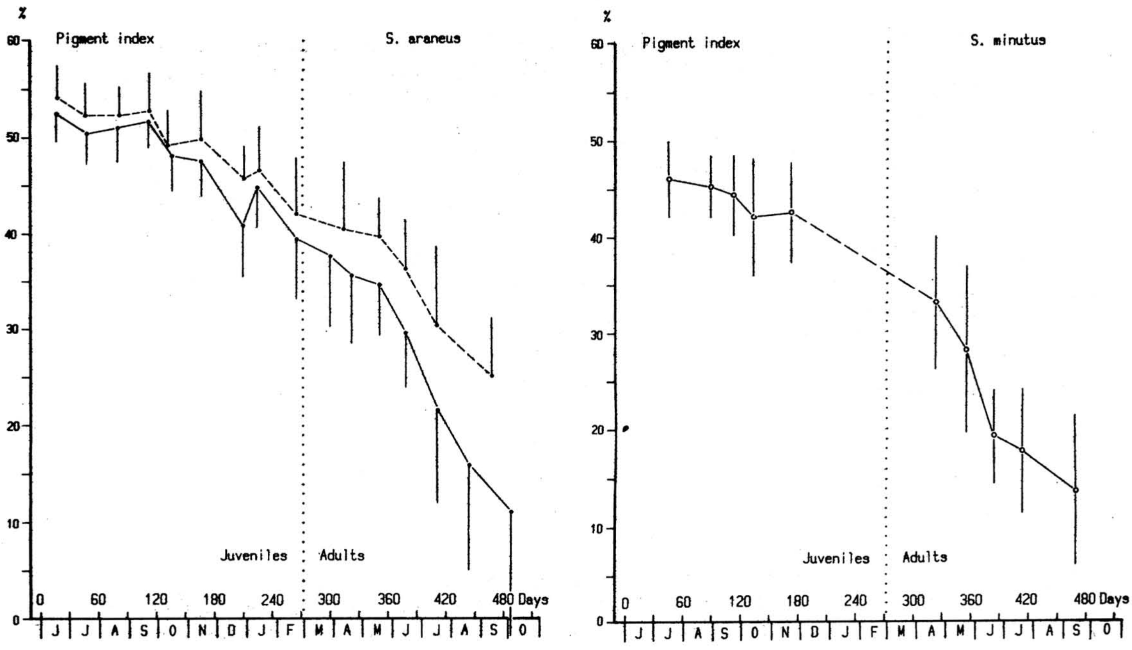

Fig. 5. The change in monthly means (±*SD*) of pigment index according to the life span of *S. araneus* and *S. minutus*. In *S. araneus* solid lines = males, broken lines = females. In *S. minutus* sexes are pooled (samples are totally lacking from December to March). For sample size and other details, see Figs. 3 and 4.

Table 4. Regression coefficients (*b*) for rate of change (30 days) in tooth dimensions and pigment index according to age of the shrew after the 15th of August in the year of birth. In the regression analyses the independent variable is "age" from the 1st of June in the year of birth and the trapping date of the individual; the dependent variable is tooth measurement in microns (pigment index in percentages). *S. araneus*: N=681, *S. minutus*: N=164. Significance symbols as in Table 2.

	S. araneus		*S. minutus*	
Height (μm)	−38.5	***	−24.6	***
Cusp (μm)	−38.6	***	−26.2	***
Base (μm)	+0.0	ns	+1.6	*
Pigment index (%)	−2.6	***	−2.4	***

the effect of individual age on these comparisons was eliminated by analysis of covariance (ANCOVA), but the results were almost similar (Table 6). Females have greater values in tooth height, cusp, and pigment index; in tooth base males have higher means. The difference between sexes is usually statistically significant and is greater in adults than in juveniles (Table 6).

Juvenile females have higher means, especially in the pigmented cusp (Table 6). This indicates that the difference between sexes in juveniles is only partly a consequence of different tooth size, but mainly of differences in the pigmented area of the tooth. Accordingly, the pigment index (describing the percentage of the pigmented area) is much higher in females. There is usually no sexual dimorphism in body size (length and weight) of *S. araneus*, but adult females weigh more than adult males (Table 6). This evidently is a result of weight increase due to embryos and to mammary gland tissue, especially because there is no difference in body length between the sexes.

In *S. minutus*, the trends in sexual dimorphism of tooth dimensions are usually the same, but the differences are smaller than in *S. araneus* and they are not statistically significant. Sexes differ only in body weight, which in juveniles is higher in males and in adults higher in females.

Table 5. Comparison of molar wear speed (regression coefficient for tooth measurement versus time in days between the 1st of June in the year of birth and the trapping date of the individual) between juvenile and adult shrews. For details, see Table 4. Significance symbols as in Table 2.

Variable	Regression coefficients (b) Juveniles		Adults		Ratio b_{Ad}/b_{Juv}	F	P
S. araneus							
Height (µm)	−30.8	***	−53.8	***	1.7	19.87	***
Cusp (µm)	−32.3	***	−51.9	***	1.6	14.81	***
Base (µm)	+1.4	ns	−1.8	ns	..	1.38	ns
Pigment index (%)	−1.8	***	−4.6	***	2.5	41.75	***
S. minutus							
Height (µm)	−17.3	**	−33.2	***	1.9	2.43	o
Cusp (µm)	−16.2	**	−38.9	***	2.4	5.10	**
Base (µm)	−1.2	ns	+5.6	o	..	1.09	ns
Pigment index (%)	−1.1	*	−4.5	***	4.2	12.23	***

Table 6. Comparison of tooth measurements and body size between sexes in *S. araneus* during the period April–September. Mean ± *SD*, dimorphism (100 × (female mean – male mean)/female mean) and statistical significance of the difference (*t*-test or Kruskal-Wallis-test). ANCOVA was calculated over a longer period (April–November), because the effect of "age" (time in days after the 1st of June in the year of birth of the individual) was eliminated. Samples from cone trappings (1975–80) only. N = sample size in *t*-tests (in body length and weight there are 0–3 missing values/group). Significance symbols as in Table 2.

	Females	Males	Dimorphism		ANCOVA
Juveniles					
Height (µm)	1242.8 ± 69.2	1232.1 ± 68.8	0.87	o	*
Cusp (µm)	656.3 ± 67.3	631.0 ± 63.9	4.02	***	***
Base (µm)	586.5 ± 37.0	601.2 ± 36.2	−2.44	***	***
Pigm. index (%)	52.71 ± 3.34	51.12 ± 3.22	3.12	***	***
Body length (mm)	67.06 ± 1.93	67.08 ± 2.08	−0.03	ns	ns
Body weight (g)	7.819 ± 0.53	7.798 ± 0.56	0.28	ns	ns
N	223	238			
Adults					
Height (µm)	905.9 ± 96.4	844.3 ± 107.5	7.30	***	***
Cusp (µm)	331.3 ± 92.2	249.5 ± 102.7	32.76	***	***
Base (µm)	574.6 ± 42.2	594.8 ± 45.1	−3.39	**	**
Pigm. index (%)	35.98 ± 7.29	28.52 ± 9.92	26.18	***	***
Body length (mm)	75.49 ± 3.91	76.38 ± 2.97	−1.16	ns	ns
Body weight (g)	11.730 ± 2.02	11.147 ± 1.14	5.22	**	**
N	63	189			

3.3. Differences between years

The dimensions of tooth and body

Variation between the years (1975–80) in tooth measurements and body size (body length and weight) were studied by ANCOVA. The trends in juvenile shrews during a period of six years are shown in Fig. 6. The figure is based on "adjusted means", which are corrected with regard to the age of the individuals. If the effect of age is not significant (e.g., body size in Fig. 6), the adjusted means are very close to the actual means.

The differences between the years were statistically significant in all the measurements of juvenile shrews, except body weight in *S. minutus* (Fig. 6). In

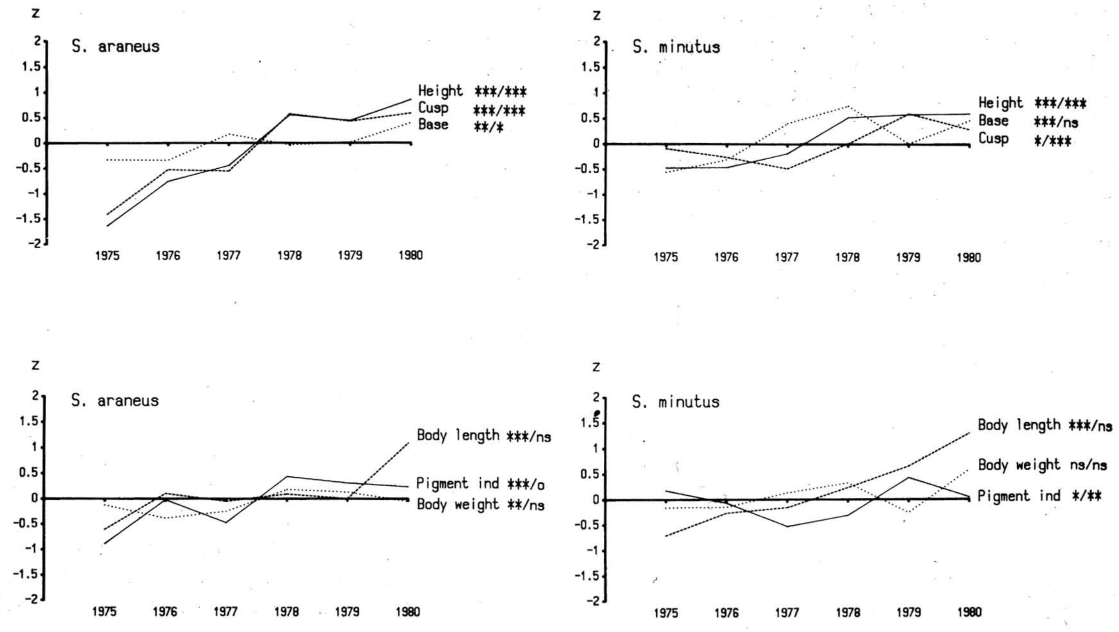

Fig. 6. Annual differences in juvenile tooth measurements and body size of the two shrew species during 1975–80. In order to compare annual variation between the measurements of quite different ranges, the means were standardized by calculating standard normal deviates (Sokal & Rohlf 1981:105). The means and standard deviations used for these calculations were the "adjusted" ones produced by ANCOVA ("age" as a covariate), see text). Asterisks after the variable names indicate statistical significance: the first indicate differences between the years, the second indicate differences due to "age", i.e. the covariate. Sample size (June – November): *S. araneus* N=515, *S. minutus* N=129.

adult shrews the comparison was possible only in *S. araneus*, in which there were differences between the years in body length and weight, but not in the tooth measurements.

There clearly is an increasing trend (low values in 1975–77, high values in 1978–80) during the six years in the tooth measurements of juveniles in both species of shrews (Fig. 6). In *S. araneus* the tooth measurements are lowest in 1975 and highest in 1980. These two years are extreme also regarding body length. The general trend is also seen in body weight. There is an analogous growth trend, though not equally clear, in the dimensions of *S. minutus*. The mean of body length especially, increased evenly during the study period (Fig. 6).

There is a tendency towards positive correlation between the annual means in body size and tooth measurements (Table 7). Although rather high, the correlations are usually not statistically significant, because the number of years is low. Sexual maturation is associated with a remarkable increase in body size in shrews (e.g., Crowcroft 1957). This occurs in spring, when the teeth of the individual are already considerably worn (cf. Figs. 3–5). Body size of the shrew evidently reflects the food conditions and general suitability of the environment during the trapping year, whereas tooth measurements reflect the situation in the previous year. Therefore, in adult shrews (adults 1 in Table 7) the correlation coefficients of annual means were calculated between body size in the year X and tooth measurements in the year X+1. This procedure is essential, if environmental conditions (such as food resources) are assumed to affect both body size and tooth wear in shrews. The correlations between adult body size and juvenile tooth dimensions for the same year also tend to be positive (adults 2 in Table 7).

The effect of weather and population density

Explanations for annual differences in tooth and body dimensions described above may be found in annual weather conditions or in the fluctuations of

Table 7. Correlation coefficients between the annual means of tooth measurements and body size. The calculations are based on the "adjusted means" produced by ANCOVA (year as a grouping variable, "age" as a covariate, sexes pooled). In adults, the correlation coefficient was calculated in two ways: 1) by using the mean of the year X in body size but the mean of the year X+1 in tooth measurements, and 2) between adult body size and *juvenile* tooth dimensions in the same years. The degrees of freedom are usually 4, but in adults 1 $df = 3$. Juveniles from June to November, adults from April to October. The six annual means are based on samples of the following size: *S. araneus*, juveniles N=515, adults N=251; *S. minutus* N=129.

	Height	Cusp	Base	Pigment index
Body length				
S. araneus				
Juveniles	+0.774 o	+0.725	+0.758 o	+0.633
Adults 1	+0.824 o	+0.906 *	–0.040	+0.959 **
Adults 2	+0.632	+0.707	+0.887 *	+0.384
S. minutus				
Juveniles	+0.819 *	+0.606	+0.593	+0.192
Body weight				
S. araneus				
Juveniles	+0.615	+0.646	+0.296	+0.652
Adults 1	+0.750	+0.896 *	–0.255	+0.825 o
Adults 2	+0.686	+0.707	+0.391	+0.723
S. minutus				
Juveniles	+0.301	–0.200	+0.720	–0.570

population density. The correlation coefficients between the annual means and the three important weather factors (precipitation, saturation deficit and temperature) or population density are given in Table 8. The results are rather similar in both species of shrews. The correlations are usually positive as regards precipitation, negative as regards temperature and saturation deficit (the latter describes the dryness of the air). Statistical significance is usually not reached (best in saturation deficit) due to a low number of years. Moreover, the great number of statistical tests increase the probability to obtain a significant correlation by chance alone. There are the same trends both in tooth dimensions and body size, and this increases the reliability of the results, because they are measurements of different quality and were taken by different people.

During the six-year study period, the relative population density (catch index) of *S. araneus* fluctuated, but decreased rather steadily in *S. minutus* (Pankakoski 1985). In *S. minutus* body length, tooth height and tooth base were greater in years of lower population density; in *S. araneus* the correlations are also negative, but not significant (Table 8).

4. Discussion

4.1. Rate of tooth wear

Differences between age groups

Most authors assume — usually without analyzing their data — that the rate of tooth wear in shrews is relatively constant throughout life (e.g., Conaway 1952). In the present study, a clear difference in tooth wear between the two age groups is seen: wear accelerates in older age. Dapson (1968a) observed a curvilinear relationship between age and tooth wear in *Blarina*, but it proceeds more rapidly in young individuals. However, there are differences in the mechanism of tooth wear between *Blarina* and *Sorex* species, as pointed out by Pruitt (1954).

Adamczewska-Andrzejewska (1966) studied variations in tooth hardness of *S. araneus*. The enamel of the tooth is hardest on its outer surface, as is the case in the softer inner part of the tooth, the dentin. Thus, hardness of the tooth decreases towards the core of the tooth. The dentin is also softer in old specimens than in young (Adamczewska-Andrzejewska 1966). Both of these hardness variations should lead to greater tooth wear in old age.

Greater wear in adult shrews can also be a consequence of change with age in energy needs or food quality. Both Croin Michielsen (1966) and Hawes (1977) have shown in *Sorex* species that the home range of the individual is greatly increased when the animal attains sexual maturity. When moving activity increases, the energy needs doubtlessly increase. Consequently, when the animal eats more, its teeth wear more. Reproduction as such also increases energy consumption.

Differences between sexes

Tooth wear is usually assumed to be equal in both sexes. However, sexual dimorphism in tooth measurements was evident in the present study. On the

Table 8. Correlation coefficients between the annual means of the measurements, and weather conditions of the summer or relative population density (1975–80). The calculations are based on the "adjusted means" of tooth and body measurements of juveniles, produced by ANCOVA (year as a grouping variable, "age" as a covariate, sexes pooled; same samples as in Fig. 6). The meteorological data used for calculations were obtaind from the Meteorological Institute of Finland (Porla station) and the values were sums over the May–August period of each year (the sum of saturation deficit and the temperature sum were calculated by pooling the values of daily mean values). Annual mean values of catch index (= individuals/ 100 trap nights during the two first days of the trappings) were used as a estimate of relative population density. Df=4.

	Precipitation	Saturation deficit	Temperature	Population density
S. araneus				
Height	+0.691	–0.904 *	–0.325	–0.308
Cusp	+0.714	–0.898 *	–0.311	–0.328
Base	+0.385	–0.662	–0.288	–0.127
Pigment index	+0.725	–0.863 *	–0.300	–0.346
Body length	+0.118	–0.638	–0.254	–0.658
Body weight	+0.673	–0.472	+0.196	+0.277
S. minutus				
Height	+0.713	–0.830 *	–0.062	–0.908 *
Cusp	+0.434	–0.607	+0.515	–0.497
Base	+0.623	–0.615	–0.654	–0.852 *
Pigment index	–0.044	–0.123	+0.847 *	+0.106
Body length	+0.445	–0.840 *	–0.057	–0.883 *
Body weight	+0.034	–0.282	–0.359	–0.629

basis of this material it is not possible to decide whether the difference between sexes in tooth height of juveniles is a result of different tooth wear or different initial tooth size. The possibility of initial tooth size is supported by the fact that there is sexual dimorphism also in the lower margin of tooth pigment, a part, on which wear has no effect. The unpigmented base of the tooth was lower in females.

In the present study, no sexual dimorphism was observed in body length or weight of juvenile shrews, except in the weight of *S. minutus* (males are heavier). Young males have been shown to be somewhat larger in some studies (Pucek 1955, Dapson 1968b, Kifer & Korybska 1971). The situation is contradictory in the tooth dimensions of the present study: females have higher means. In the muskrat, the difference between the sexes in tooth wear is related to the difference in body size (Pankakoski 1986). Thus, there might be differences in the amount of tooth wear even in juvenile shrews.

In the mole (*Talpa europaea*), males are bigger than females in each year class, which is also seen in tooth dimensions (Grulich 1967). However, sexual dimorphism in tooth wear is low. The average total wear from year class 0 to 5 years of age is 1.13 mm in males and 1.10 mm in females. Grulich (1967: Table 2) gives higher wear values in males in four out of six year classes, particularly in the three first year classes, which comprise over 80% of the total catch. Unfortunately the author does not give standard deviations of his data (Grulich 1967).

Adamczewska-Andrzejewska (1966) observed no differences between the sexes in the hardness of tooth enamel in *S. araneus*. However, there were great differences in the hardness of dentin among the years, although no differences were found in enamel hardness. Adamczewska-Andrzejewska (1966) do not give results concerning possible sexual dimorphism in dentin hardness.

In adult shrews, tooth wear is more severe in males than in females. If there is sexual dimorphism in the amount of wear or in the hardness of the teeth as early as in young shrews, tooth wear in males may be even more rapid in adults, when the wear reaches the softer inner parts of the tooth. It is also possible that greater wear in adult males at least partly is connected with differences between sexes in moving activity. Adult males have larger home ranges than adult females (Croin Michielsen 1966, Hawes 1977) and reproductive females often stay stationary during periods of gestation or lactation (Crowcroft 1957, Pankakoski, unpubl., in *Blarina*, Dapson 1968a). It does not seem probable that teeth of males wear more than females as a consequence of greater energy needs and food consumption, because females need much food for producing their litters. However, there might be differences in food quality due to different activity between sexes. Tardif & Gray (1978) have shown in *Peromyscus* that feeding diversity is greater in dispersing individuals than in resident individuals. Thus the more vagrant adult males may be obliged to feed on more diverse and abrasive food.

Annual differences

Adamczewska-Andrzejewska (1966) showed the annual differences in dentin hardness to be great in *S. araneus*, but no differences were seen in enamel hardness. Variation in dentin hardness is responsible for differences between the years in tooth wear (Adamczewska-Andrzejewska 1966). This is perhaps the main reason for different tooth heights in the present study. Tooth hardness is evidently affected by food quality and availability: dentin may be harder in years with a good supply of high quality food. Another possible factor for different tooth heights between years (without excluding the possible differences in tooth hardness) is different wear of teeth due to annual variation in food.

Earthworms (lumbricids) are important food for *S. araneus* (e.g., Pernetta 1976, Butterfield et al. 1981, Bauerova 1984). During rainy summers, earthworms are available in great numbers and they then comprise a greater part of the diet of *S. araneus* than during sunny and warm summers (Churchfield 1982). In the present study, tooth height had a tendency to show greater means in years of high rainfall and low saturation deficit. If the summer is rainy, the supply of earthworms is good, resulting in good breeding success of *S. araneus*, as indicated by Pankakoski (1985) on the basis of the present samples. Tooth wear may be lower when the food situation is good. On the other hand, Pearson (1945) and Morris (1972) consider grit-filled earthworms to be especially abrasive food that accelerates wear of teeth. It is also possible that wear is greater in dry summers, because there is less lubrication between the wearing surfaces of teeth (Rabinowicz 1962), when all the food is drier.

If animal size is great due to good food resources, this should be reflected also in initial tooth size of the individual. Tooth measurements and body size really seem to correlate positively in the present study. On the other hand, the same pattern of differences between the years were evident in the pigment index, which is a relative value and do not depend on size.

Food resources, on which weather conditions may have a great effect, are perhaps the main factor that affects body and tooth size, as well as tooth wear, of the shrews. High breeding success — typical in rainy summers (Pankakoski 1985) — increases population density. Thus good food resources should lead, on the one hand to high population densities, on the other hand to high values for tooth height and body size. A negative correlation between population density and tooth height was observed, however, at least in *S. minutus* (Table 8). The availability of earthworms is perhaps not important for *S. minutus*, because it feeds mainly on other invertebrates (Pernetta 1976, Grainger & Fairley 1978, Butterfield et al. 1981, Bauerova 1984). During the six-year period tooth height and body length of *S. minutus* increased, but the relative population density decreased. The decrease of population density perhaps improved the living conditions for individual shrews, which are, therefore, bigger both in body and in tooth size.

4.2. Tooth wear as an ageing method in shrews

In his review of mammalian age determination methods, Morris (1972) considers the method based on tooth wear as an easy and quick tool for assessing age of individual mammals. However, there are serious drawbacks in the method: tooth wear will vary with the nature of the diet and there may be regional differences or even genetic variations in dental structure and hardness (Morris 1972, Pucek & Lowe 1975). Although ageing insectivores by tooth wear is a widely used method, few attempts have been made to estimate variation due to sex, age groups or years, which is the main aim of the present study.

In shrews (*Sorex*, *Blarina*, *Crocidura*) there is almost a complete turnover of individuals in the population during one year. In the summer, the population comprises two year classes: one born in the current summer and the other born one year earlier; during the winter the population consists solely of individuals born during the previous summer (e.g., Crowcroft 1957). The maximum life span of a shrew is usually assessed to be ca. 16–18 months; shrews can live through their second winter only exceptionally (Pearson 1945, Conaway 1952, Clothier 1955, Rudd 1955, Dapson 1968a, Hutterer 1977, Skarén

1979, Jeanmaire-Besancon, 1986). It is probable that the two male *S. araneus* of the present material (excluded from calculations) with very worn teeth found in spring, have overwintered twice. The two younger age groups are easily separated on the basis of their tooth wear during the summer, but a more accurate classification of individuals into subsequent litters is not possible. Crowcroft (1956; *S. araneus*), as well as Gairdey & Fairley (1978; *S. minutus*), both measuring only one tooth per jaw, share this conclusion. Therefore, Pernetta (1977) has the opinion that taking only one measurement is not sufficiently sensitive to divide animals into more than year classes. Most authors have not been able to distinguish cohorts of juveniles even when several measurements have been taken (e.g., Jeanmaire-Besancon 1986).

According to Adamczewska-Andrzejewska (1966), variability in the amount and intensity of tooth pigment is great in *S. araneus* (see also Skarén 1979, Vogel 1984). This was also evident in the present study, in which the great variability partly proved to be a result of difference between sexes. The height of the pigmented cusp, measured either absolutely ("cusp") or relatively ("pigment index") is influenced by the variation of the lower border of pigment, which is independent of age. This greatly reduces the usefulness of tooth pigment as an indicator of tooth wear. In age class separation, more reliable results are obtained when the total height of the tooth is measured. On the other hand, pigment index evidently is independent of the absolute size of the tooth, a fact that may be useful when absolute size of the tooth greatly vary according to different body size. If pigment index, despite its drawbacks, is used for age classification, the sexes must be treated separately.

Variability was lowest in tooth height values (Section 2.4.). The differences between sexes and between the two measurers (Section 2.3.) were also smallest in that trait. In the actual age determination of shrews the measuring of total height of several teeth is recommended, bearing in mind any differences between sexes and years.

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