

Anatomical response to the vole population cycles in the Swedish red foxes (*Vulpes vulpes*)

Jan K. Å. Englund

ABSTRACT. The size of animals is often related to food abundance in the year an individual is born and thus the mean size of the animals often varies between birth cohorts. Neglecting these complications may result in false conclusions in analysis of morphological variation. In this study I examine how the lengths of the skulls and the long bones of red foxes *Vulpes vulpes* varied between birth cohorts and in relation to fluctuations in their main food (voles). Foxes, born in the northern half of Sweden when the voles are extremely common, have larger skulls and longer legs than foxes born when the voles are scarce. The relation between the abundance of voles and the size of the skulls and the long bones is less pronounced southwards and ceases in central Sweden. Neglecting these complications may result in false conclusions. When the voles are scarce the reduction of the size of the skull is larger counted as a percentage, than the shortening of the long bones. This indicates that in northern areas with much snow and long winters it is more important for the foxes to retain the length of the legs than to keep the length of the skulls.

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KEY WORDS: food abundance, skull and long bone sizes, snow depth, vole cycles, *Vulpes vulpes*, birth cohorts.

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Анатомические изменения у шведских лисиц (*Vulpes vulpes*) в зависимости от популяционных циклов полевков

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РЕЗЮМЕ. Размеры животных бывают связаны с обилием пищи в год рождения особи, отсюда и вариабельность средних значений признаков, часто наблюдаемая между когортами рождения. Пренебрежение этим обстоятельством может приводить к ложным выводам при анализе морфологической изменчивости. В этой работе я исследовал, как варьировали размеры черепов и длинных костей конечностей лисиц *Vulpes vulpes* в зависимости от года рождения и в связи с колебаниями численности основной добычи (полевки). Лисицы, родившиеся в северной части Швеции в годы, когда полевки были чрезвычайно многочисленны, имеют более крупные черепа и более длинные конечности, чем лисы, рожденные в годы малой численности полевков. Соотношение между численностью полевков и размерами черепов и длинных костей лисиц менее выражено к югу и отсутствует в центральной Швеции. Когда полевки редки, относительное уменьшение размера черепа *V. vulpes* выражено сильнее, чем укорочение длинных костей. Это указывает на то, что в северных районах с большим количеством снега и продолжительной зимой, для лисиц важнее сохранять неизменной длину ног, чем длину черепов.

КЛЮЧЕВЫЕ СЛОВА: обилие пищи, размеры черепа и длинных костей, глубина снега, циклы полевков, *Vulpes vulpes*, когорты рождения.

Introduction

Mammalian species with a wide geographic distribution occurs in very different ecological environments, which they have to adapt to. But it concerns not only different challenges in different geographical areas. Such species must also adapt to the annual changes, which occur in some areas. At the edges of a species' range

the availability of food often varies strongly. Such an example is the amount of voles, which regularly shows large variations in numbers (Hörnfeldt, 1991) in the northern areas, which affects the productivity and survival rate of predators (Englund, 1970; Hörnfeldt, 1991). In addition, the ability to grow in size may be affected by the availability of voles. Some years the voles are extremely common and in other years they are so few that the young predators are starving.

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This paper deals with the anatomical response in red foxes *Vulpes vulpes* to the vole population cycles within three different areas from northern to central Sweden. In all regions voles are their most important prey.

Material and methods

The present paper is based on data from 4058 foxes collected for ecological work during the years of 1966 through 1979 (Englund, 1970, 1980a). The material is divided into three geographically distinct areas, S1, S2 and S3 (Fig. 1). Northern Norrland (S1, 62–68° N) where most of the material come from the provinces of Jämtland and Härjedalen (62–64° N) and southern Norrland (S2) including the provinces of Värmland and the western part of Västmanland (59.5–60.2° N) situated on both sides of the border between the northern and the southern coniferous belt. These two areas have a very low productivity and little agricultural land. Other foxes come from the

central part of Sweden (S3, 58.5–60° N), which is more productive and have rather much agricultural land.

In northern Norrland (S1) the ground is covered with snow (mean of 1950 to 1980) about 150 to 225 days a year, and the mean depth in February 15 was 400–800 mm. The corresponding figures for southern Norrland (S2) are 100–150 days with 300–500 mm and for central Sweden between 75–125 days and 100–300 mm (Eriksson, 1989).

Northern Norrland (S1)

According to the game warden Sven Swahn in Jämtland the voles (mostly *Microtus agrestis* and *Arvicola amphibius*) were extremely abundant the whole year 1966 and the winter 1966–1967 (personal communication 1967, Englund, 1970). In March–April 1967 there were 1.6 voles per stomach ($n=5$; Englund, 1970). In late winter–spring 1967 the vole population crashed (Borg *et al.*, 1969). In November–December 1967 there were 0.2 voles per stomach ($n=25$) and fell to 0.1 in January–February 1968 ($n=80$; the lowest number I ever have found, Englund, 1965, 1970, 1980a). In November–December 1968, there were 0.5 voles per stomach ($n=24$).

The calculated mortality rate for the fox cubs was 70% in 1967, 34% in 1968 and 7% in 1969 (Englund, 1970, 1980a). This also indicates that the food situation was very bad in the spring and summer 1967 and 1968.

In January–February 1970 it was 1.6 voles per stomach and in February–March it was 0.8 indicating that the vole population recovered very much in the spring–summer 1969.

For reasons mentioned I expect that foxes born 1966 in S1, when the voles were extremely common, grew larger than foxes born 1967 and 1968 when the voles were extremely few. I also expect that foxes born 1969 and 1970 should grow larger than foxes born in 1967 and 1968.

Southern Norrland (S2)

In the winter 1965–1966 nearly 3000 two years old spruce plants were destroyed by voles on a 20 hectare plantation at Hällefors in S2, compared with ten plants the year before (personal information in 1966 from forester Gåssté). The mean number of voles per stomach in March–April 1966 was 1.0 ($n=23$), which is high. In June as many as 28 uneaten voles together with large preys still with meat were found at seven active fox dens, and the mean number of voles per scat collected at active dens was 1.0 ($n=247$; Englund, 1980b). The mean number of voles per scat in October–November 1966 was 1.4 ($n=64$) and the mean number of voles per stomach in September–October 1966 was 1.7 ($n=11$) and in January–February 1967 it was 0.9 ($n=23$; Englund, 1970). Thus voles were very common in 1966.

In late winter–spring 1966/1967 the vole populations crashed in whole Norrland including S2 (Borg *et al.*, 1969). In May–June 1967 the mean number of voles per scat was 0.7 ($n=122$) and no vole carcasses were found

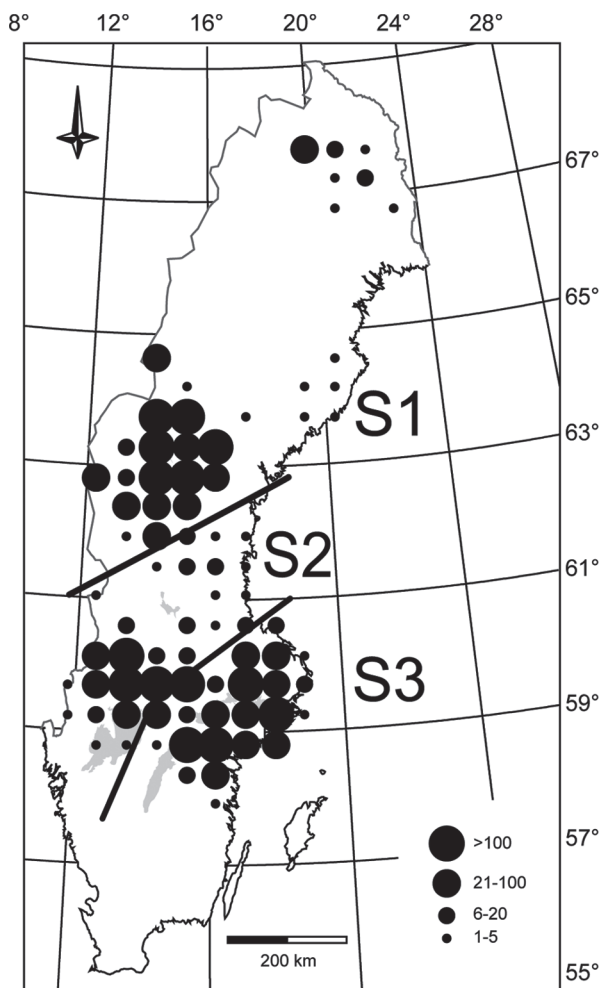


Fig. 1. The distribution of the material per 50×50 km squares within the three areas of Sweden. S1 – northern Norrland, S2 – southern Norrland, S3 – central Sweden. Size of black circles show the number of studied fox specimens.

at any of the 12 active fox dens visited. And there were no remnants with meat from large preys. Furthermore all cubs in one litter caught in the spring died during the few hours it took to catch and tag the cubs. And all cubs were very emaciated (Englund, 1980b). Thus there was very little food available for the fox cubs in the spring 1967.

In the autumn–winter 1967/1968 the voles were scarce. The mean number of voles per stomach in two months periods from September–October 1967 up to and including March–April 1968 was no more than 0.2, 0.3, 0.3 and 0.1 (19, 19, 39 and 65 stomachs). However, it was a little better food situation than in S1 (0.2, 0.1, 0.2 in November to April (25, 80, 10 stomachs)). In May–June 1968 the mean number of voles per scat from active dens was 0.2 ($n=76$). Furthermore there were no voles or other food remnants at the two active dens examined that spring. Thus there were very few voles in the spring 1968. However it was a little better than in S1.

Many farmers reported that they often saw voles in the autumn 1968 and that many mice invaded their houses (personal communication 1968). The mean number of voles per stomach in September–December 1968 was 0.6 ($n=70$) indicating that the food situation was good and a little better than in S1 (0.5; $n=25$). In March–April 1969 it was 0.4 voles per stomach and in May–June 1969 it was 0.8 voles per scat ($n=248$) from active dens (Englund, 1980b). However, there were no vole carcasses at any of the seven active fox dens examined 1969 (Englund, 1980b). The data from the stomachs and the scats indicate that voles were more common in the spring 1969 than in 1968.

I expect that foxes born 1966 in S2, when the voles were extremely common, grew larger than foxes born 1967 and 1968 when the voles were very few. I also believe that the cubs born 1969 grew somewhat larger than cubs born the two years before, since the data from the stomachs and the scats collected in 1969 indicate, that the vole numbers were increasing again. Furthermore I believe that the differences in size between foxes born different years in S2 was less than in S1, since the number of voles was not that few as in S1.

Central Sweden (S3)

In the agricultural area in central Sweden the number of voles fluctuates heavily, but not as much as in the two northern areas. In the winter 1965/1966 up to and including the autumn 1966 voles were extremely common according to many farmers, hunters and own field observations (Englund, 1970). The mean number of voles per stomach in January–April 1967 was 1.1 ($n=21$), which is high. In September–October 1967 they still were very common (1.0; $n=12$) but in the winter 1967–1968 they were somewhat less with 0.5 voles per stomach ($n=190$) in January through April 1968 (Englund, 1970, 1980a). According to several farmers there were few voles in the spring and early summer 1968, but from midsummer they often saw voles in the fields. In September–October 1968 the mean number of rodents per stomach was 1.6 ($n=15$), which is very high, and in November–December

1.4 ($n=86$). In January–April 1969 there were 0.7 voles per stomach ($n=208$). In January–April 1970 it was 0.6 voles per stomach indicating that the food situation was about the same in the summer 1970 as in 1969 (Englund, 1970, 1980a).

Furthermore there are more alternative preys like insects, birds, hares and roe deer in central Sweden compared with the northern areas (Englund, 1965). Therefore I expect that foxes born all years in S3 will grow to the same size.

Juveniles were distinguished from older foxes by the open sutures in the long bones or by the presence of an open suture between the basioccipital and basisphenoid bones in the cranium (Churcher, 1960). Older foxes were aged by the incremental annuli in the tooth cement of the canines.

Cranial measurements are from adults (killed later than June in their second summer of life) as well as from juvenile foxes that are at least seven months old (killed later than about 7.5 months after that 50% of the cubs were born; Lloyd & Englund, 1973). However, skulls where the suture between the basioccipital and the basisphenoid bones is open or where the sutures of the long bones are wide open were omitted. Thus most of the yearlings that were born very late are excluded.

When calculating the mean length of the long bones only data from foxes, where the long bones are supposed to be full grown according to the sutures, are used.

The condylobasal length of skull (CBL) and the length of the long bones have been measured to the nearest 0.1 mm as described by von den Driesch (1976).

To examine whether the large variation in the amount of food from year to year affected the possibility for the fox cubs to grow, ANOVA-tests followed by Hochberg's GT2 post hoc tests were carried out. Figures were drawn using the software package PIA (Bignert, 2013). Differences in measurements are considered significant when $p<0.02$.

Results

The size of the skulls

Male and female foxes that were born 1966 in northern Norrland, when the rodents were extremely abundant, had on average 5.9 and 4.6 mm longer skulls than those born in 1967 and 1968 when there were extremely few rodents ($p<0.001$; Fig. 2, Appendices 1, 2, 3 and Englund, 2006). And cubs born 1969, when the voles had increased in number, grew larger than the foxes born 1967 and 1968.

The situation in southern Norrland is not as clear as in northern Norrland. The males born in 1966 when rodents were extremely common, did not have significantly longer skulls than those born in 1967 (0.5 mm, $p>0.05$) when the voles were very few (Fig. 2, Appendix 1). However, they were 2.3 mm longer than those born in 1968 when voles had increased somewhat in numbers ($p<0.01$) but still were very few.

On the other hand, the average skull length in females born 1966 was 2.6 mm larger than in those born 1967

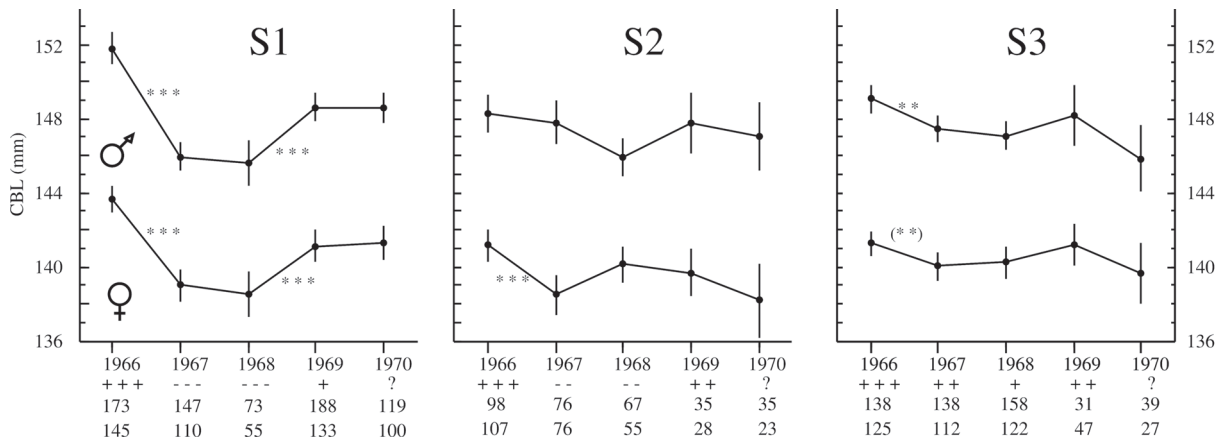


Fig. 2. Mean length of the skulls (mm) of *Vulpes vulpes* in different birth cohorts. Indexes of the amount of voles: +++ = small rodents extremely common, ++ = very common (1.0 vole/stomach), + = rather good (0.5 vole/stomach), - = very rare (0.2 to 0.3 vole/stomach), --- = extremely rare (≤ 0.1 vole/stomach). The error bars specify the 95% confidence interval of the mean. The significance of the differences in the means are shown by asterisks: (**) = $p < 0.02$, (*) = $p < 0.01$ and (***) = $p < 0.001$. The number of specimens in the figures (males and females) is given below the indexes of the abundance of voles.

Table 1. Differences in length (%) between foxes born 1966 and 1967 and for S3 also 1966 and 1968. Mean shows the mean of the four long bones. (**) = $p < 0.02$, (*) = $p < 0.01$ and (***) = $p < 0.001$.

Males	Birth cohorts	CBL		Humerus		Ulna		Femur		Tibia		Mean
S1	1966–67	- 3.8	***	- 2.4	***	- 2.4	***	- 3.6	***	- 2.7	***	- 2.8
S2	1966–67	- 0.5		0.7		- 0.2		- 0.3		0.3		0.1
S3	1966–67	- 1.0	**	- 0.4		- 0.7		- 0.7		- 1.0		- 0.7
S3	1966–68	- 1.2	***	- 0.6		- 0.8		- 0.6		0.2		- 0.5
Females	Birth cohorts	CBL		Humerus		Ulna		Femur		Tibia		Mean
S1	1966–67	- 3.1	***	- 2.3	***	- 2.4	***	- 3.4	***	- 3.1	***	- 2.8
S2	1966–67	- 1.8	***	- 0.8		- 1.3	(**)	- 2.0	(**)	- 1.7		- 1.5
S3	1966–67	- 0.9	(**)	- 0.2		- 0.6		- 0.7		- 1.3		- 0.7
S3	1966–68	- 0.8		- 0.3		- 0.6		- 0.7		- 0.5		- 0.5

($p < 0.001$). But it was not significantly larger than that of females born 1968 (however, the skulls in question were 1.0 mm longer but with $p > 0.05$; Fig. 2, Appendix 2).

The voles were extremely abundant in central Sweden (S3) in 1966. The skulls in male foxes born that year and shot in central Sweden, were 1.5 mm longer than in males born in 1967 ($p < 0.01$). This in spite of that the rodents were still very abundant in the spring and summer period 1967 (1.0 vole per stomach). And the skulls in males born 1968, the year the rodents were fewest, were 1.8 mm shorter than those born 1966 ($p < 0.001$). In females the variation in the size of the skulls was less (Fig. 2, Appendix 2).

The long bones

The foxes that were born 1966 in northern Norrland (S1), when the rodents were extremely abundant, had longer legs than those born in 1967 and 1968 (2.3 to 3.6%, $p < 0.001$). The diagrams for all long bones look about the same as for femur (Fig. 3, Appendices 1, 2).

The length of all long bones was about the same for all birth cohorts in males from south Norrland ($p > 0.02$). However, in the females born 1967 when the voles were very few, all long bones with one exception, were shorter than in the other birth cohorts ($p < 0.02$ for ulna, radius and femur; Appendix 2).

In the central part of Sweden (S3) the long bones in all birth cohorts, males as well as females, were of about the same length irrespective of the variation in the amount of voles ($p > 0.02$; Fig. 3 and Appendices 1, 2).

Discussion

The skulls in S1

In northern Norrland there is a strong relation between the amount of voles during the spring–summer period and the size of the skulls in foxes and it probably concerns their head and body lengths as well. Foxes born in years when the voles are extremely common will grow larger than foxes born in years with very few voles.

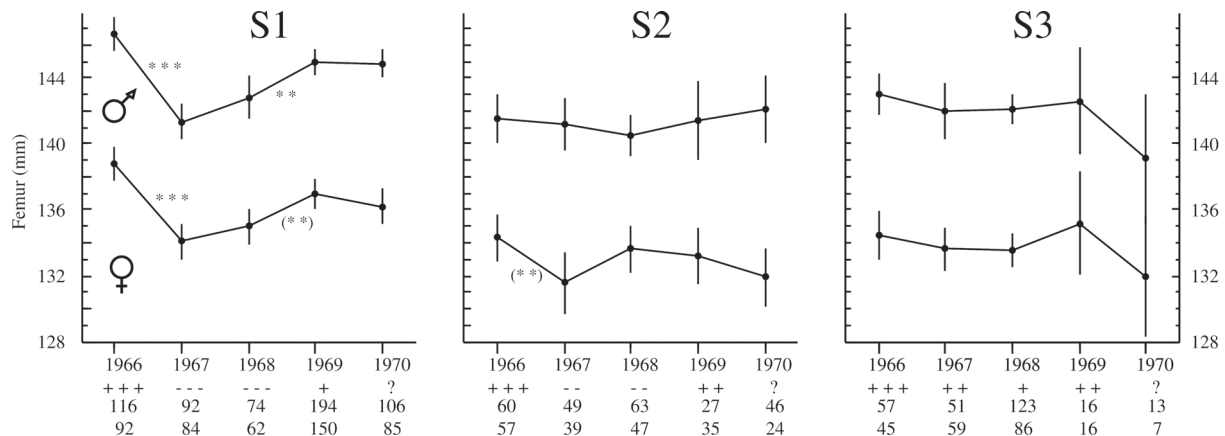


Fig. 3. Mean length of femur (mm) of *Vulpes vulpes* in different birth cohorts. Indexes of the amount of voles: +++ = small rodents extremely common, ++ = very common (1.0 vole/stomach), + = rather good (0.5 vole/stomach), - = very rare (0.2 to 0.3 vole/stomach), --- = extremely rare (≤ 0.1 vole/stomach). The error bars specify the 95% confidence interval of the mean. The significance of the differences in the means are shown by asterisks: (**) = $p < 0.02$, * = $p < 0.01$ and *** = $p < 0.001$. The number of specimens in the figures (males and females) is given below the indexes of the abundance of voles.

The skulls in S2

In southern Norrland voles would never be that extremely scarce as further north, when the vole populations have crashed, and furthermore there are more alternatives, since the habitats there are somewhat richer and the summers are longer.

In the spring and summer 1966 voles were extremely common, but in 1967 there were very few voles. As a result of the food shortage, the skulls in the females born 1967 got 2.6 mm shorter than in 1966 ($p < 0.001$, Fig. 2, Appendix 2).

Males on the other hand, did not show any significant difference between the years. A possible explanation for the difference in growth between the sexes may be that the smaller, and thus weaker females, had difficulties in the competition of the food. Males on the other hand, could get enough food to grow as large as those, who were born 1966. Another possibility is that small young males disperse more often than other groups of foxes, when the food is very scarce. This means that the remaining males born 1967 are larger than those who have dispersed.

The skulls in S3

In the central part of Sweden voles also vary strongly in numbers between years, but they would never be as scarce as in the two northern areas (0.4 voles per stomach in autumn–winter periods is the lowest number found in nine years material; Englund, 1965, 1970 and unpublished data). And the good supply of alternative preys means that foxes always have plenty of food available (Englund, 1965).

In spite of that males born 1967 when the voles still were very common (1.0 voles per stomach) had shorter skulls than males born 1966 ($p < 0.01$, Fig. 2). If the small males, as it was supposed here above left S2 in 1967, had immigrated into central Sweden it could explain the problem.

But why were the males born 1968 and shot in S3 so small compared with foxes born 1966 ($p < 0.001$)? If it was the case that small males born 1968 come from S2 that year, the remaining males in S2 should not have been small (Fig. 2). A possible explanation for the problem that the males born 1968 and shot in S2 were small is that small young males born 1968 dispersed southwards from northern Norrland (S1) into S2 at the same time as small males born 1968 in S2 dispersed into S3. The amount of food was very bad in both areas in the north that year.

However, if small males dispersed from S1 into S2 in 1968, the same kind of dispersal might have happened in 1967 too. And thus males born 1967 and shot in S2 should have been small. So why were males born 1967 and shot in S2 large? A possible explanation is that fewer small males dispersed from S1 in 1967 than in 1968.

I do not know how many yearlings there were in S1 in the autumn of 1967 compared with the number of yearlings in 1968. However, the calculated mortality rate among young foxes in S1 was 70% in 1967, compared with 34% in 1968 (Englund, 1970, 1980a). Thus, the hypothesis that a dispersal of young small males from northern Norrland was higher in 1968 than in 1967 is far from impossible.

The fact that males born 1966 and 1967 and shot in southern Norrland (S2) had the same size of the skulls while they differed with 2.6 mm in females ($p < 0.001$) may have been caused just by chance. And that the skulls in males born 1966 and 1967 and shot in central Sweden differed in length with 1.5 mm ($p < 0.01$) may also have been caused by chance. And that males born 1968 and killed in central Sweden had 1.8 mm shorter skulls than males born 1966 ($p < 0.001$) may of course also be incidental.

There is no evidence if small males disperse more often than other groups of foxes or if they disperse more often when the voles are scarce, and thus I do not have the slightest idea if my theory is correct. However, the theory gives a possible explanation of the problems observed in

S2 and S3. The good thing with the theory is that one does not have to reject several highly significant differences.

The length of the long bones in S1–S3

Foxes born in northern Norrland when the voles were few got 2.3 to 3.6% shorter legs than foxes born when the voles were very common ($p < 0.001$, Fig. 3, Table 1, Appendices 1, 2). In seven comparisons out of eight among the foxes from northern Norrland (foxes born 1966 compared with the cohort from 1967), the long bones decreased less in size than the skulls (Table 1).

There was no significant decrease in length of the male long bones in southern Norrland (S2) but in the females there was a 0.8% to 2.0% decrease four times out of four with $p < 0.02$ for ulna and femur (Table 1). The absence of a significant decrease in length of the male long bones is supposed to be a result of the dispersal of small young males from southern Norrland 1967. Therefore the long bones among male foxes born in southern Norrland in 1967 probably got shorter, than the data in Fig. 3 and Appendix 1 indicate. In that case the long bones will get shorter in foxes born in S2 as in S1 when the voles are scarce, but the differences in S2 will be smaller compared with the differences in S1 (Fig. 3, Table 1, Appendices 1, 2). In seven times out of eight the long bones in the material showed less reduction in length than the skulls ($p > 0.02$; Table 1).

In the richer provinces in the central part of Sweden (S3) voles were extremely abundant in 1966, very common in 1967 and common in 1968. The mean length of the long bones was about the same for foxes born all years ($p > 0.02$; Table 1, Appendices 1, 2).

Conclusions

When the amount of food is reduced to a critical level the skulls are getting smaller. The length of the long bones is not affected until the food availability is very low or extremely low. Obviously it is more important to keep a proper length of the legs, than to keep the length of the skulls. In areas with long winters and deep snow it is very important to have long legs, if the snow problems cannot be solved with a decreased body weight combined with large paws.

The data presented show that foxes living near the northern boundaries of their geographical distribution vary in size depending on when in the vole cycle the foxes are born. They also show that the differences do increase closer to the border. Furthermore they show that in more central areas of their geographical range, where the habitats are more complicated with less variation in food availability, the foxes born different years will

grow to the same size, irrespective of the variation in vole numbers that normally occur there.

Neglecting these complications when studying for example Bergmann's rule may cause false conclusions, at least if the question is if the foxes are adapted to the harsher conditions, that normally exist close to the border of their geographical range.

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Appendix 1. The condylobasal length (CBL) and the length of the long bones (mm) in red fox males born 1966–1970 in northern Norrland (S1), southern Norrland (S2) and central Sweden (S3).

	Born	1966			1967			1968			1969			1970		
		mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n
CBL	S1	151.8	5.56	173	146.0	4.61	147	145.6	5.22	73	148.5	4.78	188	148.6	4.26	119
	S2	148.3	5.16	98	147.6	5.28	76	146.0	4.06	67	147.9	4.63	35	147.1	4.89	35
	S3	148.8	4.37	138	147.3	4.18	138	147.0	4.52	158	148.0	4.21	31	146.1	5.20	39
Humerus	S1	138.7	5.18	165	135.4	4.97	131	134.9	4.79	70	137.1	5.31	175	137.9	4.93	81
	S2	134.7	5.32	111	135.6	4.97	70	134.2	4.42	57	134.5	5.86	23	136.0	4.95	37
	S3	135.2	4.64	122	134.6	5.18	109	134.4	4.54	114	134.1	4.41	11	132.7	5.92	11
Ulna	S1	153.4	5.55	233	149.7	5.40	194	149.5	5.46	86	151.6	5.18	231	152.4	5.13	122
	S2	149.2	5.36	131	148.9	5.45	75	148.0	4.73	73	148.2	5.33	29	150.0	5.77	51
	S3	150.0	4.61	146	148.9	4.98	142	148.8	5.03	176	149.8	4.19	26	147.4	6.09	41
Radius	S1	130.8	4.77	241	128.0	4.65	207	127.4	4.48	104	129.1	4.85	255	129.8	4.45	137
	S2	127.1	4.42	141	126.8	4.49	81	126.2	4.58	82	126.7	4.56	31	127.7	5.16	55
	S3	127.5	4.02	144	126.8	4.27	146	126.7	4.09	178	127.3	3.95	26	125.3	5.12	45
Femur	S1	146.6	5.63	116	141.3	5.31	92	142.8	5.68	74	145.0	5.53	194	144.9	4.65	106
	S2	141.6	5.77	60	141.2	5.60	49	140.5	5.11	63	141.4	5.84	27	142.1	6.69	46
	S3	143.0	4.64	57	142.0	6.01	51	142.1	5.14	123	142.6	5.94	16	139.1	6.27	13
Tibia	S1	160.1	6.39	157	155.7	6.34	125	157.6	5.97	54	159.8	5.58	97	158.8	6.18	110
	S2	154.1	5.93	51	154.6	6.41	48	155.0	5.75	24	153.4	6.70	28	155.9	6.74	32
	S3	156.1	5.58	68	154.6	5.60	64	156.4	5.93	70	156.9	6.72	25	153.9	5.38	18

Appendix 2. The condylobasal length (CBL) and the length of the long bones (mm) in red fox females born 1966–1970 in northern Norrland (S1), southern Norrland (S2) and central Sweden (S3).

	Born	1966			1967			1968			1969			1970		
		mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n
CBL	S1	143.6	4.44	145	139.1	4.30	110	138.6	4.42	55	141.1	4.63	133	141.1	4.33	100
	S2	141.1	4.47	107	138.5	4.73	76	140.1	3.49	55	139.7	3.23	28	138.2	4.51	23
	S3	141.3	3.92	125	140.0	3.87	112	140.2	4.54	122	141.2	3.81	47	139.7	4.12	27
Humerus	S1	130.5	4.26	148	127.5	4.35	112	128.0	4.19	71	128.9	5.42	126	129.3	3.88	60
	S2	126.6	4.71	114	125.6	5.46	73	126.3	4.95	44	125.7	4.61	28	123.5	4.55	16
	S3	126.8	3.98	110	126.5	4.57	104	126.4	4.54	91	127.6	4.41	15	125.7	3.82	14
Ulna	S1	144.0	4.62	194	140.5	4.66	162	140.6	4.78	76	141.9	5.75	178	143.1	4.62	109
	S2	140.3	5.03	130	138.5	5.81	87	139.6	5.32	68	139.6	4.41	28	138.9	4.31	17
	S3	140.6	4.53	130	139.7	5.01	129	139.7	5.43	131	141.5	4.70	49	140.2	4.21	36
Radius	S1	122.9	3.92	206	120.2	3.94	172	120.0	4.31	82	121.1	5.07	201	122.1	4.24	118
	S2	119.5	4.28	137	118.0	4.93	91	118.9	4.42	71	118.7	3.86	29	117.8	4.24	21
	S3	119.7	3.93	138	119.0	4.28	135	119.1	4.56	129	120.2	4.29	50	119.7	3.58	36
Femur	S1	138.8	4.97	92	134.1	4.94	84	135.0	4.16	62	137.0	5.63	150	136.2	4.91	85
	S2	134.3	5.33	57	131.6	5.82	39	133.6	4.78	47	133.2	5.02	35	131.9	4.08	24
	S3	134.5	4.63	45	133.6	4.94	59	133.5	4.78	86	135.2	5.65	16	131.9	3.63	7
Tibia	S1	151.0	5.14	123	146.3	5.47	100	147.6	5.24	43	149.2	6.38	83	148.6	6.00	80
	S2	145.7	5.67	54	143.2	6.05	38	145.2	6.12	37	145.1	4.19	27	145.4	4.69	21
	S3	147.2	6.15	56	145.3	5.17	72	146.4	5.97	73	147.7	5.09	40	145.6	4.97	31

Appendix 3. The year the red foxes were born in S1 to S3, the number of voles per stomach (voles/st), the condylobasal length in mm (mean), the number of specimens (*n*), the change in mm between foxes born different years (Diff), and the significance of the differences.

S1	Born	1966	1966	1966	1967	1967	1967	1967	1968	1968	1968	
	months	1-4	9-12		1-4	5-8	9-12	1-4	5-8	9-12		
	voles/st	high	high		1.6	few	0.2	0.1	few	0.5		
			mean		Diff		mean		Diff	mean	<i>n</i>	
	males	---	151.8	173	-5.8	$p<0.001$	146.0	-0.4	$p>0.02$	145.6	73	
	females	---	143.6	145	-4.5	$p<0.001$	139.1	-0.5	$p>0.02$	138.6	55	
	Born	1966	1966	1966	1967	1967	1967	1968	1968	1968	1968	
	months	1-4	9-12		1-4	5-8	9-12	1-4	5-8	9-12		
	voles/st	1.0	1.4		0.9	few	0.2	0.2	few	0.6		
			mean		Diff		mean		Diff	mean	<i>n</i>	
males	---	148.3	98	-0.7	$p>0.02$	147.6	-1.6	$p>0.02$	146.0	67		
females	---	141.1	107	-2.6	$p<0.001$	138.5	+1.6	$p>0.02$	140.1	55		
S2	Born	1966	1966	1966	1967	1967	1967	1968	1968	1968	1968	
	months	1-4	9-12		1-4	5-8	9-12	1-4	5-8	9-12		
	voles/st	high	high		1.0	good	0.6	0.5	good	1.4		
			mean		Diff		mean		Diff	mean	<i>n</i>	
	males	---	148.8	138	-1.5	$p<0.01$	147.3	-0.3	$p>0.02$	147.0	158	
	females	---	141.3	125	-1.3	$p<0.02$	140.0	+0.2	$p>0.02$	140.2	122	
	S3	Born	1966	1966	1966	1967	1967	1967	1968	1968	1968	1968
		months	1-4	9-12		1-4	5-8	9-12	1-4	5-8	9-12	
		voles/st	high	high		1.0	good	0.6	0.5	good	1.4	
				mean		Diff		mean		Diff	mean	<i>n</i>
males		---	148.8	138	-1.5	$p<0.01$	147.3	-0.3	$p>0.02$	147.0	158	
females		---	141.3	125	-1.3	$p<0.02$	140.0	+0.2	$p>0.02$	140.2	122	