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Cranial and skeletal growth patterns in red foxes (*Vulpes vulpes* L., 1758)

Jan Englund

ABSTRACT. Different year-classes of red foxes (*Vulpes vulpes*) grow to the same mean size during their first autumn of life in areas with a good food supply. Most parts of the cranium, mandible and long bones stop growing during the September-November period in yearlings. The zygomatic width is an exception and continues to grow throughout the winter. Several parts of the cranium and mandible continue to increase for many years.

KEW WORDS: *Vulpes vulpes*, skeletal growth, age, food abundance.

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Особенности роста черепа и скелета у лисицы (*Vulpes vulpes* L., 1758)

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РЕЗЮМЕ. Лисицы (*Vulpes vulpes*) различных возрастных групп достигают в среднем сходных размеров в течение первой осени жизни в районах с хорошей кормовой базой. У сеголеток большинство отделов черепа, нижней челюсти и длинных костей конечностей прекращает расти к сентябрю–ноябрю. Исключение составляет лишь скуловая ширина, которая продолжает увеличиваться в течение зимы. Некоторые отделы черепа и нижней челюсти продолжают увеличиваться в течение многих лет.

КЛЮЧЕВЫЕ СЛОВА: *Vulpes vulpes*, череп, скелет, рост, возраст, обилие пищевых ресурсов.

Introduction

Huson & Page (1980) showed that several parts of Welsh red fox (*Vulpes vulpes*) crania grow in size up to the age of four years. In female foxes, fewer parts increase in size than in males, and the changes are proportionally smaller. Swiss foxes from Berne reach their maximum total skull length by November of the first year. In contrast, the weight of the skull only reaches 80 to 90% of adult weight by that time, and does not continue to grow during the winter (Lüps, 1974). Slovakian adult male foxes have larger skulls than yearlings. There is, however, no corresponding difference between old and young females (Hell *et al*., 1989).

According to Lindström (1983) the growth of the mandible stops in November-December for subadult female foxes living in the southern part of the coniferous belt in Sweden. When food is scarce, the vixens will not be fully grown at that time. These foxes presumably in contrast to others he says compensate for this delay by further growth later in life.

The contents of fox stomachs show that the availability of small rodents varied a little between years in the studied area in southern Sweden, but at a high level and to a lesser degree than in northern Sweden. There is also ample alternative food available in the south, and therefore the food supply is relatively stable at a high level year after year (Englund, 1965, 1970, 1980).

The present paper addresses the question of whether or not foxes living under such food conditions continue to grow for several years or not.

Material and methods

The present paper is based on data from skulls, mandibles and long bones measured on 1800 foxes shot between 1965 and 1971 in the agricultural counties of Uppland, Södermanland, and Östergötland in southern Sweden. These provinces are situated between 58.5°and 60° N latitude.

Although the material was collected during all months of the year, the majority of the specimens were shot between November and March, with less than 100 foxes, including the juveniles, having been shot between May and September.

Because the carcasses were collected from hunters often the long bones were missing or parts of the skeleton were destroyed. This explains the varying sample size among variables (see Tables).

The skeletal parts were simmered for several hours in water with domestic detergent before cleaning.

Table 1. Age specific means of some cranial measurements in a sample of male foxes from an agricultural area in southern Sweden. Ages are given as years and the week numbers during which the foxes were killed. Means in mm; standard deviations and the number of foxes are given in parentheses.

Ages	Greatest cranial length	Condylobasal length	Palatal length	Braincase width	Mastoid width	Zygomatic width	P4 length
0.18–0.21	88.3 (–/1)	78.9 (–/1)	40.6 (–/1)	42.6 (–/1)	37.2 (–/1)	51.2 (–/1)	–
0.22–0.26	111.2 (–/1)	–	49.6 (–/1)	–	–	–	–
0.27–0.30	128.5 (5.37/2)	121.4 (7.50/2)	60.4 (–/1)	46.6 (1.10/3)	45.7 (0.88/4)	–	–
0.31–0.35	144.7 (7.47/4)	138.0 (5.61/4)	73.8 (1.55/3)	48.5 (1.69/4)	46.9 (2.88/5)	74.2 (1.13/2)	14.1 (0.49/4)
0.36–0.39	151.7 (4.75/10)	145.2 (2.98/ 9)	74.8 (3.18/11)	47.7 (1.38/17)	48.1 (1.34/17)	75.6 (1.52/4)	14.2 (0.55/22)
0.40–0.44	153.5 (3.95/26)	145.6 (3.90/25)	76.0 (2.54/30)	48.7 (1.34/38)	48.7 (1.43/40)	77.1 (1.77/19)	14.3 (0.54/54)
0.45–0.48	153.2 (5.27/45)	145.8 (4.59/41)	75.8 (2.79/49)	48.4 (1.23/41)	48.4 (1.29/44)	78.8 (2.72/21)	14.3 (0.61/57)
0.49–0.53	154.2 (5.55/46)	146.9 (5.13/46)	76.3 (3.19/55)	48.2 (1.24/43)	48.3 (1.46/45)	79.0 (2.81/23)	14.2 (0.54/57)
0.00–0.04	155.8 (5.11/48)	148.2 (4.99/41)	76.3 (3.00/63)	49.0 (1.41/44)	48.7 (1.45/48)	80.7 (2.74/37)	14.5 (0.52/68)
0.05–0.08	154.3 (4.30/79)	147.0 (3.84/76)	76.4 (2.39/93)	48.8 (1.09/76)	48.7 (1.29/77)	80.9 (2.15/63)	14.5 (0.58/98)
0.09–0.13	154.0 (4.90/109)	146.7 (4.42/108)	75.8 (2.79/122)	48.5 (1.23/105)	48.6 (1.55/109)	81.0 (2.56/77)	14.4 (0.63/127)
0.14–1.26	154.4 (4.58/26)	146.6 (4.69/24)	76.0 (2.69/29)	49.0 (1.15/25)	48.8 (1.45/24)	81.6 (2.77/21)	14.3 (0.59/30)
0.49–1.26	154.4 (4.87/308)	147.0 (5.50/295)	76.1 (2.78/362)	48.7 (1.24/293)	48.6 (1.45/303)	80.7 (2.59/221)	14.4 (0.59/380)
1.27–2.26	155.8 (5.40/168)	148.3 (4.77/160)	76.9 (3.34/187)	49.0 (1.20/156)	49.0 (1.57/162)	83.1 (2.41/155)	14.4 (0.58/189)
2.27–3.26	155.9 (4.77/92)	148.4 (4.45/89)	76.9 (2.67/106)	49.1 (1.39/92)	49.0 (1.47/95)	83.7 (2.47/93)	14.5 (0.58/110)
3.27–4.26	158.0 (5.44/33)	149.6 (4.97/29)	78.0 (2.99/37)	49.3 (1.26/36)	49.1 (1.21/36)	83.8 (2.14/33)	14.4 (0.58/42)
4.27–5.26	157.9 (4.77/26)	150.0 (4.60/25)	77.7 (2.87/29)	49.4 (1.13/27)	49.4 (1.51/29)	85.2 (2.42/26)	14.4 (0.63/33)
5.27–6.26	160.9 (4.81/7)	153.2 (4.31/7)	79.5 (3.08/8)	49.9 (1.18/11)	49.8 (1.32/11)	85.4 (2.98/11)	14.4 (0.50/13)
6.27–	158.9 (5.12/12)	151.8 (5.27/10)	79.9 (2.45/14)	49.7 (1.43/17)	49.4 (1.71/18)	86.7 (2.99/15)	14.4 (0.70/18)
Change/year	0.9	0.8	0.5	0.2	0.2	1.0	–
p-value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	> 0.492
Correlation	0.24	0.23	0.24	0.22	0.18	0.51	–
SE	5.0	4.6	2.9	1.2	1.5	2.6	–

Juveniles were distinguished from older foxes when possible by open sutures in the tibia or by the presence of an open suture between the basioccipital and basisphenoid bones in the cranium (Churcher, 1960). Other foxes were aged by the incremental annuli in the tooth cementum of the canines. The technique used was that described by Jensen & Nielsen (1968) and modified by Englund (1970).

Cranial measurements taken are as follow (the codes in parentheses correspond to those given in von den Driesch, 1976): greatest length (akrokranion-prosthion) (1); condylobasal length (2); palatal length (the median point of intersection of the line joining the deepest indentations of the choanae to the prosthion) (13a); greatest width of the braincase (29); mastoid width (23); zygomatic width (30); and length of the right upper P4 (L).

Mandibular measurements are: total length (from infradentale to the midpoint of the condyle) (1); distance between the alveoli of the canine c1 and the p1; length of p1–p4 (11), and of m1–m3 (10) both measured along the alveoli; thickness of the mandible below the middle of the m1; and length of the crown of m1 (13).

Greatest length (GL) was measured on the humerus, the ulna, the radius, and the tibia. Femural length (GLC) was measured from the superior surface of the femoral head to the most distal point of the bone, which for foxes is the greatest length in the femur.

Measurements were recorded to the nearest 0.1 mm using calipers connected to a computer (Billfors & Jacobsen, 1974).

Age-specific means and standard deviations for the different variables, as well as the number of foxes measured, are given in Tables 1–6. The ages are given in years followed by the week during which the animals were killed.

The relationship between skull, mandibular, and long bone sizes and age was analyzed quantitatively for each sex by regression analysis using SPSS/PC+. In all tests yearlings killed earlier than December were excluded.

Table 2. Age specific means of some cranial measurements in a sample of female foxes from an agricultural area in southern Sweden. Ages are given as years and the week numbers during which the foxes were killed. Means in mm; standard deviations and the number of foxes are given in parentheses.

Ages	Greatest cranial length	Condylobasal length	Palatal length	Braincase width	Mastoid width	Zygomatic width	P4 length
0.18–0.21	–	–	–	–	–	–	–
0.22–0.26	–	–	48.7 (1.77/2)	44.7 (–/1)	42.7 (–/1)	–	–
0.27–0.30	114.3 (–/1)	–	56.1 (–/1)	46.7 (1.91/2)	45.7 (2.61/2)	–	–
0.31–0.35	130.2 (–/1)	125.4 (–/1)	65.8 (–/1)	46.4 (0.21/2)	46.5 (1.56/3)	–	13.5 (0.47/5)
0.36–0.39	146.7 (5.80/6)	139.1 (5.53/6)	71.9 (3.67/7)	48.3 (0.74/8)	47.1 (0.50/8)	76.0 (–/1)	13.8 (0.51/12)
0.40–0.44	146.2 (4.72/10)	139.1 (4.64/10)	72.4 (2.69/11)	48.1 (1.57/12)	46.8 (1.71/14)	73.8 (2.82/6)	14.1 (0.70/18)
0.45–0.48	146.9 (3.95/19)	139.2 (3.87/18)	72.4 (2.63/21)	47.9 (1.21/20)	46.4 (1.43/21)	75.6 (1.64/15)	13.5 (0.58/23)
0.49–0.53	146.0 (4.02/16)	139.6 (3.42/16)	72.1 (1.77/20)	47.6 (1.20/11)	46.8 (1.70/14)	75.0 (1.92/7)	13.7 (0.59/22)
0.00–0.04	146.2 (4.15/37)	139.7 (3.47/31)	72.1 (2.20/48)	47.7 (1.07/37)	47.0 (1.47/36)	75.7 (2.45/34)	13.8 (0.62/52)
0.05–0.08	146.9 (5.08/79)	140.2 (4.54/77)	73.0 (2.90/98)	47.7 (1.12/79)	46.9 (1.32/84)	76.4 (2.30/67)	13.7 (0.58/101)
0.09–0.13	146.2 (4.55/107)	139.4 (4.27/95)	72.7 (2.71/128)	47.6 (1.27/95)	46.8 (1.33/97)	76.5 (2.36/79)	13.7 (0.53/131)
0.14–1.26	147.4 (5.49/26)	141.3 (5.02/23)	73.0 (2.72/28)	48.0 (1.24/25)	47.2 (1.79/26)	77.5 (2.50/23)	13.7 (0.53/30)
0.49–1.26	146.5 (4.72/265)	139.9 (4.30/242)	72.7 (2.66/322)	47.7 (1.18/247)	46.9 (1.41/257)	76.4 (2.39/210)	13.7 (0.56/336)
1.27–2.26	147.7 (4.31/143)	141.0 (3.91/139)	73.3 (2.38/168)	47.7 (1.24/139)	47.1 (1.26/143)	78.2 (2.15/139)	13.8 (0.58/176)
2.27–3.26	148.4 (4.15/83)	141.9 (3.79/80)	73.7 (2.32/91)	48.0 (1.17/79)	47.3 (1.44/81)	78.6 (1.74/75)	13.8 (0.53/92)
3.27–4.26	147.5 (4.31/51)	140.9 (4.39/47)	73.2 (2.77/61)	48.0 (1.33/51)	47.1 (1.34/54)	79.3 (2.42/48)	13.7 (0.52/65)
4.27–5.26	150.4 (4.33/28)	142.9 (3.92/26)	74.0 (2.25/31)	48.2 (1.05/27)	47.4 (1.31/26)	79.8 (2.19/27)	14.0 (0.67/35)
5.27–6.26	149.7 (3.78/20)	143.0 (3.21/19)	74.7 (2.25/23)	48.4 (0.78/21)	47.5 (1.09/22)	80.1 (1.84/23)	14.0 (0.58/26)
6.27–	149.6 (3.09/15)	142.5 (2.69/14)	73.8 (2.38/19)	48.0 (0.95/23)	47.5 (0.85/23)	79.5 (2.33/18)	13.7 (0.37/26)
Change/year	0.6	0.5	0.3	0.1	0.1	0.7	–
p-value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.002	< 0.001	> 0.045
Correlation	0.21	0.21	0.17	0.14	0.13	0.44	–
SE	4.4	4.0	2.5	1.2	1.3	2.3	–

Results

The mean length of the skulls and bones examined did not vary significantly in size among foxes born in different years (p>0.05). Foxes born in 1968, when the rodent population was at a low (Englund, 1970), reached approximately the same mean size during their first autumn as foxes born in other years when rodents were more common. Foxes of all year classes therefore were lumped together for further treatment.

Some parts of the crania and mandibles of yearlings stop growing in November (Tables 1–6). Other dimensions such as the length of the palate, the width of the braincase and the mastoid width, the length of toothrows p1–p4 and m1–m3 of the mandible, mandibular thickness, and the length of the long bones stop growing even earlier (Tables 1–6 and Fig. 1). Zygomatic width on the other hand increased in size throughout the entire winter (Tables 1, 2 and Fig. 2).

The mean length of most parts of the skulls and mandibles studied were larger among older foxes of both sexes. This was especially apparent for the zygomatic width and the distance between c1 and p1 in the mandibles (Tables 1–4 and Fig. 2). In fact the increase in the distance between c1 and p1 corresponds to nearly half of the total increase in the length of the mandible. Whether half the mandibular growth takes place between c1 and p1, or if that increase of length is just a result of movements of the teeth, is not known.

The mean of the mandibular distances m1–m3 and probably also p1–p4 are not greater in older foxes (1.27+) compared with young foxes (0.49–1.26).

Among males most distal long bones increased in size with age. Old vixens, on the other hand, did not have longer bones than yearlings (Tables 5, 6).

For most variables little of the total variation in size (3–6%) is explained by the age (Tables 1–6). However, variation in the zygomatic width is explained by age in 26 and 20% of males and females respectively, and corresponding figures for the distance between c1 and p1 in the mandible are 20 and 21%.

Table 3. Age specific means of some mandibular measurements in a sample of male foxes from an agricultural area in southern Sweden. Ages are given as years and the week numbers during which the foxes were killed. Means in mm; standard deviations and the number of foxes are given in parentheses.

Ages	Total length	c1–p1 length	p1–p4 length	m1–m3 length	Thickness	m1 crown length
0.18–0.21	58.8 (5.53/4)	–	–	–	4.9 (0.88/4)	–
0.22–0.26	–	–	–	–	–	–
0.27–0.30	90.3 (3.30/5)	3.8 (–/1)	32.3 (1.11/3)	21.9 (–/1)	7.4 (1.05/5)	–
0.31–0.35	102.3 (8.42/6)	3.9 (0.53/6)	33.8 (1.30/5)	27.6 (1.00/4)	7.8 (0.48/6)	16.4 (0.71/6)
0.36–0.39	109.9 (3.44/19)	3.1 (0.81/20)	34.8 (1.57/20)	27.9 (1.26/19)	7.5 (0.52/20)	16.5 (0.63/22)
0.40–0.44	111.6 (3.74/36)	3.2 (0.90/41)	34.7 (1.31/41)	27.9 (0.93/39)	7.2 (0.55/44)	16.6 (0.74/54)
0.45–0.48	112.3 (3.67/50)	3.2 (0.80/50)	34.8 (1.41/51)	28.1 (1.17/48)	7.1 (0.37/52)	16.8 (0.73/58)
0.49–0.53	113.5 (4.00/50)	4.0 (1.09/49)	34.5 (1.65/49)	27.5 (1.11/45)	7.1 (0.36/49)	16.5 (0.73/ 57)
0.00–0.04	114.2 (4.14/55)	3.9 (1.02/54)	35.0 (1.57/55)	27.8 (0.96/54)	7.2 (0.50/55)	16.8 (0.63/64)
0.05–0.08	113.3 (3.19/87)	4.2 (0.82/88)	34.8 (1.28/89)	27.7 (0.86/84)	7.3 (0.42/89)	16.7 (0.69/95)
0.09–0.13	113.3 (3.66/117)	4.1 (0.85/118)	34.6 (1.47/118)	27.6 (1.17/110)	7.3 (0.45/117)	16.5 (0.69/128)
0.14–1.26	113.2 (3.21/24)	4.2 (0.89/25)	34.6 (1.33/25)	27.3 (0.86/21)	7.2 (0.42/25)	16.6 (0.77/30)
0.49–1.26	113.5 (3.65/333)	4.0 (0.91/334)	34.7 (1.46/336)	27.6 (1.03/314)	7.2 (0.44/335)	16.6 (0.70/374)
1.27–2.26	114.8 (3.69/158)	5.0 (1.00/158)	34.8 (1.44/158)	27.4 (1.09/154)	7.3 (0.48/163)	16.5 (0.70/187)
2.27–3.26	115.1 (3.71/86)	5.1 (0.85/83)	34.8 (1.49/84)	27.6 (1.16/85)	7.4 (0.48/88)	16.7 (0.73/106)
3.27–4.26	116.4 (3.64/29)	5.8 (0.98/26)	35.0 (1.43/26)	27.3 (1.12/28)	7.6 (0.47/31)	16.6 (0.67/40)
4.27–5.26	117.3 (4.24/20)	5.6 (1.55/15)	35.0 (1.90/15)	27.5 (1.03/18)	7.6 (0.46/21)	16.6 (0.63/32)
5.27–6.26	116.1 (3.93/5)	5.8 (1.74/6)	35.4 (1.50/6)	27.3 (0.97/7)	7.6 (0.33/8)	16.7 (0.47/11)
6.27–	119.6 (2.99/11)	5.7 (1.02/8)	36.3 (1.70/8)	27.2 (1.10/11)	7.7 (0.60/13)	16.4 (0.78/15)
Change/year	0.9	0.4	0.1	–	0.1	–
p-value	< 0.001	< 0.001	< 0.004	> 0.136	< 0.001	> 0.417
Correlation	0.30	0.45	0.11	–	0.26	–
SE	3.7	1.0	1.5	–	0.5	–

Discussion

During their first year of life, most parts of the skeleton in yearlings stop growing in November; the zygomatic width is being an exception. However, the mean lengths for many of the variables measured were larger among foxes older than one year. Are these differences caused by growth during the second summer in life or later, or are they a result of biased sampling or of something else?

Could the natural mortality rate for small foxes be higher than for large ones, or are small ones more likely to be shot? In both cases, large specimens would survive longer and be represented more often among older foxes. This would give a false impression of growth after the first year of life.

Had the small foxes disappeared faster from the population than the large ones for any of the reasons mentioned, there should have been a steady increase in size throughout the winter among yearlings. Such an increase was not observed except for the zygomatic width.

Some structures, such as the length of P4 in the upper jaw and m1 in the mandible cannot grow in size in adult foxes. Furthermore, the correlation coefficient between the condylobasal length and the length of P4 is 0.33 for adult males, and 0.32 for adult females ($p<0.001$ for both sexes). Thus foxes with larger teeth have longer skulls. Therefore, had small foxes for one reason or another disappeared faster from the population than the large ones, the mean size of the teeth should have been larger among older foxes. No such difference was found (Tables 1, 2).

My conclusion therefore is that several parts of the skull, mandible and long bones grow in size for more than the first year, at least for foxes living under good food conditions as foxes are in the area studied. This growth is for nearly all skeleton parts supposed to take place only during the summer-autumn period, perhaps caused by the better food supply during that time.

Being larger and stronger probably increase the chance of advancement in the hierarchy. This is very important in populations with intensive social interac-

Table 4. Age specific means of some mandibular measurements (mostly lengths) in a sample of female foxes from an agricultural area in southern Sweden. Ages are given as years and the week numbers during which the foxes were killed. Means in mm; standard deviations and the number of foxes are given in parentheses.

Ages	Total length	c1–p1 length	p1–p4 length	m1–m3 length	Thickness	m1 crown length
0.18–0.21	64.9 (8.11/4)	–	–	–	4.9 (0.43/4)	–
0.22–0.26	72.0 (2.37/3)	–	–	–	6.5 (0.21/3)	–
0.27–0.30	85.5 (5.26/5)	2.8 (–/1)	–	–	6.8 (0.89/5)	–
0.31–0.35	98.9 (6.85/4)	3.9 (1.21/5)	32.2 (1.99/5)	26.5 (0.67/4)	7.4 (0.57/6)	15.6 (0.22/6)
0.36–0.39	104.0 (5.09/11)	3.2 (0.82/11)	32.8 (1.25/11)	27.4 (0.83/11)	7.2 (0.50/11)	16.0 (0.68/12)
0.40–0.44	105.2 (4.90/12)	3.0 (0.77/14)	33.0 (1.67/14)	27.3 (1.08/12)	7.1 (0.45/15)	16.4 (0.72/18)
0.45–0.48	106.2 (4.07/21)	3.1 (1.06/21)	32.7 (1.17/21)	26.8 (1.01/20)	6.8 (0.46/21)	15.8 (0.59/22)
0.49–0.53	106.3 (2.97/21)	3.6 (0.57/21)	33.1 (1.29/21)	26.5 (0.80/20)	6.8 (0.41/21)	15.9 (0.70/21)
0.00–0.04	107.5 (3.03/45)	3.7 (0.64/45)	33.1 (1.10/45)	26.6 (1.13/45)	7.0 (0.39/45)	16.0 (0.73/50)
0.05–0.08	108.3 (3.69/93)	3.8 (0.77/95)	33.3 (1.46/93)	26.8 (1.10/89)	6.9 (0.43/96)	16.0 (0.69/99)
0.09–0.13	107.5 (3.43/120)	3.9 (0.71/119)	33.2 (1.51/119)	26.6 (0.91/116)	7.0 (0.48/120)	15.9 (0.60/127)
0.14–1.26	108.5 (3.68/27)	3.8 (0.73/27)	33.7 (1.30/27)	26.7 (0.97/23)	7.0 (0.39/26)	15.9 (0.57/30)
0.49–1.26	107.7 (3.47/306)	3.8 (0.72/307)	33.2 (1.41/305)	26.7 (1.00/293)	7.0 (0.44/308)	15.9 (0.65/327)
1.27–2.26	108.9 (2.94/150)	4.6 (0.81/146)	33.4 (1.32/147)	26.7 (0.87/147)	7.0 (0.47/153)	16.0 (0.64/171)
2.27–3.26	109.7 (3.38/76)	4.9 (0.73/78)	33.5 (1.34/79)	26.7 (0.94/82)	7.1 (0.41/82)	16.0 (0.68/91)
3.27–4.26	108.5 (3.41/49)	4.9 (0.98/47)	33.1 (1.27/48)	26.5 (1.01/50)	7.3 (0.44/52)	15.9 (0.69/60)
4.27–5.26	110.7 (3.28/26)	4.9 (0.97/25)	33.9 (1.60/26)	26.7 (1.22/23)	7.3 (0.55/30)	16.2 (0.65/34)
5.27–6.26	110.6 (2.13/12)	5.2 (1.44/12)	33.6 (1.32/13)	26.7 (1.27/13)	7.4 (0.59/13)	16.2 (0.49/23)
6.27–	109.6 (2.57/10)	5.1 (0.72/12)	33.4 (1.55/13)	26.5 (0.98/16)	7.6 (0.50/21)	15.8 (0.61/23)
Change/year	0.5	0.3	–	–	0.1	–
p-value	< 0.001	< 0.001	> 0.082	> 0.530	< 0.001	> 0.561
Correlation	0.21	0.46	–	–	0.32	–
SE	3.3	0.8	–	–	0.5	–

tion. Low ranking vixens are less likely to reproduce in these populations, and there will be lower survival value for their genes (Macdonald, 1977).

Such social interaction pressure was probably present in the area studied, as a high proportion of the vixens were unproductive in spite of a good food supply. Among one-year old vixens 40–60% were unproductive, as were 20–25% of older ones (Englund, 1970, 1980).

The yearly increase of the zygomatic width in older foxes was larger than for the other variables studied. Furthermore that measurement, which also represents the greatest skull width, in contrast to other skeleton parts increased throughout the whole winter, at least among yearlings (Tables 1, 2). The growth of the skull breadth thus seems to be the most important factor for competition with other foxes.

Foxes that feed cubs may grow more slowly, and this should be especially obvious in lactating vixens. This may be the reason for the smaller growth in females shown here and by others (Huson & Page, 1980; Hell *et al*., 1989).

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Table 5. Age specific means of the length of long bones in a sample of male foxes from an agricultural area in southern Sweden. Ages are given as years and the week numbers during which the foxes were killed. Means in mm; standard deviations and the number of foxes are given in parentheses.

Ages	Humerus	Ulna	Radius	Femur	Tibia
0.18–0.21	–	–	53.7 (–/1)	–	–
0.22–0.26	–	–	–	–	–
0.27–0.30	–	–	–	–	–
0.31–0.35	–	142.7 (–/1)	–	–	–
0.36–0.39	–	148.8 (4.28/5)	–	–	157.6 (–/1)
0.40–0.44	134.8 (4.44/9)	149.2 (5.96/11)	127.3 (3.54/20)	139.8 (7.80/3)	156.7 (5.03/12)
0.45–0.48	134.6 (3.82/27)	149.5 (3.77/28)	127.0 (3.73/38)	141.8 (3.70/26)	155.7 (4.97/28)
0.49–0.53	134.3 (4.18/32)	148.4 (5.24/40)	126.1 (4.41/43)	142.0 (4.70/24)	154.7 (6.18/34)
0.00–0.04	135.8 (5.47/37)	149.2 (5.95/51)	127.1 (4.84/50)	142.0 (5.01/21)	155.1 (5.72/37)
0.05–0.08	135.4 (4.27/63)	148.9 (4.82/72)	127.0 (3.96/75)	142.3 (5.06/46)	154.6 (4.95/53)
0.09–0.13	133.6 (5.00/66)	148.1 (5.06/95)	126.3 (4.29/87)	140.2 (5.34/42)	154.9 (5.50/73)
0.14–1.26	133.8 (4.50/19)	148.1 (5.07/24)	126.1 (4.29/25)	137.2 (5.52/8)	151.4 (6.60/8)
0.49–1.26	134.6 (4.76/217)	148.6 (5.18/282)	126.6 (4.32/280)	141.3 (5.21/141)	154.7 (5.56/205)
1.27–2.26	135.2 (4.77/110)	149.5 (4.90/138)	127.2 (4.34/140)	143.3 (5.24/53)	155.7 (6.11/88)
2.27–3.26	133.8 (4.90/66)	149.4 (4.82/79)	127.0 (4.22/78)	142.1 (5.28/33)	154.9 (5.62/49)
3.27–4.26	135.6 (5.95/17)	149.2 (4.74/18)	127.0 (4.55/22)	142.9 (7.19/9)	156.2 (7.09/14)
4.27–5.26	136.0 (4.42/20)	151.4 (4.30/23)	128.8 (4.01/22)	143.5 (5.58/11)	157.8 (5.33/17)
5.27–6.26	139.2 (2.75/6)	152.0 (4.50/11)	129.9 (4.80/11)	146.5 (4.49/5)	159.2 (6.41/8)
6.27–	137.6 (6.26/11)	151.3 (6.72/15)	129.2 (5.02/14)	142.2 (6.66/8)	159.6 (7.52/8)
Change/year	–	0.5	0.4	–	0.6
p-value	> 0.028	< 0.002	< 0.002	> 0.085	< 0.003
Correlation	–	0.13	0.14	–	0.15
SE	–	5.0	4.3	–	5.8

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Table 6. Age specific means of the length of long bones in a sample of female foxes from an agricultural area in southern Sweden. Ages are given as years and the week numbers during which the foxes were killed. Means in mm; standard deviations and the number of foxes are given in parentheses.

Ages	Humerus	Ulna	Radius	Femur	Tibia
0.18–0.21	–	–	–	–	–
0.22–0.26	–	–	–	–	–
0.27–0.30	–	–	–	–	–
0.31–0.35	–	134.0 (–/1)	–	–	–
0.36–0.39	130.7 (0.78/2)	141.2 (2.87/4)	122.0 (–/1)	–	–
0.40–0.44	130.1 (5.25/5)	140.9 (3.74/6)	120.0 (3.44/8)	137.0 (3.12/3)	150.0 (4.15/4)
0.45–0.48	126.7 (4.63/17)	138.9 (5.43/14)	118.5 (4.70/15)	133.1 (4.48/14)	146.9 (4.01/15)
0.49–0.53	125.5 (3.62/17)	138.4 (4.78/18)	117.8 (3.81/16)	132.9 (4.64/8)	144.5 (4.50/13)
0.00–0.04	126.1 (2.79/22)	140.3 (4.43/35)	119.2 (3.78/35)	134.9 (4.70/12)	147.5 (4.85/28)
0.05–0.08	126.7 (5.05/48)	140.4 (5.50/69)	119.6 (4.53/68)	133.8 (5.44/33)	146.7 (6.21/60)
0.09–0.13	126.1 (4.84/66)	139.9 (4.94/98)	119.2 (4.24/94)	133.3 (6.22/35)	145.3 (5.88/70)
0.14–1.26	127.4 (5.39/18)	140.3 (6.50/21)	120.2 (5.34/23)	137.0 (7.31/5)	147.0 (9.63/9)
0.49–1.26	126.3 (4.62/171)	140.0 (5.16/241)	119.3 (4.34/236)	133.8 (5.67/93)	146.1 (6.00/180)
1.27–2.26	126.9 (4.30/97)	140.6 (4.63/131)	119.7 (4.12/128)	133.9 (4.50/42)	146.3 (5.13/84)
2.27–3.26	127.6 (4.35/59)	141.1 (4.50/76)	120.1 (4.11/75)	134.9 (4.01/32)	147.1 (4.89/51)
3.27–4.26	126.6 (4.13/40)	139.7 (4.46/48)	119.6 (3.74/46)	132.5 (4.72/29)	144.8 (6.50/35)
4.27–5.26	127.3 (4.34/18)	141.5 (4.97/21)	120.1 (4.08/23)	137.4 (6.38/11)	148.8 (6.37/16)
5.27–6.26	129.1 (3.76/16)	142.4 (4.00/16)	121.5 (3.65/17)	135.4 (3.29/13)	146.8 (4.92/11)
6.27–	126.2 (3.39/14)	139.4 (3.63/22)	119.1 (3.40/20)	134.3 (3.44/11)	146.3 (4.98/16)
Change/year	–	–	–	–	–
p-value	> 0.131	> 0.390	> 0.175	> 0.261	> 0.575
Correlation	–	–	–	–	–
SE	–	–	–	–	–

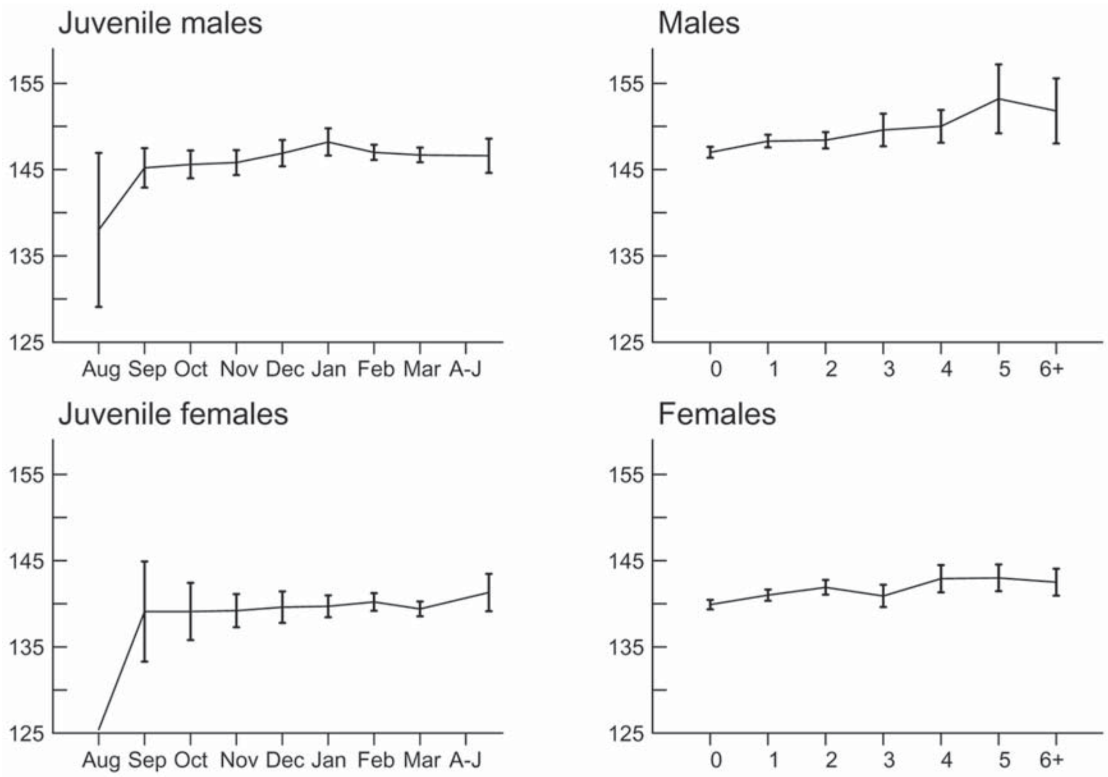

Figure 1. Condylobasal length in mm (mean ± 95% confidence limits of the mean) in foxes from the counties of Uppland, Södermanland, and Östergötland. Yearlings include foxes killed from December through June of the following year. Older ones up to 6+ years in age, include foxes killed all year round (July 1 – June 30).

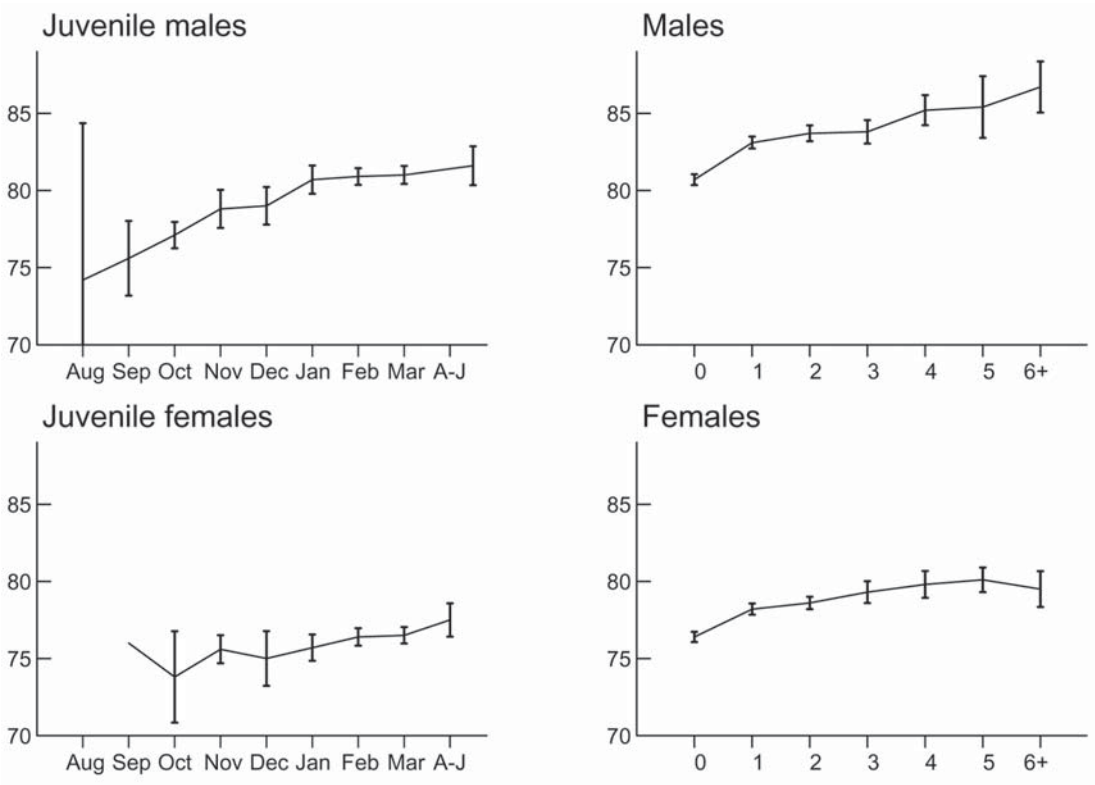

Figure 2. Zygomatic width in mm (mean ± 95% confidence limits of the mean) in foxes from the counties of Uppland, Södermanland, and Östergötland. Yearlings include foxes killed from December through June of the following year. Older ones up to 6+ years in age, include foxes killed all year round (July 1 – June 30).