



The Red fox in Norway: Morphological adaptation or random variation in size?

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Abstract

LUND (1959) collected red foxes *Vulpes vulpes* from different sites in Norway. We reanalysed his data on body mass, body length, tail length and condition in an attempt to study some factors influencing size variation in foxes. Sexual dimorphism was most significant, with regional variation followed by yearly and seasonal variation. Males were larger (4–5%) and heavier (14%) than females, but not in better condition. Foxes increased in size from south to mid Norway, but were smallest in north Norway. Sexual dimorphism in mass decreased progressively from south to north. Yearly variation was greatest in males. Both males and females were in better condition during autumn and winter, and in poorer condition in the spring. Seasonal changes in mass were similar, but less systematic. Environmental factors that change most from south/mid Norway to north Norway are climatic with lower temperatures, longer winters and lower primary productivity to the north. A smaller northern fox may need a shorter period of growth and conserve energy during the winter.

Key words: Size variation, environmental factors, *Vulpes*

Introduction

The red fox *Vulpes vulpes* is a highly adaptable carnivore, distributed throughout most of the northern hemisphere. Local and large scale variation in size have been found (e.g., DAVIS 1977; KOLB 1978; DAYAN et al. 1989; HUSON and PAGE 1980; LÜPS and WANDLER 1983), last summarized by CAVALLINI (1995). Although finding both increased mass, head and body length, and tail length with latitude, CAVALLINI (1995) concluded that body size reflected phylogenetic distance more than ecological conditions. Geographical variation in size has also been found in other fox species, e.g. arctic foxes *Alopex lagopus* (FRAFJORD 1993 a), Blanford's foxes *Vulpes cana* (GEFFEN et al. 1992) and Chilean foxes *Dusicyon* sp. (FUENTES and JAKSIC 1979), but none of these supported Bergmann's rule. Bergmann's rule that "races from cooler climates tend to be larger" has been much debated (e.g., KOLB 1978; CLUTTON-BROCK and HARVEY 1983, GEIST 1987; DAYAN et al. 1989). Even in cases where a positive relationship between body size and latitude has been found, other explanations were sought (e.g., CAVALLINI 1995). As pointed out by CLUTTON-BROCK and HARVEY (1983), although relative surface area is smaller in large animals, absolute surface area is larger, and a larger animal will not save energy in absolute terms. Alternative explanations for the red fox include population density, interspecific competition, size of prey, type of prey, the length of the dark winter night, and productivity of the area.

Norway stretches through 13 degrees of latitude, from 58° to 71°N. Generally, the climate is colder with longer winters towards the north (the northernmost part being subarctic), which implies a lower productivity and a shorter growing season. In north Norway

the midnight sun shines during May–July. The red fox is found throughout Norway, in a wide variety of habitats and climatic regimes. According to LUND (1962) it preys primarily on small rodents, hares, and birds. Carcasses of larger mammals may be an important source of food during the winter. Regional variation in prey type and size is most likely small. The terrestrial fauna is similar from south to north, but there are some small variations. For instance, wood mice *Apodemus* sp. are absent in north Norway (LURA et al. 1995), and carcasses of domestic reindeer *Rangifer tarandus* are more available in the north. The importance of vegetable matter in the diet of the Norwegian red fox is unknown.

This study presents analyses of size variations in the Norwegian red fox, attempting to find some of the sources of variation.

Material and methods

All the data came from LUND (1959), who examined red fox carcasses collected from hunters, the largest sample in Norway. LUND (1959) presented data on body size, mass, condition and sex ratio and compared them to reports in the literature. He provided only averages and minima and maxima, and made no statistical analysis in those pre-computer times. Fortunately, he also presented all the original data in a table, which we recalculated to verify some of his conclusions and to look further into some sources of variation. All our analyses and presentations are different from those of LUND (1959), except that we also include our averages for comparison.

LUND (1959) included capture site, date, age (adult or juvenile), sex, mass, total length, tail length (excluding tail hairs), and condition. We pooled capture site by county, used only adult-sized foxes (from October, $n = 348$) and calculated body length as total length minus tail length. Condition was given as a “fat index”, based on the amount of subcutaneous and visceral fat (LUND 1959): 1 very fat, 2 fat, 3 lean, 4 very lean. Most foxes ($n = 293$, 84.4%) came from only six counties in three regions (Fig. 1): Akershus and Telemark (south Norway), Sør-Trøndelag and Nord-Trøndelag (mid Norway), and Troms and Finnmark (north Norway). In all regions there are large altitudinal gradients in vegetation and fauna, but most red foxes were probably caught in lowland, forested regions.

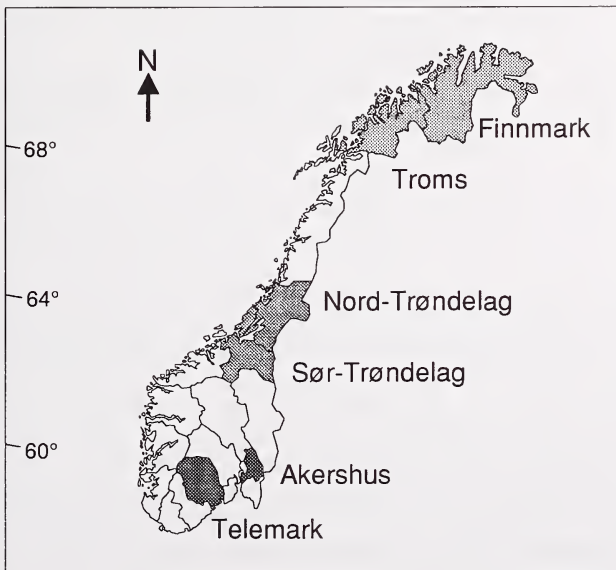


Fig. 1. Map of the counties in Norway, the six counties representing three regions are outlined.

Mass, body length and tail length were normally distributed, but condition was not (K-S Lilliefors tests). We used parametric tests (Student's t-test, ANOVA with Scheffé multiple comparison test) for normal variables and the Mann-Whitney U-test (z score) and Kruskal-Wallis one-way ANOVA (κ^2) for condition. All tests were two-tailed. We include the entire samples in the figures, but in statistical analysis and conclusions only groups with more than 10 foxes are used.

Results

Males were significantly heavier (14%) and larger (4–5%) than females, but not in better condition (Tab. 1). Sexual dimorphism in mass was about three times larger than in length. The three measurements mass, body length and tail length were significantly correlated with each other, as was also the condition index except with tail length (Tab. 2). Our results are slightly different from those of LUND (1959), possibly because we used a slightly smaller sample size.

Table 1. Mean mass, body length, tail length and condition of male and female red foxes, the ratio of male/female (R), and test between the sexes.

	Males			Females			R	t	p
	\bar{x}	SD	n	\bar{x}	SD	n			
Mass (g)	5887	962	192	5186	948	155	1.14	6.79	<0.001
Body length (cm)	68.6	3.6	188	65.8	3.9	154	1.04	6.82	<0.001
Tail length (cm)	43.8	3.0	188	41.8	3.0	154	1.05	5.97	<0.001
Condition index	2.90	0.6	185	2.88	0.7	149	1.01	0.30	>0.05*

* Mann-Whitney U-test

Table 2. Pearson's correlations between mass, body length, tail length and condition in the red foxes (minimum pairwise n = 328). ** = p < 0.001.

	Mass	Body length	Tail length
Body length	0.64**		
Tail length	0.45**	0.37**	
Condition	0.49**	0.19**	0.06

The general pattern of regional variation was similar for mass, body length, tail length and condition (Fig. 2). Within sexes, significant variation between counties was found for male body mass. Males from Finnmark were lighter than those from Nord-Trøndelag, Sør-Trøndelag and Akershus ($F = 7.03$, d.f. = 5,155, $p < 0.001$, Scheffé test).

Combining the 6 counties into 3 regions, an overall tendency of larger foxes in mid Norway and smaller foxes in north Norway becomes clearer. Northern males were lighter ($F = 12.7$), and had shorter body length ($F = 5.7$) and tail length ($F = 7.2$) than males from mid Norway, and were lighter than males from south Norway. Northern females were lighter ($F = 3.3$) and had shorter tails ($F = 7.2$) than females from mid Norway, and females from south Norway had shorter tails than those from mid Norway. A similar overall regional variation was also found for female body length ($F = 3.3$), but no two regions were significantly different from each other. Regional variation was also found in male

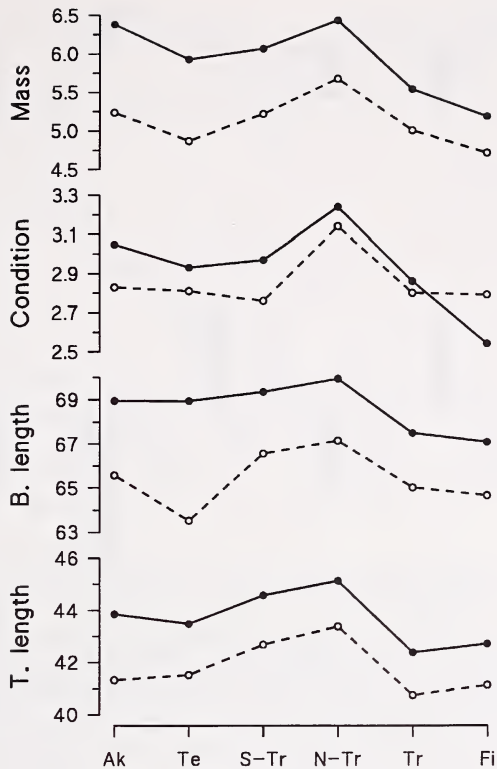


Fig. 2. Average mass (kg), condition index, body length (cm), and tail length (cm) of male (●) and female (○) red foxes from six counties (Ak-Akershus, Te-Telemark, S-Tr-Sør-Trøndelag, N-Tr-Nord-Trøndelag, Tr-Troms, and Fi-Finnmark).

condition ($\kappa^2 = 11.77$, $p < 0.01$). If males vary more than females, one might expect a reduced sexual dimorphism northwards. This was most pronounced in mass (male/female ratio 1.17, 1.14 and 1.09 for south, mid and north Norway) and less in condition, body length or tail length.

Yearly variation in mass and size through 1950–1956 was most pronounced in males (Fig. 3). Most foxes were caught in the years 1951 to 1954. We excluded the years 1950 and 1955–1956 from the analyses of yearly variation, using only 1951–1954 so that no group (by year by sex) contained less than 16 foxes. No significant yearly variation was found in female mass, body length or tail length. Males, on the other hand, were particularly small in 1954, being lighter ($F = 7.7$) with shorter tails ($F = 4.9$) than in 1951 and 1952, and smaller body length ($F = 3.5$) than in 1952. Yearly variation in condition was also found in males ($\kappa^2 = 13.89$, $p < 0.01$, Fig. 3).

No seasonal differences were found in body mass for either males or females, although values were nearly significant (males: $F = 3.2$, d.f. = 3,188, $p = 0.06$, females: $F = 2.4$, d.f. = 3,151, $p = 0.07$). Seasonal differences were found in male condition ($\kappa^2 = 16.06$, $p = 0.001$), but not in female condition. Males were in poor condition in the spring (2.56 ± 0.63 , $n = 41$) and in best condition in the autumn (3.08 ± 0.64 , $n = 66$).

The data were split into groups by the two sexes, three regions, and four seasons. For each group, mass and condition were calculated as percent deviation from the average within the group. Sample sizes were notably small and inconclusive for the summer sea-

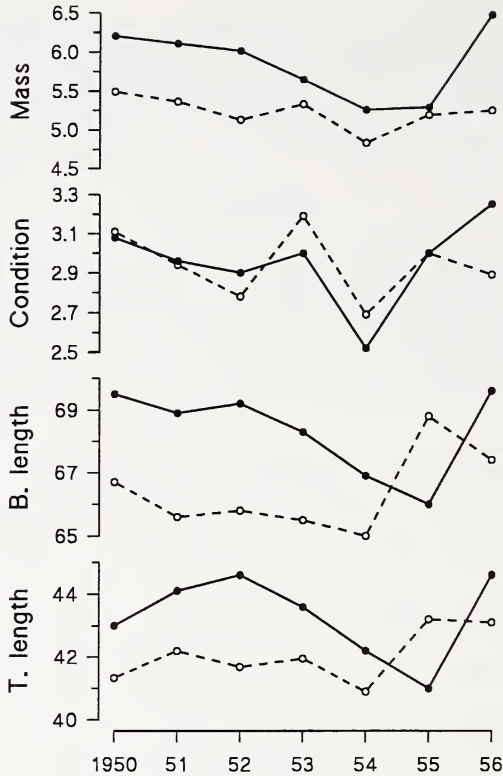


Fig. 3. Average mass, condition index, body length, and tail length of male (●) and female (○) red foxes through different years.

son (Fig. 4). Males were heaviest in the winter in all regions and in north Norway in the autumn (Fig. 4). Female mass appeared to vary less systematically, but females in south Norway were notably light in winter and heavier in spring and autumn (Fig. 4). To some extent, a similar pattern was found for the condition index, with foxes in better condition in autumn and winter and in poorer condition in spring (Fig. 5). The patterns for males and females were more similar for condition than for mass.

The data were not evenly distributed. Of the 82 foxes collected in north Norway, 96.3% were collected in 1953 and 1954. In mid Norway, 89.2% of the 111 foxes were collected in 1951 and 1952. In south Norway, 63.1% of 149 foxes were collected in 1951 and 1952. Thus, more of the smaller foxes in north Norway were collected in what may have been “bad” years for the red fox, implying that regional variation may be somewhat obscured or exaggerated by the effect of yearly variation. In an ANOVA of mass with sex, region, year and season as independent variables, only sex had a significant influence ($F = 42.4$, $F = 2.1$, $F = 0.7$, and $F = 1.3$, respectively). No two-way interactions of these factors were significant for mass.

For males and females we calculated the ratio maximum/minimum for each group (Tab. 3). The ratios of mass and condition were about three times higher than the ratios for body and tail lengths, i.e. the variation in the four measurements were proportional. In some cases, females of the largest group were larger than males of the smallest group. Male ratios averaged \pm SD 1.09 ± 0.08 and female ratios 1.07 ± 0.05 ($z = 0.06$, $p > 0.05$).

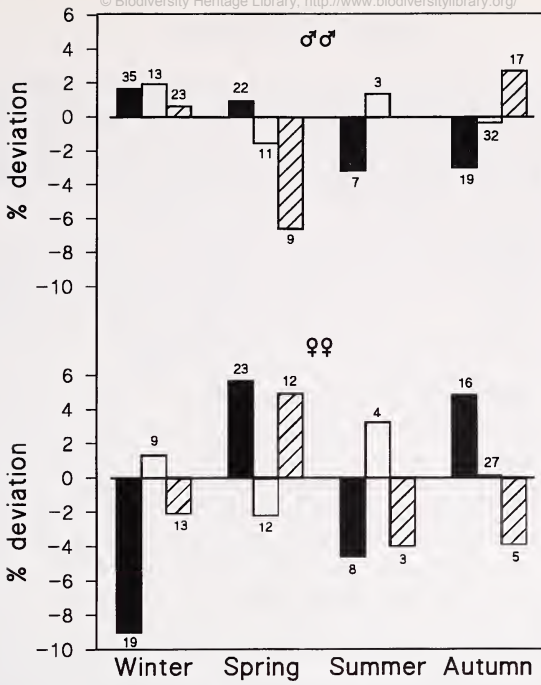


Fig. 4. Average seasonal deviations from the mean mass in male and female red foxes in south Norway ■, mid Norway □, and north Norway ▨: Numbers represent sample size. Winter = December–February, Spring = March–May, Summer = June–August, Autumn = September–November.

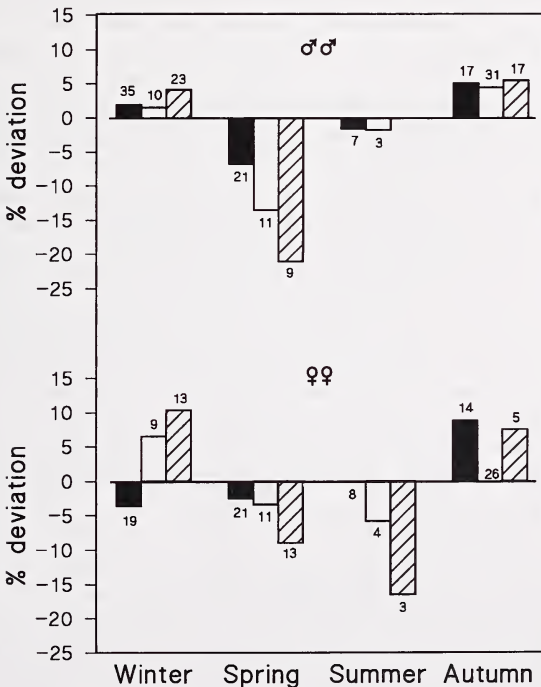


Fig. 5. Average seasonal deviations from the mean condition in male and female red foxes in south Norway ■, mid Norway □, and north Norway ▨: Numbers represent sample size. Seasons as in Fig. 4.

Table 3. The ratio maximum/minimum in each group of male (n = 162–192) and female (n = 126–155) red foxes from three regions, four years (1951–1954) and four seasons.

	Mass	B. length	T. length	Condition
Males				
Regions	1.16	1.03	1.03	1.14
Years	1.16	1.03	1.06	1.19
Seasons	1.02	1.02	1.01	1.20
Females				
Regions	1.11	1.03	1.05	1.05
Years	1.11	1.01	1.03	1.19
Seasons	1.10	1.03	1.06	1.10
Average all	1.11	1.03	1.04	1.15

Discussion

The abundance, distribution, and type of food have often been cited as determinants of behaviour and social organization in red foxes (e.g., MACDONALD 1981; LINDSTRÖM 1986; CAVALLINI and LOVARI 1991). Relationships between home range size and metabolic needs have been found in carnivores (GITTLEMAN and HARVEY 1982), as well as between body size and behaviour in canids (BEKOFF et al. 1981). HARRIS and STEUDEL (1997) found that prey-capture behaviour affected the evolution of carnivore hind-limb length most, and that home range size, daily distance moved, prey size, and latitude were less important. In long-legged carnivores, like the red fox, stalking with pouncing or chasing predominates (HARRIS and STEUDEL 1997). The red fox probably uses this method when hunting most vertebrate prey species, but it may be most crucial when hunting small mammals (voles and hares). A possible relationship between red fox size and the proportion of vertebrates in the diet has not been examined. In Wales, HUSON and PAGE (1980) related geographical variation in size to some unknown ecological factor, and altitude was suggested as a possible factor. KOLB (1978) found that foxes in Scotland grew larger from south to north, and the most important factor was suggested to be the length of the winter night rather than climate, prey size or productivity of the area. DAYAN et al. (1989) suggested that competition with other canids could influence size variation in foxes through character displacement. Within central Italy, CAVALLINI (1995) found smaller foxes in the south than in the north. This was attributed to a higher density of foxes in the south, and not to food supply or climate because the variation in these factors was small. CAVALLINI (1995) suggested that the similar result of KOLB (1978) in Scotland may also be explained by population density. On the larger scale of Europe and North America CAVALLINI (1995) suggested that phylogenetic distance was more important than ecological conditions to explain an increase in body mass and length with latitude.

We ordered the proximate factors into three groups. 1) Environmental factors: latitude/climate, length of the winter, length of snow cover, snow depth, length of the winter night, altitude, interspecific competition. 2) Prey availability: prey type, productivity/food abundance, proportion of vertebrates in the diet. 3) Intrinsic factors: population density, behaviour, social organization. Which factors influence the size of the Norwegian red fox most? Climate, length of the winter, and primary productivity are most likely to be the factors that differ most within south, mid, and north Norway. As conditions deteriorate to the north Norway, foxes most likely experience a cooler climate, a longer winter and a re-

duced food supply. The reduced size and mass are then means of reducing energetic costs (MCNAB 1980), possibly also resulting in a reduced period of growth. This fits well with what has been found in the arctic fox (FRAFJORD 1993 a) and in the common shrew *Sorex araneus* (FRAFJORD et al. 1994). Energetic constraints may possibly also reduce population density, but the influence of density on size is uncertain. A high density may reduce the amount of food per fox and select for small foxes, but a high density may also increase competition and select for more competitive and larger foxes. HERSTEINSSON and MACDONALD (1992) suggested that the northern limit of the red fox is determined by resource availability, a theory that was supported by our study.

Lower temperatures or higher latitudes have been associated with greater body mass in the red fox (DAYAN et al. 1989), but the determinants of the variation may be complex (CAVALLINI 1995). There may be a threshold level of temperature or latitude below or above which size cannot increase because of the overall lower productivity further north. This may explain the increase in red fox size from south to mid Norway, and the smaller size of foxes in north Norway (including a reduced sexual dimorphism in the north). Thus, the size of the red fox may follow Bergman's rule in the southern part, with climate as an indirect factor, but not in the north (sensu GEIST 1987). It would have been interesting to know whether limb length is proportional to body length in the three regions, or relatively larger in north Norway. A shortening of limbs has been associated with adaptation to a cooler climate, acting independent of body length. An effect against a shortening of limbs is perhaps snow depth. Because tail length was proportional to body length in the three regions, such any adaptation is unlikely.

Males varied in size and mass more than females both between regions, between years and between seasons. It was difficult to separate the effects of these three variables, and some bias was possibly due to different sampling among regions and years. The vole cycles are not synchronised throughout Norway (CHRISTIANSEN 1983), so a bad year with few voles in one region may be a good year with many voles in another region. The amount of variation in the size of the red fox is similar to that found within other countries (including a study of Norwegian red fox skulls, FRAFJORD 1993 b), but smaller than between countries (CAVALLINI 1995). Larger variation in males may indicate greater environmental influence on the size of the larger sex. Seasonal variation in mass and condition are also related to differential energy expenditure in reproduction by males and females. Males use more energy early, i.e. in late winter and spring, when they defend territories most intensively. Females use most energy in late spring and summer, in the final stages of pregnancy and during lactation and feeding of pups. This was partly indicated by the data, with both males and females being in poor condition in the spring. Reproduction may possibly start 1–2 months earlier in south Norway than in north Norway.

Body mass of the red fox may vary as much as 75% between populations, and length 24% (from CAVALLINI 1995). The red fox in Norway is of medium size, but of comparatively smaller mass (CAVALLINI 1995), which indicates that it is a slender fox. Sexual dimorphism is small compared to other populations (CAVALLINI 1995). However, because we used foxes collected from October onwards, some not fully mature juveniles may have been included (sensu TRAVINI and DELIBES 1995). The growth curves of pup mass reach an asymptote in October–November (LUND 1959).

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Zusammenfassung

Der Rotfuchs in Norwegen: Morphologische Anpassung oder zufällige Größenvariation?

Daten zum Körpergewicht, zur Körper- und Schwanzlänge, sowie zur Kondition von 348 Rotfüchsen *Vulpes vulpes* aus drei verschiedenen Regionen (Süd-, Mittel- und Nord-)Norwegens wurden statistisch bearbeitet (Originaldaten: LUND 1959). Rüden wiesen in den Maßen, nicht aber in der Kondition signifikant höhere Werte auf als Fähen. Im Süden waren die Füchse kleiner als in Mittelnorwegen, am kleinsten und geschlechtsspezifisch am wenigsten dimorph waren sie im Norden des Landes. Bei den Rüden war die jährliche Variation größer. Im Herbst und Winter wiesen beide Geschlechter höhere Werte auf als im Sommer.

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