

Variation in the body size of the red fox

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Foxes were measured in a small (75 by 52 km) area of Central Italy. Males were larger and heavier than females, while age variation was insignificant. Males were both longer and heavier in the northern than in the southern part of the study area, whereas females were slightly longer, but not heavier in the north than in the south. The difference cannot be attributed to either cooler climate or larger food supply, and may be related to lower population density. Body mass, head and body length, and tail length are sufficient to separate fox populations studied worldwide in three clusters corresponding to geographical origin (North American, British, and Continental European). External morphology appears therefore to reflect phylogenetic distance more than global ecological conditions.

1. Introduction

In its enormous distribution range, the red fox *Vulpes vulpes* (L.) inhabits extremely diverse habitats, from Arctic tundra (e.g. Jones & Theberge 1982) to hot desert (e.g. Lindsay & Macdonald 1986). The morphology is also variable among areas (external measurements: Kolb & Hewson 1974, Storm et al. 1976, Lloyd 1980; skull: Huson & Page 1979, Huson & Page 1980), and at least 36 subspecies (of dubious validity) have been described (Burrows 1968). The external morphology has been studied in Central and Northern Europe (including British Isles) and in North America (e.g. Tetley 1941, Hoffman & Kirpatrick 1954, Lund 1959, Fairley 1970, Kolb & Hewson 1974, Storm et al. 1976, Kolb 1978, Lloyd 1980, Allen & Gulke 1981, Lüps & Wandeler 1983), whereas there is less in-

formation in the Mediterranean area (Lewis & Lewis 1968, Travaini & Delibes 1995). In the palearctic region, fox teeth and skull size is negatively correlated with temperature and positively with latitude (Davis 1977, Dayan et al. 1989), following Bergmann's rule. In the extreme south of its range (the Saharo-Arabian region), the rate of size decrease is much lower, possibly because of competition with other canid species (Dayan et al. 1989).

On a smaller scale (within Scotland), however, body size is correlated to latitude only, not to climate, prey dimensions or environmental productivity. In this area, lower food availability led to a body size decrease, followed by a slow increase. Larger size of foxes in northern latitudes was interpreted as a consequence of the longer winter nights, and consequently longer periods available for hunting during the period of food stress (Kolb 1978).

Ecological factors, and especially food distribution and abundance, have been recognised as important in shaping the various facets of the biology of Carnivores (e.g. Macdonald 1983), including morphology (e.g. Kruuk & Parish 1983). However, the relative importance of ecological and genetic factors in determining morphological differences in canids is unclear. For instance, the size increase in coyotes (*Canis latrans*) in the eastern USA has been attributed to genetic factors, higher food availability or predation on larger preys (Thurber & Peterson 1991, Larivière & Crete 1993, Peterson & Thurber 1993).

This paper aims to answer the following questions: (a) what are the sources of body size variation within a sample of Mediterranean red foxes? (b) what is the pattern of body size variation across the distributional range of the red fox?

2. Study area, material and methods

Foxes were killed by hunters in the Pisa province (43°N, 10–11°E), Central Italy, from January to May 1992, during the main fox hunting season. The study area (52 km E–W by 75 km N–S; 2 448 km²) was divided in 4 sections (Cavallini 1994b; in north to south order): (1) a coastal belt (500 km²), flat, with very high human population (> 400 × km⁻²), scarce woodlands (20% of total area) and large cultivated areas (> 50%); (2) internal valleys (713 km²), mostly flat, with high human population (> 200 × km⁻²), scarce woodlands (22%) and large cultivated areas (> 50%); (3) coastal hills (412 km²; up to 400 m a.s.l.) with low human population (36 × km⁻²), more even percentages of woodlands (38%) and cultivated fields (45%); (4) southern hills (823 km²), higher (up to 800 m a.s.l.), with the lowest human population density (33 × km⁻²), the highest proportion of wooded areas (51%) and least cultivated fields (33%). For some analyses, I aggregated sections 1 and 2 (hereafter "north"), and sections 3 and 4 (hereafter "south").

The climate is Mediterranean, with mild winters and dry, hot summers. In 1992, minimum temperatures (monthly average) ranged from 3.4°C to 19°C, and maximum temperatures from 12°C to 31°C. Rainfall is heavier in autumn (35.9% of total rainfall), in winter (28.9%) and in spring (23.7%), whereas only 11.5% of total rain occurs during summer. Inter-annual variation is large (Cavallini 1994b).

I collected foxes from hunters within 6 hours of death and stored them in plastic bags (≤ 48 hours, -2°C) until dissection. Foxes were weighed (body mass: hereafter BM; to the nearest 50 g) and measured (head and body length, from the tip of the nose to the first vertebra of the tail, hereafter HBL; tail length, from the first vertebra to the tip of the tail, TL; chest girth, immediately behind the fore legs, CG; to the nearest 0.5 cm). Age was determined by counting

incremental annuli in canine teeth and measuring the width of the pulp cavity of canines and the mass of eye lens (Cavallini & Santini 1995). Owing to the small number of older foxes (Cavallini & Santini 1995a), foxes ≥ 5 years old were pooled in a single class. The sample was pooled in two age classes for some analyses: yearlings (1 year old at the time of sampling) and adults (≥ 2 years old). In the study area, most births occur around 26 February (Cavallini & Santini 1995b).

I collected 330 foxes (125 females and 205 males), but due to physical damage during hunting, sample size was reduced for several variables. Forty-three foxes (13% of total sample) had been skinned by hunters. Therefore 13 other foxes (7 males and 6 females; BM ranging from 4 200 to 6 600 g) were weighed, skinned, and re-weighed. A regression line predicting total BM from skinned BM was fitted to data (BM = -0.0146 + 1.168 × skinned BM; $r^2 = 0.99$; $p < 0.0001$). These coefficients were used to estimate the total BM of skinned foxes.

2.1. Statistical analyses

Results are presented as average ± 1 standard deviation. Normality of distributions was evaluated by Lilliefors test (a modified version of the Kolmogorov-Smirnov test; statistics MAXDIF; Lilliefors 1967). I used non-parametric tests (Mann-Whitney's *U*) for non-normal variables, and parametric tests (Student's *t*-test, linear regression, ANOVA, MANOVA, cluster analysis) for normal ones. All tests were two-tailed.

3. Results and discussion

3.1. Local variation

Average mass was 5 450 ± 950 g (range: 3 250–8 150 g; $N = 327$), HBL was 64.3 ± 4.2 cm (range: 51–78 cm; $N = 309$), TL was 37.7 ± 3.1 cm (range: 24–45 cm; $N = 318$), and CG was 35.1 ± 2.9 cm (range: 26.5–46.5 cm; $N = 269$). Most measurements were normally distributed:

	MAXDIF	<i>p</i>
BM	0.028	0.97
HBL	0.062	0.19
CG	0.076	0.09

but tail length deviated significantly from normality (MAXDIF = 0.102, $p = 0.003$). Males were on average about 5 to 6% larger than females (HBL: 65.7 ± 3.9 cm vs. 62.0 ± 3.6 cm; $t = 10.64$, $p < 0.001$, $N_{\text{males}} = 193$; $N_{\text{females}} = 116$; CG = 35.9 ± 2.9 cm vs. 33.7 ± 2.5 cm; $t = 6.55$, $p = 0.001$, $N_{\text{males}} = 167$;

$N_{\text{females}} = 102$, $TL = 38.6 \pm 3.0$ cm vs. 35.9 ± 3.2 cm; $U = 18170$, $p < 0.001$, $N_{\text{males}} = 198$; $N_{\text{females}} = 121$; $BM: 5,750 \pm 953$ g vs. $4,940 \pm 680$ g; $t = 8.32$, $p < 0.001$, $N_{\text{males}} = 204$; $N_{\text{females}} = 123$). Average mass did not significantly increase with age (males: from 5 650 g at 1 year to 5 880 g at ≥ 5 year; $F = 1.53$, $p = 0.15$, $N = 194$; females: from 4 909 at 1 year to 5 300 g at ≥ 5 year; $F = 0.40$, $p = 0.85$, $N = 119$); no interaction was apparent between sex and age class (MANOVA, $F_{\text{sex}} = 60.59$, $p < 0.0001$, $F_{\text{age}} = 1.55$, $p = 0.15$, $F_{\text{interact}} = 0.17$, $p = 0.68$, $N = 314$). No linear measurement was different between age classes, neither for males nor for females ($t < 0.5$, $U < 4 130$, $p > 0.14$).

Males were progressively larger and heavier the more north (BM: from 5 500 g in section 4 to 5 980 g in section 1; $F = 3.52$, $p = 0.02$, $N = 198$; HBL: from 64.5 cm in section 4 to 66.5 in section 1; $F = 3.54$, $p = 0.02$, $N = 188$), but CG was similar throughout the area ($F = 2.31$, $p = 0.08$, $N = 162$). Females had the same BM throughout the study area ($F = 0.50$, $p > 0.5$, $N = 123$) and the same CG ($F = 0.40$, $p > 0.5$, $N = 101$), but were longer in the north (62.5 ± 4.1 cm) of the area than in the south (61.3 ± 2.4 cm; HBL, $t = 2.064$, $p = 0.041$, $N = 116$). The lack of significance for body mass of females was not caused by the confounding effect of pregnancy because also the body mass of females killed before the mating period (Cavallini and Santini 1995b) did not differ between north and south ($t = 0.657$, $p = 0.5$, $N = 44$).

Within the sample from Central Italy, age had therefore an insignificant effect on body mass. Previous authors (Lloyd 1980, Allen & Gulke 1981) reported an increase in BM with age, but did not statistically test for it. Within this small study area, the general trend of larger foxes in the north is significant, especially for males. For females, results are less clear. The differences in body size between the two sections of the study area are surprising considering: (1) the small dimensions of the area (75 km north to south; 50 km between the centres of the northern and southern areas), and consequently the relative homogeneity of climate; in fact, the winters in the south of the study area are more severe, because of higher elevations (Cavallini 1994b); (2) the absence of barriers, and the consequent continuous distribution of foxes; (3) the magnitude of the difference (almost 500 g for BM and 2 cm for HBL of males); (4) the body condition of

males were constant throughout the area, whereas those of females were higher in the south (Cavallini 1994b), where foxes were shorter; (5) the lack of consistent differences in the consumption of main food items among the sections of the study area (Cavallini 1994b). The difference cannot therefore be attributed to either cooler climate or better nutrition in the north of the area. Small scale variation has been reported for HBL over longer distances (7 cm for males and 5 cm for females along 350 km north to south; Kolb 1978) and for cranial measurements (within a 180 by 70 km area; Huson & Page 1980). In the first case, food seems an important factor explaining the difference (Kolb 1978). Body size is inversely related to population density, at least in herbivorous mammals (Damuth 1981, Leberg & Smith 1993). Although accurate population density estimates are difficult to obtain in large areas, fox density appears higher in the south of the Pisa province (Cavallini 1994a, Cavallini 1994b). This factor could therefore explain the larger body size of foxes in the north of the study area. Also within Scotland fox density was higher in the south (Hewson & Kolb 1973), where foxes were smaller (Kolb 1978).

3.2. Geographic variation

I studied geographic variation of the morphology of the red fox within its whole range by using literature data and results from the present study (Table 1). Variation among areas was large, average BM ranging from 4 300 g to 7 600 g for males and from 3 600 g to 6 500 g for females; average HBL ranged from 59 to 72 cm for males, and from 55 to 68 cm for females, and TL from 36 to 44 cm (males) and from 34 to 42 cm (females; Table 1). Males were invariably larger, heavier and more massive (higher BM/HBL ratio) than females. Average dimorphism (percentage difference respect to males; cubic roots of masses were used) was about 5–6%.

Fox populations studied originate from three geographical areas: Eurasia (excluding British Isles; N of populations including the present one = 8), British Isles ($N = 7$), and North America ($N = 5$). Red foxes from North America are comparatively light, rather long for their mass and with a high sexual dimorphism. British foxes are heavy but relatively short, whereas European foxes are closer to the gen-

eral average among populations (Table 1). Foxes from Central Italy are the smallest among European foxes (larger however than Lebanese red foxes, which are exceptionally small), but their body proportions (BM/HBL ratio) are close to the general average. In accordance with Bergmann's rule, BM and HBL are positively related to latitude, both for males (BM: $r^2 = 0.351$, $p = 0.006$, $N = 20$; Fig. 1. HBL: $r^2 = 0.341$, $p = 0.046$, $N = 12$; Fig. 2) and for females (BM: $r^2 = 0.396$, $p = 0.003$, $N = 20$; Fig. 1. HBL: $r^2 = 0.428$, $p = 0.002$, $N = 12$; Fig. 2). There is a slight evidence of reduction of appendixes with increasing latitude: tail length was positively related to latitude (males: $r^2 = 0.524$, $p = 0.01$, $N = 11$; females: $r^2 = 0.460$, $p = 0.06$, $N = 11$; Fig. 3), but the increase was slightly lower than that relating HBL to latitude (TL: slope = 0.210 and 0.178; HBL: slope = 0.243 and 0.259 cm/degree of latitude for

males and females, respectively).

The geographical origin have an effect on body mass larger than latitude (multiple regression; BM males: $r^2 = 0.720$, $p_{\text{latitude}} = 0.4$, $p_{\text{origin}} = 0.004$, $N = 19$; BM females: $r^2 = 0.808$, $p_{\text{latitude}} = 0.16$, $p_{\text{origin}} = 0.001$, $N = 19$; Fig. 1). Unfortunately, many studies reported different measurements, thus limiting sample sizes for multivariate analyses. Similar analyses for HBL and TL did not show a significant effect of geographical area (all $p > 0.5$, $N \leq 12$). The effect of latitude on body mass and size was not evident within each geographic area (particularly within Eurasia), but only when considering all areas together (Figs. 1–3). The rate of increase in HBL with latitude (males: 0.243 cm/degree of latitude, i. e. about 0.22 cm per 100 km; females: 0.259 cm/degree of latitude, i. e. about 0.24 cm per 100 km; Fig. 2) is one order of magnitude lower than the rate of

Table 1. External morphology of red foxes in various areas (BM = body mass; HBL = head & body length; TL = tail length), grouped according to geographical area, and ordered from north to south within each area. Studies with $N < 10$ for each sex were excluded. The percentage of dimorphism is calculated as the ratio of the difference between measurements (on the larger measurement). The cubic root of mass was used instead of original measurements for the calculation of mass dimorphism.

Location	BM (g)		%	HBL (cm)		%	TL (cm)		%	Ratio BM/HBL		Ref.
	M	F		dimorph.	M		F	dimorph.		M	F	
Australia	6300	5500	4.4	65	62	4.6	40	38	5.0	96.9	88.7	(1)
UK (Scotland)	7300	6200	5.3	71	68	4.2	44	41	6.8	102.8	91.2	(2)
UK (Scotland)	7225	5950	6.3	—	—	—	—	—	—	—	—	(3)
UK (Ireland)	6900	5800	5.6	72	68	5.6	37	35	5.4	95.8	85.3	(4)
UK (England)	6670	5410	6.7	67	63	6.0	41	39	4.9	100.0	85.7	(2)
UK (England)	6446	5540	4.9	—	—	—	—	—	—	—	—	(3)
UK (England)	7380	6485	4.2	—	—	—	—	—	—	—	—	(3)
UK (Wales)	6401	5540	4.7	67	62	7.5	41	38	7.3	95.5	89.4	(3)
USA (N Dakota)	5341	4542	5.3	—	—	—	—	—	—	—	—	(5)
USA (Iowa)	4822	3938	6.5	64	61	4.7	36	34	5.6	75.3	64.6	(6)
USA (Illinois)	5250	4128	7.7	66	62	6.1	37	35	5.4	79.5	66.6	(6)
USA (Indiana)	5253	4213	7.1	—	—	—	—	—	—	—	—	(7)
USA (Maryland)	4352	3610	6.0	60	58	3.3	38	36	5.3	72.5	62.2	(8)
Norway	5896	5183	4.2	68	66	2.9	44	42	4.5	86.7	78.5	(9)
Denmark	7600	6100	7.1	—	—	—	—	—	—	—	—	(3)
E Germany	6872	5700	6.0	—	—	—	—	—	—	—	—	(3)
The Netherlands	5960	5100	5.1	—	—	—	—	—	—	—	—	(3)
Switzerland	7080	5930	5.7	—	—	—	—	—	—	—	—	(10)
Spain	6330	5124	6.8	71	66	7.0	—	—	—	89.4	77.8	(11)
Lebanon	—	—	—	59	55	6.8	37	36	2.7	—	—	(12)
Central Italy	5750	4940	4.9	66	62	6.1	39	36	7.7	87.2	79.7	(13)
Average (excl. Italy)	6283	5263	5.7	66	63	5.1	40	37	6.3	89.4	79.0	

(1) McIntosh 1963, (2) Kolb and Hewson 1974, (3) Lloyd 1980, (4) Fairley 1970, (5) Allen and Gulke 1981, (6) Storm et al. 1976, (7) Hoffman and Kirpatrick 1954, (8) Nelson and Chapman 1982, (9) Lund 1959, (10) Lüpés and Wandeler 1983, (11) Travaini and Delibes 1995, (12) Lewis and Lewis 1968, (13) This study.

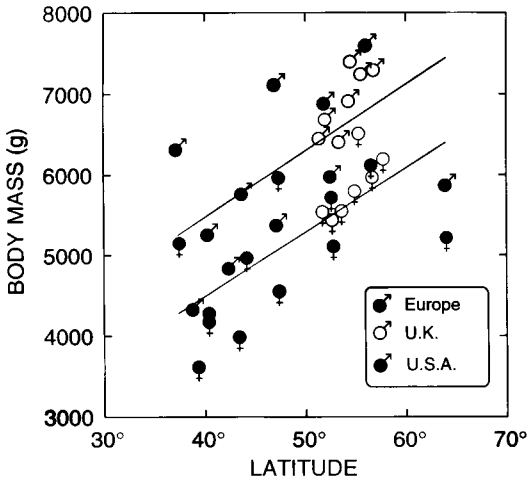


Fig. 1. Relationship between body mass and latitude in male and female red foxes, divided by geographical units. Regression lines for males ($y = 69.0x + 2897.9$) and females ($y = 64.5x + 2107.2$) are shown. For references to individual studies, see Table 1.

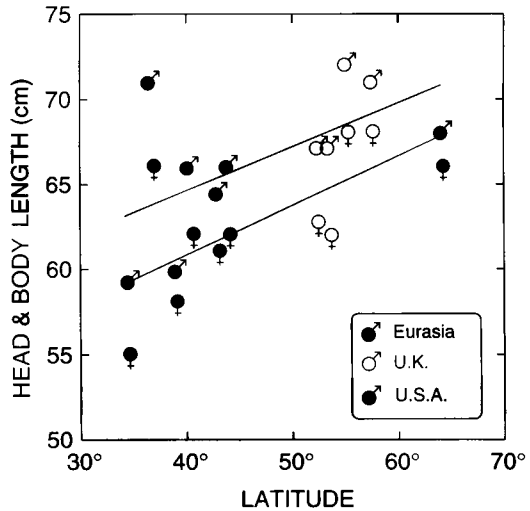


Fig. 2. Relationship between head & body length and latitude in male and female red foxes, divided by geographical units. Regression lines for males ($y = 0.243x + 55.14$) and females ($y = 0.259x + 50.85$) are shown. For references to individual studies, see Table 1.

local increase found both in Central Italy (males: 4 cm/100 km; females: 2.4 cm/100 km; this study) and in Scotland (males: 2 cm/100 km; females: 1.5 cm/100 km; Kolb 1978). It is therefore likely that the determinants of local variation (e.g. population density, food supply) are different from those causing the trend observed at the geographic level (phylogenetic origin, climate).

The degree of sexual dimorphism is not related to either latitude (BM dimorphism: $r^2 = 0.127$, $p = 0.12$, $N = 20$; HBL dimorphism: $r^2 = 0.074$, $p = 0.39$, $N = 12$; TL dimorphism: $r^2 = 0.194$, $p = 0.175$, $N = 11$) or geographical origin (BM dimorphism: $F = 2.63$, $p = 0.10$, $N = 20$; HBL dimorphism: $F = 0.37$, $p = 0.70$, $N = 12$; TL dimorphism: $F = 2.39$, $p = 0.15$, $N = 11$). The three measures most commonly reported (BM, HBL, TL, separated by sex, for a total of six variables) are sufficient to clearly separate foxes in three clusters (cluster analysis by Euclidean distance, Ward minimum variance method): North American, British, and European red foxes (Fig. 4). British foxes are more similar to the European than to the American ones. External morphology of populations appears therefore to reflect phylogenetic distance more than global ecological conditions. An indirect test is provided by the recent (mid 1 800) introduction of English and Welsh foxes in Australia: despite widely

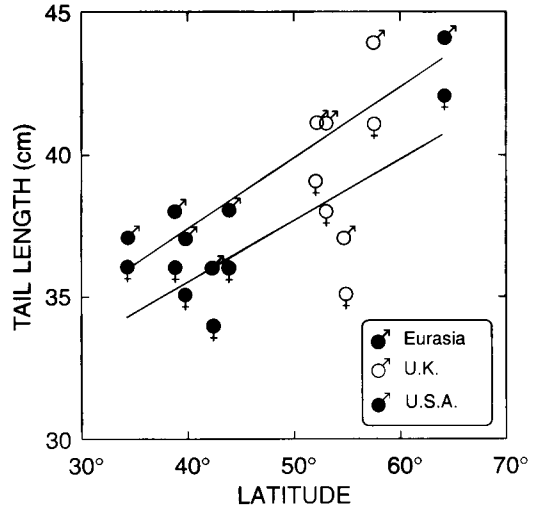


Fig. 3. Relationship between tail length and latitude in male and female red foxes, divided by geographical units. Regression lines for males ($y = 0.210x + 29.493$) and females ($y = 0.178x + 28.901$) are shown. For references to individual studies, see Table 1.

different environmental conditions in the newly colonised environment, the external morphology of introduced foxes still groups them clearly with their British ancestors. Bergmann's rule (which has been

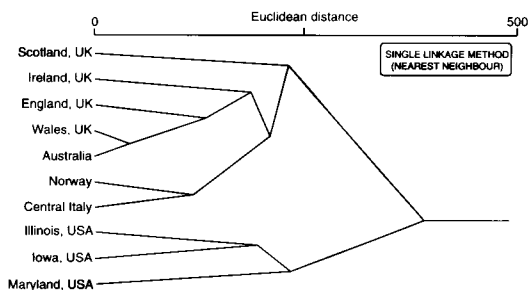


Fig. 4. Tree diagram of various populations of red foxes, as resulting from cluster analysis external morphological variables (body mass, head & body length, tail length, separated by sex; cluster analysis by Euclidean distance, Ward minimum variance method).

heavily criticised, e.g. Geist 1987) explains part of the variability, but its causal factors remain unexplained (e. g. greater fasting endurance of larger individuals: Mugaas & Seidensticker 1993). Exceptions are numerous (e.g. the light Norwegian foxes), and require additional explanations (e. g. character displacement by other carnivores: Dayan et al. 1989, Dayan et al. 1992; influence of prey dimension: Fuentes & Jaksic 1979, Schmitz & Lavigne 1987). For all variables, variation within populations is greater in Eurasia than in other areas (Figs. 1–3), as could be expected given the Eurasian origin of the red fox (Kurtén 1968).

Main conclusions of this study are: (1) body size of the red fox may be variable even within a small area; (2) the determinants of such variation are complex, and may be related to population density; (3) at larger (geographical) scale, the general trend of larger individuals at higher latitudes results both from differences among continents (or subcontinents) and from trends within each continent; (4) body size seems to reflect phylogenetic distance more than ecological conditions. More data should be collected, both in different areas and with different methods (e.g. cranial measurements, genetic sampling) to test these views.

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